Universitat Autònoma
de Barcelona
Departament de Biologia Animal, de
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Unitat d'Antropologia Biològica

Institut Català de Paleontologia
Miquel Crusafont

Miocene Carnivorans from the Vallès-Penedès Basin (NE Iberian Peninsula)

Josep Maria Robles Giménez
Tesis Doctoral
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Els carnívors del Miocè de la conca del Vallès-Penedès (NE de la península Ibèrica)

Memòria presentada per Josep Maria Robles Giménez per optar al títol de Doctor en Biologia, dins del programa de doctorat en Biodiversitat del Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia de la Universitat Autònoma de Barcelona, dirigida pel Dr. David M. Alba de l'Institut Català de Paleontologia Miquel Crusafont.

Signat a Bellaterra el 11 de juliol de 2014.

JOSEP MARIA ROBLES GIMÉNEZ
Doctorand

DAVID MARTÍNEZ ALBA
Director

SALVADOR MOYÀ-SOLÀ
Tutor

A mi padre y familia.

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Preface and Acknowledgments

Siempre me acordaré perfectamente. Fue a la temprana edad de 6 años cuando supe lo que quería ser de mayor: paleontólogo. Fue en una clase cualquiera de gimansia en la escuela, en un campo cercano donde nos llevaron a brincar, correr... disfrutar, vamos. Aquel día tocaba jugar al escondite y me escondí en una hondonada del terreno, a cual trinchera, detrás de una piedra a ras de suelo. Fue en ese momento cuando miré hacia esa "piedra" que tenía delante y mi mirada se fijó en una concha, perfectamente conservada con sus ornamentaciones y forma, tal y como tantas otras veces las había visto en la playa. Desde ese momento, y durante todo el tiempo que duró el juego, estuve completamente absorto planteándome toda una serie de dudas: ¿cómo había llegado aquella concha allí, donde no había mar alguno? ¿porqué estaba tan dura como una piedra, si yo ya había roto algunas con la mano en la playa? Etcétera. Desde ese mismo momento, supe que quería conocer todas las respuestas a las preguntas que rodeaban a esa concha. Cuando llegué a casa, se lo conté eufórica y repetidamente a mi madre y a mi padre, los cuales, pobres, al igual que mis compañeros de clase, no supieron darme ninguna explicación convincente.

Mi tozudería hizo que, poco a poco, curso tras curso de primaria, me fuera interesando de manera intensa en todo lo referido a los fósiles y a todo lo que les rodea, hasta que le pude poner nombre: Paleontología. Esta "obsesión" hizo que quisiera estudiar Paleontología y trabajar como paleontólogo. El instituto de secundaria fue el primer lugar dónde conocí por primera vez a una persona que tenía los mismos intereses paleontológicos que yo, Mario Salerno, al cual le debo muchas tardes de charlas, excursiones a lugares cercanos con afloramientos fosilíferos (como el Papiol), libros, etc. Desgraciadamente, y por circunstancias de la vida, nuestras carreras se separaron a final de esta etapa de secundaria, cuando yo entré en la Universitat Autònoma de Barcelona a estudiar, como no, Geología, mientras que Mario se quedó en el instituto. Hasta que llegué a la universidad, sólo supe lo qué quería ser; pero durante mis estudios universitarios, ya supe cómo lo tenía que hacer. Allí tuve la oportunidad de conocer a muchísima gente que compartía mis inquietudes. A algunos de ellos aún los tengo como compañeros a día de hoy (Bernat Vila, Joan Madurell-Malapeira y Isaac Casanovas-Vilar), mientras que a otros ya no (David Franch, Oriol Pujols, Fernando Lacasta, Ornella, Marc, Manel, etc.).

Durante los estudios univeristarios, realizé prácticas de empresa en Geoterna S.L., junto con Bernat Vila, donde conocí a mucha gente del mundo de la empresa privada y recibí consejos por parte de Xavier Ros y Jordi Palomar. Fue durante estas prácticas de empresa cuando, por primera vez desde que era pequeño, pude hacer lo que siempre había querido: trabajar de paleontólogo. Fue en Incarcal, un yacimiento del Pleistoceno, donde nos llevaron a excavar a Bernat y a mí, y allí fue dónde conocí a Àngel Galobart, director de la excavación. A partir de aquí en adelante, y hasta el día de hoy (al menos, cuando la agenda me lo permite), participé como voluntario en distintas campañas veraniegas de excavaciones de dinosaurios en Isona o de mamíferos miocenos en el Vallès-Penedès. Después de finalizar, el año 2002, la carrera de Geología, gracias a la confianza de Isaac Casanovas-Vilar, empezé a trabajar en lo que continúa siendo actualmente mi trabajo: las excavaciones paleontológicas que se llevan a cabo en el Abocador de Can Mata (ACM). Allí empezé como técnico, llegando a ser director al cabo de unos años. Allí compartí trabajo, inicialmente, con Isaac Casanovas-Vilar, y también conocí a David M. Alba (director del presente trabajo) y a Jordi Galindo Torres, que entonces eran los directores de la intervención paleontológica. A lo largo de los años, con ellos he pasado innumerables horas, situaciones, explicaciones, broncas, consejos, enseñanzas, etc., que me han enseñado lo que es la profesión de paleontólogo. Lejos de lo que se ve en las películas, es un trabajo muchas veces duro, sacrificado y sufrido, aunque también es de lo más gratificante, permitiéndote recuperar fósiles de hace millones de años que nadie ha visto antes. Por el ACM han pasado multitud de personas, las cuales han aportado su granito de arena a tan magna empresa paleontológica, contribuyendo a recuperar un excepcional patrimonio paleontológico.

Durante el año 2003 y paralelamente al trabajo en el ACM, empezé el Máster de Geología Experimental por la Universitat de Barcelona. Allí conocí a Jordi Martinell, Rosa Doménech, Jordi Batllori, Núria y Jordi Maria de Gibert. Este último empezó a dirigir mi trabajo de máster, que debía versar sobre equinoideos miocénicos del Vallès-Penedès, pero que desgraciadamente no llegué a concluir, puesto que mi trabajo en el ACM copó todo mi tiempo. Finalmente, en 2007 me matriculé en el recientemente creado Máster de Paleontología de la Universitat Autònoma de Barcelona y la Unitat de Barcelona, con un trabajo sobre un grupo de carnívoros del ACM dirigido por David M. Alba. Una vez finalizado, en 2008, decidí continuar mis investigaciones en este campo en el marco de la presente tesis doctoral, que durante todos estos años he compatibilizado con mi trabajo como co-director de las sucesivas intervenciones paleontológicas en el ACM.

Son, pues, muchas las personas e instituciones a las que tengo algo que agradecer. Me gustaría empezar por dar las gracias a la institución que me acogió desde el comienzo de esta aventura personal, el Intitut Català de Paleontologia Miquel Crusafont (ICP), y muy especialmente a su director, el Prof. Salvador Moyà-Solà, por haberme permitido el acceso a un material fósil tan espectacular; por esa confianza depostiada en mí; por tener siempre la puerta de su despacho abierta para lo que necesitara (dudas, consejos, etc.), contagiándome toda su energía y su pasión por esta disciplina científica.

En segundo lugar, quisiera agradecer también al Dr. David M. Alba, director de esta tesis, toda la confianza depositada en mí durante tantos y tantos años de trabajo y de investigación. Gracias a dicha confianza, he podido trabajar de lo que siempre he querido, de paleontólogo, y tener continuidad en un trabajo muy relacionado con mi vocación. Igualmente, le doy las gracias por darme la oportunidad de trabajar con un grupo de mamíferos que siempre me ha fascinado, los carnívoros; por la paciencia que ha tenido conmigo a la hora de contestarme tantas, tantas, tantas y tantas dudas que he tenido durante tantos largos y cortos cafés; y por dirigirme este trabajo durante tanto tiempo.

En tercer lugar, quiero darle las gracias al Dr. Isaac Casanovas-Vilar por su confianza en mí, dándome la oportunidad de poder trabajar en paleontología, un campo en el cual, a día de hoy, todavía continúo al pie del cañón. Asimismo, agradecerle su paciencia conmigo a la hora de contestar mis preguntas, la gran cantidad de artículos y correos electrónicos llenos de información (que me han servido de mucho en este trabajo), y por considerarme un gran compañero de trabajo.

Por supuesto, no quiero dejarme al resto de compañeros y colegas del ICP durante todo este tiempo. Este grupo incluye a muchas personas que pasaron por el antiguo Institut de Paleontologia M. Crusafont de Sabadell de la Diputació de Barcelona, algunos de los cuales actualmente todavía trabajan en el actual ICP, así como otros que se incorporaron más tarde, y otra mucha gente, que por un motivo u otro, ya no están. Quiero agradecer de corazón las muestras de amistad, bromas, chistes, cafés, y demás buenos momentos en general, que me han proporcionado las siguientes personas: David M. Alba, Isaac Casanovas-Vilar, Joan Madurell-Malapeira, Marc Furió, Sergio Almécija, Bernat Vila, Josep Fortuny, Guillem Pons, Arnau Bolet, Judit Marigó, Josep Aurell, Laura Celià, Marta March, Jordi Galindo, Àngel H. Luján, Carolina Cancelo, Núria Guerrero, Marta Valls, Massimo Delfino, Marta Pina, Marta Palmero, Manel Méndez, Josep Marmi, Dani DeMiguel, Josep Torres, Salvador Moyà-Solà, Novella Razzolini, Pere Figuerola, Gretell García, Raef Minwer-Barakat, Joan Femenias, Ivette Susanna, Nekane Marín, Blanca Moncunill, Meike Kölher, Miriam Pérez de los Ríos, Maria Pérez, Xavi Jordana, Sandra Val, Mònica Cucurella, Maria Pereira, Manel Llenas, Inma Roig, Albert Garcia, Enric

Menéndez, Hanneke Meijer, el Sr. Farrer (conserje) y Àngel Galobart. Una mención especial merecen mi compañeras del ICP Judit Marigó, Nekane Marín y Gemma Prats, además de la Dra. Assumpció Malgosa de la Unitat d'Antropologia de la UAB, por resolverme tantas y tantas dudas con respecto al doctorado y los trámites burocráticos necesarios para llevar esta tesis a buen puerto.

Esta tesis no hubiese sido posible si no se hubiesen llevado a cabo las sucesivas intervenciones paleontológicas en el ACM, financiadas por CESPA Gestión de Residuos, S.A.U., en las que llevo trabajando desde hace ya cerca de once años (que no todo el mundo lo puede decir). Gracias a ello he tenido la oportunidad de dedicarme a mi profesión (y vocación), además de conocer a toda una serie de gente que no quiero dejar de mencionar aquí: Arsenio (el abuelo) e hijo, Silvestre, Marta, Noemí, Ramon (gerente y hombre de palabra), Juclà, Darwin, Pedro, Mercè (gracias por todas las mañanas de charlas, medio dormidos, preguntado por nuestro trabajo), y tantos otros trabajadores y trabajadoras que han pasado por allí, y otras que todavía siguen al pie del cañón día tras día.

Muy especialmente, pues, quiero dar también las gracias a mis compañeros directores de excavación en Can Mata, con los cuales, durante tantos y tantos años, día tras día, hemos estado sacando adelante el trabajo de campo. Todos ellos, en muchos momentos, me han ayudado a hacer más llevadero este duro trabajo: Jordi Galindo, Sergio Almécija, Jordi Balaguer, Juan Vicente Bertó, Cheyenn Rotgers y Raül Carmona. Y junto con ellos, también quiero recordar aquí a mis otros compañeros, como Ivette Susanna, Lluís Checa, Pau Obradó, Eudald Rifà, Montserrat Ginestí, Joan Sala, Josep Sala, Arnau Céspedes, y muchas otras personas que han pasado por Can Mata, para agradecerles la paciencia que han tenido conmigo y con mis decisiones, no siempre fáciles de aceptar, y por lo momentos que me han regalado a lo largo de este período tan largo de tiempo. Y por supuesto, le doy también las gracias a la Goretti y su restaurante, donde hemos pasado momentos inolvidables todos juntos, y donde siempre me han tratado como de la família.

No puedo olvidarme de todas las instituciones que me han acogido para poder estudiar sus colecciones, y que también has sido pues partícipes de este trabajo. Además del ICP (Laura Celià, Marta March, Mònica, María), cabe dar las gracias al Museu de Ciències Naturals de Barcelona, y en especial a Vicens Vicedo; al Museu de Geologia del Seminari Conciliar de Barcelona, y más concretamente a su director, el padre Sebastià Calzada; y al American Museum of Natural History (Nueva York, EUA).

Tampoco quiero dejar de mencionar a todos mis colegas científicos (algunos de los

cuales desde hace bastante más tiempo que yo, junto con otros que no tanto, je je je…), y que se dedican a estudiar carnívoros fósiles o a otras disciplinas afines, y que en algún u otro momento me han enviado artículos que me parecían imposibles de conseguir o me han proporcionado consejos y orientaciones de gran utilidad. Mi gratitud, pues, para Jorge Morales, Óscar Sanisidro, Gema Siliceo, Manuel J. Salesa, Mauricio Antón, Plinio Montoya, Juan Abella, Israel M. Sánchez, Alberto Valenciano, Víctor Vinuesa, Alberto Boscaini, Chinche (no te enfades, ¿eh? ¡o sí! je je je je) y Patro, Maite la "Dinoxiqueta", Miguel Garcés, Lluís Cabrera, Rosa Domènech, Jordi Batllori, Jordi Martinell, Ashley Hammond, Anneke Madern, Júlia Arias-Martorell. Un recuerdo muy especial es para el malogrado Jordi Maria de Gibert, que me ayudó muchísimo en mis inicios, y que desgraciadamente nos dejó durante la realització de este doctorado.

No quiero bajo ningún concepto dejarme tampoco a ningún amigo de Sant Cugat del Vallès… Debo agradecerles sobre todo su paciencia conmigo, a la hora de entender mi situación laboral y personal, ayudándome siempre en todo y más. ¡Gracias sobre todo a Javi, Nuria, Alexis y Marta! También a toda la gente "chunga" de "TAAAARRRRASSA", por haberme distraído durante tantos momentos de duda, y apoyado tanto a nivel personal como profesional. Gracias Marta/Alberto, inseparables, como gran pareja que son; a Moyitaaaa, que todavía esperas a día de hoy quedar conmigo para hacer una excursión en bici… ¡te la debo!; a Cantón, por darme conversación y distraerme en diferentes momentos dificiles de este largo trabajo; a Guillem, por estar ahí también; y a toda la gente que he conocido.

Por todos los momentos, que no son pocos (bueno, malos y regulares) que me han hecho pasar los miembros de MI FAMILIA, quería agradecerles a todos su gran apoyo y confianza en mí y en mi "afición", ya desde pequeño, a raíz del encuentro fortuito de una concha fósil cerca de mi casa natal, que me llenó de ilusión y pasión, hasta el día de hoy. Sobre todo, darle las gracias a mi padre, que desgraciadamente ya no está, pero a quien dedico este trabajo, porque siempre estuvo apoyándome, ayudándome y aconsejándome en todo lo que se refería a la Paleontología (¡aunque siempre le tuviera que explicar a lo que me dedicaba! Je je je je). Y también a mis hermanos, madre, y tíos, por estar ahí y, simplemente, no preguntar, sino ayudar y ya está. ¡GRACIAS, ABRAZOS, BESOS Y MÁS DE TODO!

También quiero darle las gracias a Júlia Solé Berlanga y su familia, por la ayuda que me brindaron en su día al soportar todas mis neuras, dudas, etc., que pudieron asomar en mí durante este largo trabajo de tesis, así como por abrirme las puertas de su casa. En este sentido, dar las gracias también a la familia Cancelo Fernández, por haberme dado tanto, y haberme acogido como a uno más.

Finalmente, quiero darle las gracias a Carolina Cancelo, a la que tengo la suerte de conocer desde hace ya tiempo, y con la que, de siempre, nos hemos "llevado" muy bien. Gracias por estar ahí preguntado por mi trabajo/tesis, por aguantarme todos mis momentos (malos y buenos), por hacerme reír, por hacerme disfrutar de todo lo que me rodea, y por aconsejarme siempre de corazón y de la mejor manera. Por tu gran afición y pasión a tu trabajo, que me contagias, y por tu gran visión global de todas las cosas y saber sintetizarlas en "la frase". Esta tesis también te la dedico a ti.

I.–INTRODUCTION AND METHODOLOGY

Chapter 1. General introduction and aims of this dissertation

1.1. Aims and structure of this work

Motivation of this dissertation

The Vallès-Penedès Basin is one of the richest areas in fossil remains of Miocene vertebrates from the Iberian Peninsula. When the present doctoral dissertation, focused on the mammalian order Carnivora, was planned in 2009, it was already clear that no systematic research had been carried out on the extinct representatives of this group in the Vallès-Penedès for several decades. This situation contrasted with that in other areas from Iberia, and evidenced that the knowledge on the Vallès-Penedès carnivoran record was in need of profound revision. At the same time, new paleontological discoveries from the Vallès-Penedès Basin, especially from the local stratigraphic series of Abocador de Can Mata (ACM, els Hostalets de Pierola) since 2002 (Alba et al. 2006, 2007, 2009, 2010a, 2011b), had provided a huge wealth of new, unpublished carnivoran material.

From the beginning, it was clear-cut that an exhaustive revision of all the available material was beyond the possibilities of this work. This was because of several reasons: (a) the great diversity of carnivoran groups recorded from this basin; (b) the large amount of new, unpublished (and largely unprepared) material; and (c) the obsolete knowledge of this group in the Vallès-Penedès Basin, with the most recent systematic works devoted to them dating back more than thirty years ago. Given the time constraints to perform a doctoral dissertation, it was decided that the best way to approach the study would be to devote the work to selected carnivoran taxa, for which new material had been recently recovered. In this way, it would be possible to contribute to a better knowledge on the taxonomy and/or paleobiology of these taxa at a more global level while, at the same time, further contributing to a better knowledge on the Vallès-Penedès carnivorans. Particular emphasis was put on the Miocene primate-bearing sites or fossiliferous areas from the Vallès-Penedès Basin, and especially in the ACM series. At the same time, the dissertation also intended to provide an updated overview of the carnivoran record from the Vallès-Penedès Basin, which is provided in the Appendix 2 and the Discussion and Conclusions. This overview provides a new state-of-the-art summary of Vallès-Penedès Miocene carnivorans, which hopefully will serve as a starting point for further research on this topic in the near future.

The present work is therefore devoted to all the Miocene carnivorans from the Vallès-Penedès Basin, with particular emphasis on selected taxa mainly from primate-bearing localities. The dissertation has mainly a systematic perspective, being mostly devoted to the taxonomy and phylogeny of carnivorans, although other paleontological topics (such as paleobiology, biostratigraphy and paleoenvironmental reconstruction) are also included.

Type of dissertation and general overview

This work is not structured as a 'classical' dissertation, but rather as a compilation of the research previously published by the author in various journals. Each of these papers corresponds to one of the main chapters and Appendix 1 of this dissertation, which further includes several introductory chapters at the beginning, as well as a discussion, a summary of the conclusions and an appendix at the end. In total, the dissertation is structured into five blocks (Introduction, Results, Discussion and Conclusions, Literature Cited and Appendixes), which in turn make up to ten different chapters. They are the following:

I. Introduction: This first block includes a first, introductory chapter, as well as two other chapters in which the methodology and the geographic background, respectively, are discussed. Thus, in Chapter 1, both the aims and the structure of the dissertation are explained, together with an introduction to carnivorans, such as a summary on carnivoran anatomy is provided, with emphasis on the cranium, mandible and dentition—given that most of the descriptive parts of the work rely on either teeth or skulls, as well as a brief historical account on the previous work on these mammals in the Vallès-Penedès Basin. In Chapter 2, Material and Methods are provided. Finally, in Chapter 3 the geographic and geologic background of the area of study is provided.

II. Results: This block constitutes the main scientific contribution of this dissertation, with each of its six different chapters corresponding to the papers published or in press in the framework of this work. They are the following:

- **Chapter 4:** It provides an updated chronology for the Miocene hominoid radiation in Western Eurasia, with particular emphasis on Vallès-Penedès localities, and further incorporating new biostratigraphic and magnetostratigraphic data from ACM. Thus, although this chapter is mainly devoted to primates, it equally provides the necessary chronological framework for dicussing the carnivoran record from primate-bearing localities of this basin.

- **Chapter 5:** In this chapter, the extinct mustelid *Trocharion albanense* is revised from a taxonomic and phylogenetic viewpoints, based on the Vallès-Penedès remains, with particular emphasis on the previously-unpublished cranial remains from the ACM. This taxon, in spite of its wide geographical distribution throughout Eurasia, was previously known based only on scarce and fragmentary fossil remains. Therefore, the taxonomic revision and cladistic analysis provided in this chapter represent a significance addition to the knowledge of this fossil mustelid.
- **Chapter 6:** This chapter provides a systematic revision of the barbourofelid genus *Albanosmilus*—previously considered a subjective junior synonym of *Sansanosmilus*—based on the remarkable record from the Vallès-Penedès Basin, and with emphasis on the previously-unpublished cranial material from the ACM. This chapter therefore provides the first description of an almost complete cranium of this genus, which enables to provide an emended diagnosis as well as to perform a cladistic analysis focused on the internal phylogeny of the tribe Barbourofelini.
- **Chapter 7:** In this chapter, new remains of the felid genera *Pseudaelurus* and *Styriofelis* from the ACM are described. Although no taxonomic revision of these taxa is required, the newly described craniodental remains enable a considerable extension of the chronological range of these genera in the Iberian Peninsula, and further provide new anatomical details for species of *Pseudalurus*.
- **Chapter 8:** In this chapter, all of the available fossil remains of the sabertooth felid genus *Machairodus* from the Vallès-Penedès Basin are revised, including a significant amount of previously-unpublished remains from various localities of this basin. The described remains include not only craniodental, but also postcranial remains, some of which are described and figured for the first time in this taxon. Part of the described material further enables to refine the known stratigraphic range of *Machairodus aphanistus* in the Vallès-Penedès Basin.

III. Discussion and Conclusions: This block synthesizes and further discusses the data reported in the various chapters of the Block II. Chapter 9, in particular, globally discusses the main results of the dissertation, as well as its implications for the knowledge on carnivoran evolution as a whole. In turn, Chapter 10 provides a succinct summary of the dissertation's main conclusions along with prospects for the future regarding the study of fossil carnivorans from the Vallès-Penedès Basin.

IV. Literature Cited: As explained above, the various chapters from Block 2 correspond to manuscripts published or in press, and therefore each of them has its own references section. The same applies to the published paper and the unpublished manuscript reproduced in Appendixes 1 and 2, respectively. Therefore, the Literature Cited Block, which is not subdivided into chapters, provides the references cited elsewhere in this work (e.g., in Blocks I and III).

V. Appendixes: This block contains two main appendixes. In Appendix 1, a new ursid genus (*Kretzoiarctos*), based partly on fossil dentognathic remains from ACM, is described. A cladistic analysis further shows that this taxon belongs to the giant panda lineage, with significant paleobiogeographic and chronologic implications for bear evolution as a whole. Appendix 2, in turn, contains an updated review of all the Miocene carnivorans from the Vallès-Penedès Basin from a taxonomic and chronological viewpoint. This appendix not only incorporates the works reproduced in Block II and Appendix 1, but further provides the remaining unpublished results of the work performed in the framework of this dissertation.

1.2. An introduction to the Carnivora

What is a carnivoran?

Carnivoran diversity. The Carnivora Bowdich, 1821 are a mammalian order of medium diversity, with about 271 extant species (Wozencraft 2005; MacDonald & Kays 2005), of which 36 are marine (pinnipeds) (MacDonald & Kays 2005; Hunter 2011) and 245 are terrestrial (Hunter 2011).

Carnivorans vs. carnivores. The name of the group literally means "meat eater" (Turner & Antón 1997), and refers to the adaptations displayed by its members for cutting, stabbing, tearing and eating flesh with their specialized shearing teeth (the carnassials), which are the sole unique evolutionary hallmark of this order. This feature allows to distinghish carnivorans from their shrew-like ancestors (Kruuk 2001; MacDonald & Kays 2005). Althought many of the members of this group, such as some canids, felids and most mustelids are generally carnivorous (meat-eaters; e.g., *Canis simensis*), an important number of them—especially some ursids, canids and procyonids—are herbivorous (plant-eaters; e.g. *Ailuropoda melanoneuca*), insectivorous (insect-eaters; e.g., *Proteles cristatus*, *Otocyon megalotis*), frugivorous (fruit-eaters; e.g., *Nandinia binotata*, *Potos flavus*), omnivorous (e.g., *Canis adustus*) or even marine invertebrate-eaters or piscivorous (e.g., *Enhyndra lutris*). All these diverging dietary adaptations, together with other (locomotor, cognitive, etc.) specializations, have resulted in carnivorans displaying a wide geographical distribution all around the world.

Although, from an ecological viewpoint, the term ‘carnivore’ refers to any carnivorous organism (mostly animals) that regularly consumes meat as food items, many authors further employ this term as the English version of the Latin Carnivora. However, in order to avoid any misunderstanding, in this work we follow most recent authors in employing ‘carnivorans’ as the English version of Carnivora (Van Valen 1969; Flynn & Galiano 1982; Wyss & Flynn 1993; Wolsan & Bryant 2004). Such a distinction cannot be unfortunately made in many other languages, such as for example Catalan or Spanish, in which there is a single term to refer to carnivorans and to ecological carnivores.

Carnivorans and humans. Carnivorans include some of the most popular animals among humans, since both dogs and cats are frequently raised as pets in most human societies. On the other hand, several members of the carnivoran order have been sistematically killed by humans, either in order to exploit their furs, meat or bones, to prevent their pernicious effects for cattle raising or fishery exploitation, or merely for the pleasure of hunting. In the case of some felids and mustelids, these human activities have put at risk many populations and have led several species near to extinction.

Biology

Body size. In terms of body size, carnivorans are, togheter with primates (Fleagle 2013), one of the most diverse groups of mammals (Anyonge 2001; MacDonald & Kays 2005; Hunter 2011), ranging in body length from a few centimeters (*Mustela nivalis*, 11 cm) to several meters (*Mirounga leonine*, 6.9 m), and in body mass from a few grams (*Mustela nivalis*, 80 g) to almost a ton in terrestrial carnivorans (*Ursus maritimus*, 800 kg) or even more in the marine pinnnipeds (*Mirounga leonine*, 3.000 kg). Among carnivoran populations there can also be a significant amount of interindividual variation in body size, as shown for example by *Canis lupus*, which ranges from 15 to 80 kg (Ewer 1973; Savage 1977; Anyonge 2001; Kruuk 2001; MacDonald & Kays 2005; Hunter 2011).

Diet. Although many carnivorans (e.g., some canids, felids and most mustelids) are carnivorous (meat-eaters; e.g., *Canis simensis*), an important number of them (especially some ursids, canids and procyonids) are herbivorous (plant-eaters; e.g. *Ailuropoda melanoneuca*), insectivorous (insect-eaters; e.g., *Proteles cristatus*, *Otocyon megalotis*), frugivorous (fruit-eaters; e.g., *Nandinia binotata*, *Potos flavus*), omnivorous (e.g., *Canis adustus*) or even marine invertebrate-eaters or piscivorous (e.g., *Enhyndra lutris*) (MacDonald & Kays 2005; Hunter 2011). All these diverging dietary adaptations of carnivorans, together with other (locomotor, cognitive, etc.) specializations, have resulted in the wide geographical distribution of this group all around the world.

Locomotion and lifestyle. Carnivorans are mainly terrestrial, with the exception of the marine pinnipeds (seals, sea lions and walrus) and of some groups that have secondarily adapted to a (semi-)aquatic lifestyle in freshwater (*Hydrictis maculicollis*) or marine (*Enhyndra lutris*) environments (Hunter 2011). Among terrestrial carnivorans, most of them are cursorial ground-dwellers (*Canis lupus*), therefore displaying powerful limbs. However, several members of the order are arboreal (*Martes martes*), semi-arboreal (*Cryptoprocta ferox*) or fossorial (*Taxidea taxus*) (Hunter 2011). With regard to daily activity, carnivorans may be either diurnal (*Ursus arctos*) or nocturnal (*Meles meles*).

Traditionally, in relation to locomotion, carnivorans have been classified into plantigrades (walking on their soles, with the heels touching the ground; e.g., *Ursus arctos* and *Meles meles*) and digitigrades (walking on their toes; e.g., *Felis tigris* and *Canis lupus*) (Ginsburg 1961a; Ewer 1973; Savage 1977; Turner & Antón 1997; Anyonge 2001; MacDonald & Kays 2005; Sanderson & Watson 2011). Plantigrades are generally ground-dwellers, and either omnivorous or opportunistic feeders (Ginsburg 1961a; Ewer 1973), with non-retractable claws as well as short and robust limbs. Digitigrades, in contrast, display varied locomotor repertoires (from arboreal or semi-arboreal, to cursorial, with retractable claws, and more elongated limbs and metapodials (Turner & Antón 1997).

Even among carnivorous carnivorans, hunting techniques vary widely. Solitary nocturnal carnivorans, such as *Meles meles*, have a body design and other adaptations that allow them to chase prey in burrows and other refuges, using a single bite (by stabbing with their upper canine between the last cervical and the first thoracic vertebrae, to dislocate these bones, lacerate the spinal cord, and inflict paralysis or death; Anyonge 2001; Kruuk 2001; MacDonald & Kays 2005). Felids, such as *Panthera leo*, display in turn blunt and flattened faces suitable for a powerful bite, together with other adaptations enabling a powerful first punch (Anyonge 2001; Kruuk 2001). In contrast, other carnivorans, such as *Hyaena hyaena* or *Lycaon pictus*, are more diurnal pack hunters. The latter collectively run and follow their prey in open habitats, until the prey falls exhausted as is attacked by one member of the group with a non-lethal bite, while other members hold the prey until it dies (Colbert et al. 1991; Anyonge 2001; MacDonald & Kays 2005). However, it must be emphasized that not all carnivorans are carnivorous. Some taxa even use their long (*Cryptoprocta ferox*) or prehensile (*Potos flavus*) tails as a fifth limb, allowing them to move in arboreal settings and securely catch fruits (Colbert et al. 1991; Anyonge 2001; MacDonald & Kays 2005).

Main adaptations. The main adaptations displayed by carnivorans are related to food gathering and processing. These adaptations include skeletal modifications in their limbs, in overall body design and especially in the skull and teeth (see below for further details). Thus, in the carpus the scaphoid and the lunar are fusioned into a single bone (scapholunar). Carnivorans commonly display pentadactyl (sometimes tetradactyl, e.g., *Lycaon pictus*; Martínez-Navarro & Rook, 2003) limbs, with sharp claws on each digit, the first one (pollex and hallux) being non-opposable and commonly reduced or event absent (Nowak 2003). The claws can be retractable or non-retractable. Together with their specialized limbs, in many carnivorans the clays facilitate prey capture, either when covering long distances in open spaces, or when hunting in more closed areas (in burrows, such as *Meles meles*, or ambushing their preys, as in the case of *Panthera leo*).

Habitat and geographic distribution. Carnivorans as a group are adapted to inhabit almost every habitat on Earth (MacDonald & Kays 2005), ranging from deserts (e.g., *Fennecus zerda*) to grasslands (e.g., *Suricatta suricatta*), woodlands (e.g., *Helogale parvula*), tropical rain forests (*Potos flavus*) and even the Arctic icecap (*Ursus maritimus*), freshwater environments (e.g., *Lutra lutra*) and the seas (e.g., *Enhyndra lutris*, pinnipeds).

The worldwide geographic distribution and wide habitat occupation of the order Carnivora as a whole contrasts with the restricted distributions displayed by most of their individual members (Hunt 1996; MacDonald & Kays 2005). This fact is attributable to many factors (MacDonald & Kays 2005), both ecological (habitat preference, dispersal ability, sensitivity to human activity) and historical (related to the particular evolutionary history of each group as well as the geological history of Earth). It is noteworthy that there are 25 diversity hotspots around the globe, in which many carnivoran species overlap in distribution and exploit the same habitat (Macdonald & Kays 2005). The most important hostspots correspond to Sundaland (Borneo, Java and Sumatra), Madagascar, Mesoamerica, Western Ghats and Sri Lanka, and the Guinean Forests of West Africa. All these areas display a high number (22%) of endemic species (Macdonald & Kays 2005). Examples of whole endemic groups are the euplerids (Malagasian carnivorans) and the New World procyonids (Sechrest et al., 2002; MacDonald & Kays, 2005).

Systematics and phylogeny

Systematics, phylogeny and biological classification. In order to deal with the evolutionary history and fossil record of any group of organisms, it is indispensable to employ a particular classification of it. In other words, for practical reasons, it is necessary to distribute organisms into distinct classes, which are termed taxa, which are grouped into a nested hierarchy of nested taxonomic ranks. Among life sciences, systematics is the scientific discipline that deals with biodiversity and the classification of living organisms (both extant and extinct), according to pre-established principles that intend to provide with a 'natural' (as opposed to 'artificial') classification. Taxonomy, in contrast, rather deals with the practical rules (taxonomic nomenclature, taxon description, etc.) involved in the practice of systematics. Given the fact that organismal evolution is the unifying paradigm in life sciences as a whole, phylogeny plays a central role in systematics and provides the theoretical justification for the hierarchical structure of the classification system. Therefore, there is currently a universal acceptance among researchers that systematics must reflect the evolutionary relationships between organisms.

Over the years, however, the practice of systematics has experienced a significant theoretical revolution, leading to significant changes in the way higher-level taxa are defined. Thus, the more traditional school of evolutionary systematics (e.g., Simpson 1945) incorporated phylogeny but further emphasized morphological disparity in biological classification. In contrast, with the advent of the currently favored school of phylogenetic systematics or cladistics (Hennig 1966), the emphasis on biological classification shifted to phylogeny alone. Both schools agree that only similarities based on community of descent (homologous features) must be employed, but cladistics further emphasizes that only 'synapomorphies' (shared-derived features, as opposed to primitive or 'plesiomorphic' features) must be employed to define natural groups (e.g., strictly monophyletic groups, or 'clades') as taxa. There is therefore a general agreement that polyphyletic groups (including taxa that do not share a single common ancestor) cannot be considered natural, but there is some controversy on whether paraphyletic groups (including taxa that share a common ancestor but not all of its descendants) should be defined as taxa, since they represent 'grades' instead of clades.

At lower taxonomic levels, paraphyly is inevitable, for any species must have evolved from a pre-existing one (Carroll 1988). To solve this problem, adherents of the so-called phylogenetic nomenclature school have even proposed to abandon binominal nomenclature and mandatory Linnean ranks. However, such a radical transformation of taxonomic nomenclature has been criticized by many other researchers (e.g., Benton 2000). In fact, adherence to phylogenetic nomenclature implies a misunderstanding of the difference between phylogeny and biological classification. The latter must necessarily be arbitrary to some degree, because besides reflecting phylogeny it must be also practical for transmitting scientific information (see discussion in Benton 2000). Therefore, the present work adopts the use of Linnean ranks and all other provisions of the *International Code of Zoological Nomenclature* (ICZN 1999), which has the merits of being explicit, universal and stable. At the same time, this work adopts a cladistic approach not only in phylogenetic reconstruction but also in the practice of systematics, by trying to avoid the use of paraphyletic taxa at suprageneric ranks (thus recognizing that clades are more natural than paraphyletic groups).

Traditionally, supraspecific taxa were defined based on characters, until the adoption of phylogenetic systematics, which led to apomorphy-based definitions of taxa. Subsequently, clade-based definitions of taxa (based on common ancestry, instead of a set of derived features) were also proposed. Two types of clade-based definitions of taxa are possible (Benton 2000): node-based definitions and stem-based definitions. The *International Code of Zoological Nomenclature* (ICZN 1999) does not specify how taxa should be defined, so that the use of Linnean ranks is not restricted at all to character-based definitions of taxa (Benton 2000). Although different types of definition can be employed, depending on the specificities of each group, the use of stem-based definitions is favored here for groups with both extant and extinct representatives. Given a presumably holophyletic extant taxon, we may distinguish the crown group from the stem lineage (Jefferies 1979; Hennig 1981; Ax 1985), which together consitute a closed descend community termed the total group of the taxon. The crown group is the clade that includes all the extant representatives of the taxon, whereas the stem lineage is a paraphyletic assemblage of basal subtaxa that are more or less distantly related to the crown group, but which are more closely related to the latter than to its sister-group, and which are not more closely related to any members of the crown group than to others. It is sometimes difficult to determine whether a particular extinct species is a stem or crown member of a particular clade, but at least with the adoption of stem-based definitions, the inclusion of this particular species into the taxon as a whole remains stable. Whereas the crown group constitutes a clade and can be therefore formally erected as a subtaxon, the stem lineage must not necessarily constitute a clade and, hence, might conform a paraphyletic taxon if formally designated.

Carnivoran phylogeny and systematics. With the progressive change of the theoretical principles of systematics, coupled with the accumulation of knowledge on the phylogeny of both living and fossil carnivorans (e.g., Cope 1880; Trouessart 1885; Wortman & Matthew 1899; Matthew 1901; Wortman 1901; Matthew 1909; Gregory & Hellman 1939; Simpson 1945; Kretzoi 1945; MacIntyre 1966; Young 1971; Cray 1973; Tedford 1976; Savage 1977; Flynn & Galiano 1982; Wyss & Flynn 1993; Vrana et al. 1994 and Janis et al. 1998), the systematics of this group has considerably changed over the years. For this study, we will consider to simplificate the systematics of the Carnivora (Table 1.1) based on the most recent studies, such as Wesley-Hunt & Flynn (2005), Finarelli & Flynn (2006), Spaulding et al. (2010) and Tomiya (2011, 2013).

The order Carnivora Bowdich, 1821 has long been considered a clade, e.g., a strictly monophyletic (holophyletic) group, by most authors (MacIntyre 1966; Young 1971), being traditionally included into the superorder Ferae Linnaeus, 1758, together with the order Creodonta Cope, 1875. Subsequent studies, such as Tedford (1976), Savage (1977) and Flynn & Galiano (1982) excluded the creodonts from the order Carnivora, given the lack in the former of a non-ossified entotympanic bullae, as well as the position and development of the carnassials (P4/m1 and dP3/dp4 in carnivorans and M1/m2 or M2/m3 in creodonts). The morphology of the tympanic bullae has been always been of great significance for carnivoran systematics (Simpson 1945; Hough 1948; Hunt 1974; Tedford 1976; Savage 1977). Tedford (1976) stressed the presence of an ossified bulla in crown carnivorans of suborders Caniformia Kretzoi, 1943 and Feliformia Kretzoi, 1945. However, this character is absent among the basal-most carnivorans (Miacidae), so that this features is no longer considered diagnostic of the Carnivora as a whole by subsequent authors. According to Flynn & Galiano (1982) the Carnivora would be characterized by the following diagnositeic features: P4/m1 modified as the principal carnassial teeth, lacking a migratory locus for the carnassial as found in the Creodonta, but with retention of some subsidiary shear on other teeth; P4 protocone located anterolingually, far forward of the paracone; extremely elongate P4 metastyle wing with a well-developed metastyle blade and carnassial notch; well-developed, elongate p4 talonid with at least M2-M3 and m2-m3 reduced in size; processus hyoideus formed by a ventromedial prolongation of the squamosal. In turn, according to these authors, carnivorans would be primitively characterized by the following features: retention of M1-M3 and m1-m3; P4 with a small, but distinct parastyle cusp; P3 lacking a protocone; all molar talonids short, basined, with a large hypoconid as the highest talonid cusp, and an obliquely oriented cristid obliquid; molar trigonids high, with the paraconid < metaconid < protoconid size; molar paraconids and metaconids moderately closely apressed, resulting in a closed-V between the paralophid and protolophid in the trigonid; upper molars with both a paraconule and metaconule; molar hypocones absent as distinct cusps, precingulum and postcingulum not continuous around lingual base of protocone; small p4 anterior accessory cuspid; p4 lingual accessory cuspid absent; entotympanic bulla unossified; schapoid, lunar, and centrale separate; calcaneal fibular facet present; scapula without teres major process or secondary scapular spine.

Althought Flynn & Galiano (1982) established clear diagnostic features for the Carnivora, later works could not resolve the relationships between stem carnivorans (such as miacids and viverravids) and crown carnivorans (feliforms and caniforms), due to the scarcity of the available material (Flynn & Galiano 1982; Bryant 1991; Wang & Tedford 1994; Hunt & Tedford 1993; Wyss & Flynn 1993; Flynn 1996, 1998; Turner & Antón 1997; Hunt 1998a). During the 1980s and 1990s, several authors tryied to relate the origin of crown Carnivora with miacids, based on dental and basicranial features, and employing modern methods of phylogenetic reconstruction (Flynn & Galiano 1982; Gingerich & Winkler 1985; Hunt & Tedford 1993; Wyss & Flynn 1993; Wolsan 1993; Bryant 1996). These works led some authors to restrict the order Carnivora to the crown members of this group (feliforms and caniforms), which required the erection of a new clade, the Carnivoramorpha Wyss and Flynn, 1993, to include all mammals more closely related to the Carnivora than to taxa referred to Creodonta by Carroll (1988). Such a restricted definition of the Carnivora is now followed here. In other words, Carnivora are here not restricted to the crown members of the group, but further includes the members of the stem lineage, such as the families Viverravidae Wortman and Matthew, 1899 and Miacidae Cope, 1880. Whereas viverravids are considered a monophyletic group of basal-most carnivorans (carnivoramorphans), miacids (also referred to as the "non-Viverravidae group"; e.g., Spaulding et al. 2010) are considered a paraphyletic array of stem taxa closer to the crown carnivorans than viverravids (Wolsan 1993; Wyss & Flynn 1993).

The monophyletic status of Carnivora s.l. (=Carnivoramorpha) (Fig. 1.1) is currently very well supported, especially after the discovery of new postcranial remains of viverravids (Polly et al. 2006) and the description new cranial features (related to the tympanic bulla) in the non-viverravid group (Spaulding & Flynn 2009; Spaulding et al. 2010). Yet another clade has been recently erected within carnivorans, the Carnivoraformes Flynn et al., 2010, was recently erected to include all carnivorans more related to the crown group (represented by *Canis lupus*) than to Viverravidae (represented by *Viverravus*) (Flynn et al., 2010). This sublcade is primarily defined based on craniodental features (round infraorbital foramen, blunt mastoid process, rostral entotympanic, and non-elongated m2 talonid, among other features). For adherents to phylogenetic nomenclature, the erection of this clade would enable to discount the family Miacidae (or superfamily Miacoidea), which has been widely employed as a "wastebasket" (paraphyletic assemblage) of basal carnivoramorphans more closely related to crown carnivorans than viverravids (Simpson 1945; MacIntyre 1966; Young 1971; Flynn & Galiano 1982; Gingerich 1983; Gingerich & Winkler 1985; Wyss & Flynn 1993; Heinrich & Rose 1995, 1997; Wesley-Hunt & Flynn 2005; Heinrich & Houde 2006). Given the more traditional, Linnean taxonomic approach followed in this work, the family Miacidae has been provisionally maintained in this work, although recognizing that it is clearly a paraphyletic assemblage. Although no rank is attributed to carnivoraforms, this clade remains useful to distinguish all carnivorans (or carnivoramorphans) with the exclusion of the viverravids, which are well established as the basal-most members of the whole group (Spaulding et al. 2010; Tomiya 2011, 2013; Spaulding & Flynn 2012; Solé et al. 2013). Unfortunately, due to the lack of the proper fossil remains, the phylogenetic relationships between viverravids and the basal-most members of crown carnivoran lineages are not yet well established (Bryant 1991; Hunt & Tedford 1993; Wyss & Flynn 1993; Flynn 1996, 1998; Janis et al. 1998; Flynn et al. 2010).

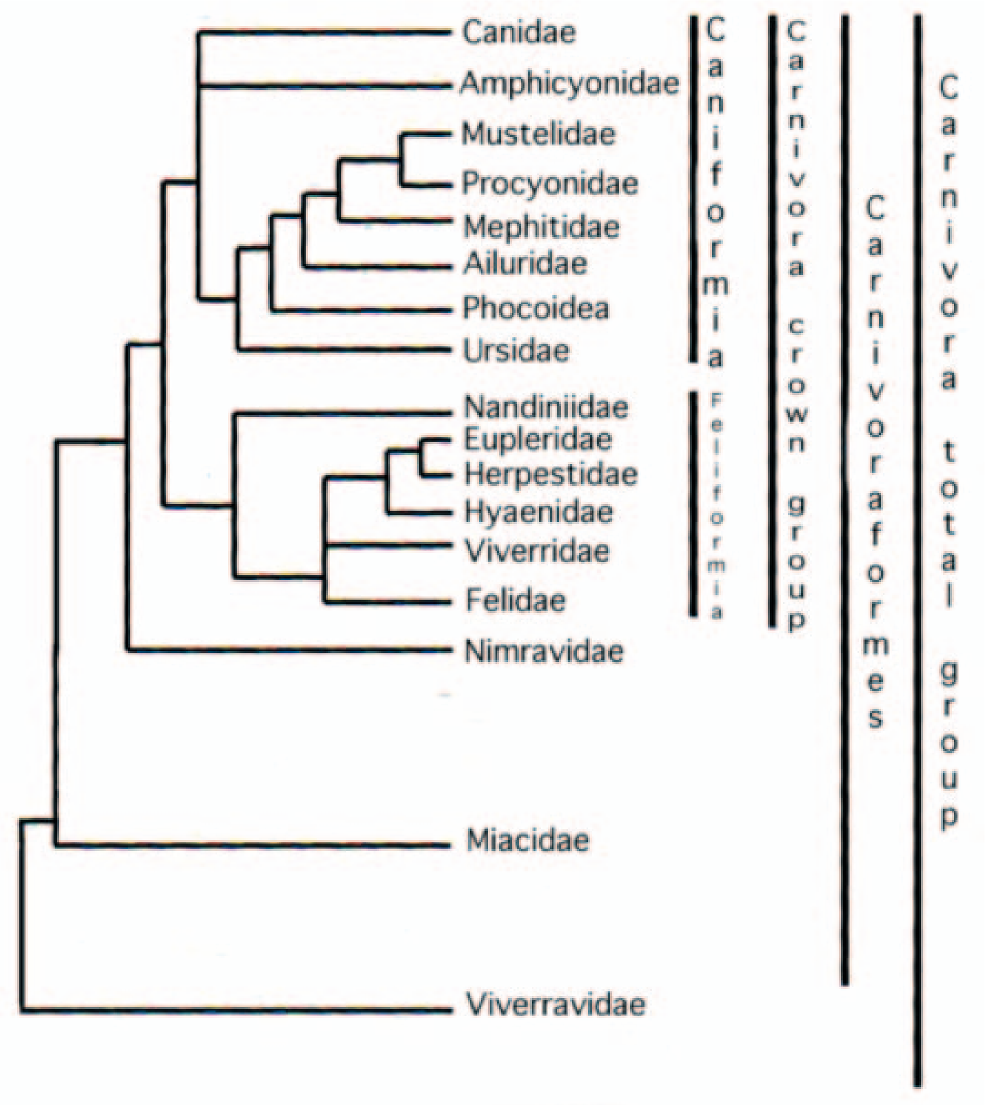

Figure 1.1. Schematic phylogeny of the Carnivora s.l. (=Carnivoramorpha). Simplified and redrawn from Flynn et al. (2010).

The division of crown group of Carnivora into two monophyletic infraorders (Feliformia and Caniformia; Fig. 1.2) is currently widely accepted (Bryant 1991, 1996; Wolsan 1993; Hunt & Tedford 1993; Wyss & Flynn 1993; Vrana et al. 1994; Wang & Tedford 1994; Flynn et al. 2000); Flynn 1998; Flynn & Nedbal 1998; Janis et al. 1998; Anyonge 2001; Sato et al. 2004, 2006; Yu et al. 2004; Wolsan & Bryant 2004; MacDonald & Kays 2005; Wang et al. 2005b; Flynn & Wesley-Hunt 2005; Wesley-Hunt & Flynn 2005; Wesley-Hunt & Werdelin 2005; Fulton & Strobeck 2006; Yu & Zhang 2006; Arnason et al. 2007; Barycka 2007; McKenna & Bell 1997; Finarelli 2008; Flynn et al.

2005, 2010; Hunter 2011; Spaulding & Flynn 2012). This contrasts with the classically division of the Carnivora by Simpson (1945) into the suborders Pinnipedia Illiger, 1811 and Fissipedia Blumenbach, 1791, based on their strikingly different adaptations to aquatic and terrestrial environments, respectively. Following Tedford (1976) and other subsequent authors (Savage 1977; Flynn & Galiano 1982), the taxon Feliformia Kretzoi, 1945 (including part of Simpson's Fissipedia) was resurrected, together with Caniformia Kretzoi, 1943 (including Simpson's Pinnipedia and the remaining Fissipedia).

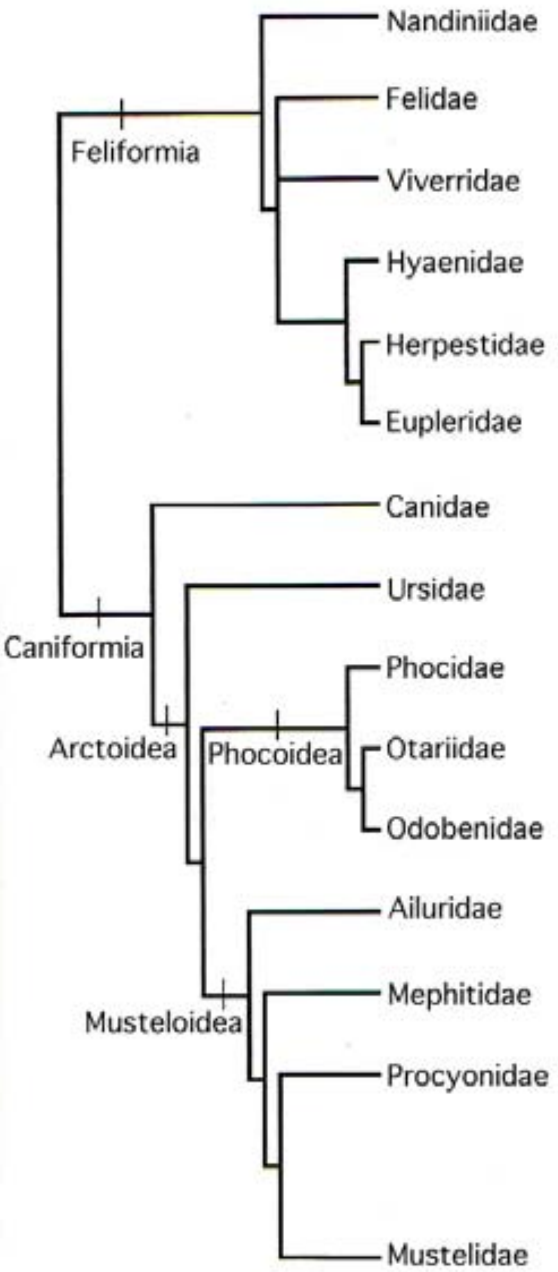

Figure 1.2. Schematic cladogram of extant Carnivora. Redrawn from Flynn et al. (2010).

Feliforms include all members of Carnivora that are more closely related to Feloidea than to Canoidea, being characterized by the following features (Flynn & Galinao 1982; Wyss & Flynn 1993; Bryant 1996: P4 parastyle enlarged; very deep, narrow, and slit-like carnassial notch in the metastyle blade of P4; M3/m3 lost; M2 reduced in size and simplified in morphology; m2 talonid extremely elongate, and entire tooth with elongate oval outline; m2 hypoconulid larger than, or equal to, hypoconid size (particularly in height). The phylogenetic relationships between feliform families are however not yet well resolved (Janis et al. 1998; Flynn & Wesley-Hunt 2005, Flynn et al. 2010; Barycka 2007), so that the most widely accepted systematic arrangement has been adopted in this study. A single superfamily Feloidea Hay, 1930 is distinguished by many authors among feliforms (Simpson 1945; Tedford 1976; Flynn & Galiano 1982; Wyss & Flynn 1993; Bryant 1996), being characterized by several cranial and postcranial features. Some authors (e.g., Hunt & Tedford 1993) have used instead the term Aeluroidea Flower, 1869, which is invalid for this superfamily (Simpson 1945; Flynn & Galiano 1982), because it is based on a genus name (*Aelurus*, currently *Ailurus*) that is considered a canoid. In spite of this fact, this term has been widely used by many authors, sometimes at the infraorder rank (Hunt 1974, 1987, 1989, 1991, 1996, 1998a, 2001; Hunt & Solounias 1991; Janis et al. 1998; Morales et al. 2000; Sato et al. 2004). Given the nomenclatural problems of this term, as well as other problems related to its definition (Barycka 2007), the term Aeluroidea is rejected here in favor of Feloidea (see also Flynn & Nedbal 1998; Wesley-Hunt & Flynn 2005; Flynn et al. 2005; Barycka 2007; Flynn et al. 2010).

Classically, feloids (Fig. 1.3) included the families Hyaenidae Gray, 1821, Viverridae Gray, 1821 and Felidae Fischer de Waldheim, 1817, but excluded the Nimravidae Cope, 1880 (Wyss & Flynn 1993; Bryant 1996; Wesley-Hunt & Flynn 2005; Flynn et al. 2010). The phylogenetic position of nimravids is still uncertain. Over the years, they have been included among feliforms (Kretzoi 1945; de Beaumont 1964; Hunt 1974, 1987; Martin 1980; Tedford 1978; Baskin 1981; Bryant 1996; McKenna & Bell 1997; Tomiya 2011), among caniforms (Flynn & Galiano 1982), as a basal taxon, sister of feliforms (Martin 1998a; Bryant 1991; Flynn & Wesley-Hunt 2005; Wesley-Hunt & Flynn 2005), and most recently as a monophyletic clade of carnivoraforms diverging before the split of crown carnivorans (Spaulding & Flynn 2012). Following the latter authors, here nimravids are provisionally considered stem carnivorans, but the possibility cannot be excluded that they are more closely related to feliforms than to caniforms, as traditionally considered.

Among the families traditionally included in the Feliformia, the Viverridae have experienced the most significant changes in content, being currently split into different families (Hunt & Tedford 1993; Wyss & Flynn 1993; Veron 1994, 1995, 2010; Flynn & Nebdal 1998; Bininda-Edmonds et al. 1999; Hunt 2001; Gaubert & Veron 2003; Yoder et al. 2003; Flynn & Wesley-Hunt 2005; Wozencraft 2005; Gaubert & Cordeiro-Estrella 2006; Koepfli et al. 2007; Barycka 2007; Flynn et al. 2010; Veron 2010; Hunter 2011). Classically (Simpson 1945; Wyss & Flynn 1993; Wolsan 1993; Wozencraft 2005; Hunt 2001), viverrids included not only genets, oyans and civets (Viverridae as conceived here), but also mongooses (Herpestidae Bonaparte, 1845), *Nandinia binotata* (Nandiniidae Pocock, 1929), linsangs (Prionodontidae Horsfield, 1821) and Malagasian carnivorans (Eupleridae Chenu, 1852). Hunt (2001) excluded the nandiniids from the Viverridae, whereas, since previous phylogenetic analyses (Flynn & Nebdal 1998; see also Gaubert & Veron 2003; Yoder et al. 2003; Gaubert & Cordeiro-Estrella 2006) concluded that they represent a unique combination of ancestral dental and auditory features, suggesting that they are the basal-most members of the Feliformia (being thus excluded from the Feloidea). Regarding prionodonts, they were traditionally included into the Viverridae due to several morphological convergences, but molecular data (Gaubert & Veron 2003) and morphological similarities with primitive felids (retractile claws, hairy metapodials, hypercarnivorous dentition, and basicranial features; Hunt 2001; Veron 2010) indicate that they constitute a distinct, monophyletic family closer to felids. Similarly, herpestids and euplerids were traditionally viverrid subfamilies, but molecular analyses and craniodental features (Veron 1994, 1995, 2010; Yoder et al. 2003) indicate that they constitute distinct groups of their own, with euplerids being the sister taxon of herpestids (Yoder et al. 2003; Flynn et al. 2005; Veron 2010), and both sharing some derived features with hyaenids (Veron 1994, 1995, 2010).

The monophyly of the Hyaenidae among feliforms is widely accepted (Werdelin & Solounias 1991; Wyss & Flynn 1993; Bininda-Edmonds et al. 1999; Hunt 2001; Gaubert & Veron 2003; Flynn & Wesley-Hunt 2005; Flynn et al. 2005; Wozencraft 2005; Gaubert & Cordeiro-Estrella 2006; Koepfli et al. 2007; Barycka 2007; Flynn et al. 2010; Veron 2010; Hunter 2011), and molecular analyses indicate that they are closely related to herpestids and euplerids (Flynn et al. 2005; Gaubert & Cordeiro-Estrella 2006). This has led to the recognition of a Herpestoidea clade (Flynn et al. 2010), which is here provisionally recognized as a superfamily distinct from feloids. However, the phylogenetic relationships between Herpestoidea, Felidae and Viverridae remain controversial (Yoder et al. 2003; Flynn et al. 2005; Gaubert & Cordeiro-Estrella 2006; Flynn et al. 2010). The Felidae, in turn, are characterized by several cranial features suggesting that they constitute the sister clade of Viverridae and Hyaenidae (Martin 1998b; Binninda-Edmonds et al. 1999; Gaubert & Cordeiro-Estrella 2006; Barycka 2007; Flynn et al. 2005, 2010). They include two extant subfamilies (Pantherinae Pocock, 1917 and Felinae Fischer de Waldheim, 1817), globally referred to as conical-toothed cats, as well as the extinct Machairodontinae, which differ from the former by their sabertoothed morphology and other cranial features (Turner & Antón 1997; Martin 1998b; Salesa et al. 2003, 2005a,b, 2012; Barycka 2007).

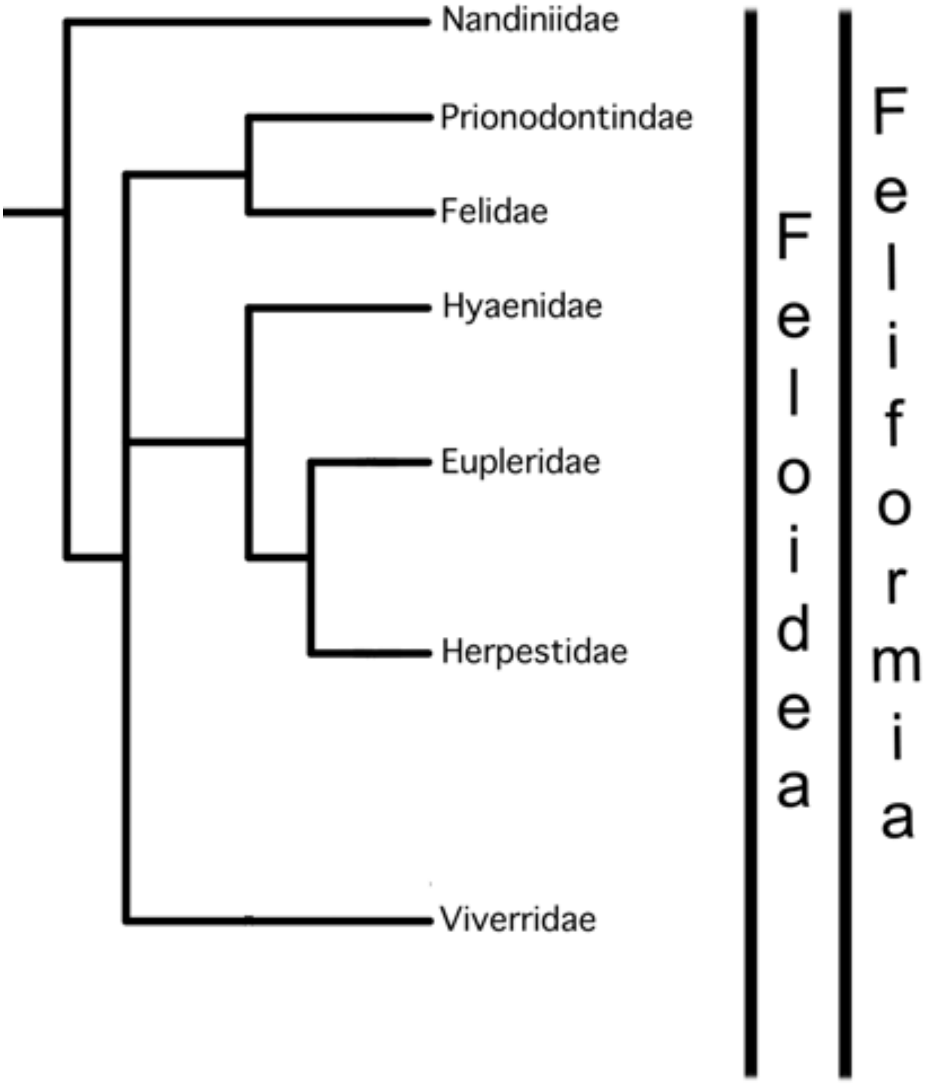

Figure 1.3. Synthetic phylogenetic tree of extant Feliformia, based on molecular and morphological data. Redrawn from Veron (2010).

Table 1.1. Systematics of the Carnivora to the family level adopted in this work, based on Wolsan (1993), Wyss & Flynn (1993), Finarelli & Flynn (2006), Finarelli (2008), Flynn et al. (2010), Veron (2010) and Hunter (2011). Extinct taxa are denoted with a dagger.

- Class Mammalia
  - Infraclass Eutheria
    - Cohort Placentalia
      - Grandorder Laurasiatheria
        - Superorder Ferae
          - Order Carnivora s.l. (=clade Carnivoramorpha)
            - Suborder incertae sedis
              - Family Viverravidae†
              - “Subclade Carnivoraformes”
                - Family Miacidae†
                - Family Nimravidae†
            - Suborder Feliformia
              - Superfamily incertae sedis
                - Family Nandiniidae
              - Superfamily Feloidea
                - Family Viverridae
                - Family Prionodontidae
                - Family Felidae
                - Family Stenoplesictidae†
                - Family Barbourofelidae†
              - Superfamily Herpestoidea
                - Family Herpestidae
                - Family Hyaenidae
                - Family Eupleridae
                - Family Percrocutidae†
            - Suborder Caniformia
              - Infraorder incertae sedis
                - Superfamily Amphicyonoidea†
                  - Family Amphicyonidae†
              - Infraorder Cynoidea

    - Superfamily Canoidea
      - Family Canidae
- Infraorder Arctoidea
  - Parvorder Ursida
    - Superfamily Ursoidea
      - Family Ursidae
      - Family Hemicyonidae†
    - Superfamily Phocoidea (=Pinnipedia)
      - Family Enaliarctidae†
      - Family Otariidae
      - Family Phocidae
      - Family Odobenidae
  - Pavorder Mustelida
    - Superfamily Musteloidea
      - Family Mustelidae
      - Family Mephitidae
      - Family Procyonidae
      - Family Ailuridae

Besides the above-mentioned, extant families, three extinct families of feliforms are distinguished: Stenoplesictidae Schlosser, 1923; Barbourofelidae Schultz et al., 1970; and Percrocutidae Werdelin & Solounias 1991. The systematic position of stenoplesictids among feliforms have been controversial, and although some authors (Morales et al. 2000) considered them as a basal subfamily of Viverridae s.l., more recently they have been considered a monophyletic group of their own (Morlo et al. 2007), even though their relationships with viverrids remain unclear. Barbourofelidae, in turn, were erected by Morlo et al. (2004) for saber-toothed carnivorans traditionally included in the Nimravidae (Neff 1983; Hunt 1987; Bryant 1991; McKenna & Bell 1997; Peigné 2003; Barycka 2007), but which are more closely related to felids (Morales et al. 2001). The distinction of barbourofelids from nimravids is supported by craniodental features (particularly from the tympanic region; Morlo et al. 2004; Tseng et al. 2010; Robles et al. 2013a,b), although their relationships with felids are still unresolved. Finally, Percrocutidae are closely related to hyaenids, from which they differ by more derived dental features (Werdelin & Solounias 1991).

With regard to the Caniformia, they are characterized by the following features (Flynn & Galiano 1982): loss of calcaneal fibular facet in the pes; great reduction or absence of parastyle in P4; reduction in size of the P4 protocone; lingual cingulum on all upper molars complete around the base of the protocone; large teres major process on the scapula. From a phylogenetic viewpoint, the Caniformia can be defined as carnivorans more closely related to Canoidea than to Feloidea (Wyss & Flynn 1993; Wolsan 1993; Bryant 1996). Two main monophyletic clades are distinguished among caniforms, here referred to as infraorders Cynoidea Flower, 1869 and Arctoidea Flower, 1869 (McKenna & Bell 1997; Janis et al. 1998). Among the former, classical studies (Tedford 1976; Flynn & Galiano 1982) distinguished a single superfamily Canoidea Fischer de Waldheim, 1817 including not only the family Canidae Fischer de Waldheim, 1817, but also the Amphicyonidae Haeckel, 1866. The latter possess several postcranial features (e.g., loss of calcaneal fibular facet in the pes) that indicate closer phylogenetic affinities with caniforms than with feliforms. However, subsequent studies (Wyss & Flynn 1993; Bryant 1996; Flynn & Nebdal 1998; Flynn et al. 2005; Wesley-Hunt & Flynn 2005; Finarelli 2008; Finarelli & Flynn 2006; Spaulding & Flynn 2012; Tomiya 2011) showed that amphicyonids are less closely related to canids than previously assumed, so that the Canoidea should be restricted to the Canidae. Many studies have therefore concluded that amphicyonids occupy an uncertain systematic position among stem caniforms (Bryant 1996; Wolsan 1993; Wyss & Flynn 1993; Janis et al. 1998; Finarelli & Flynn 2006; Flynn et al. 2010), even being excluded from the latter by some authors (Wesley-Hunt & Flynn 2005).

Arctoidea, in turn, are characterized by several craniodental features (reduction or loss of posterior accessory cusps on premolars, widening of the basioccipital, and position of the infraorbital foramen above the distal half of the P4; Bryant 1996; Wesley-Hunt & Flynn 2005; Flynn et al. 2010). From a phylogenetic viewpoint, they can be defined as the clade including the most recent common ancestor of species referred to Procyonidae Gray, 1825, Mustelidae Fischer de Waldheim, 1817, including Mephitidae Bonaparte, 1845, Ursidae Fischer de Waldheim, 1817, Ailuridae Gray, 1843 and Pinnipedia Illiger, 1811 and all its descendants (Bryant 1996; Wesley-Hunt & Flynn 2005). It must be taken into account, however, that the phylogenetic relationships between cynoids and arctoids still remain unclear (Flynn & Nedbal 1998; Wesley-Hunt & Flynn 2005; Finarelli 2008; Tomiya 2001). Two main arctoid clades are distinguished (Tedford 1976; Wolsan 1993;

Bryant 1996), Ursida Tedford, 1976 and Mustelida Tedford 1976, here distinguished as distinct parvorders.

Ursida, in turn, include two sister groups, (Wyss & Flynn 1993; Bryant 1996; McKenna & Bell 1997; Flynn & Nedbal 1998; Wang et al. 2005b; Finarelli & Flynn 2006, Yonezawa et al. 2007), here distinguished as superfamilies Ursoidea Gray, 1825 and Phocoidea (Gray, 1821) (the latter corresponding to the classical denomination of Pinnipedia, still considered a distinct order by some authors; Riedman 1990; Reeves et al. 1992; Nowak 2003). Although the monophyly of these two groups is well supported by both morphological and molecular data, their phylogenetic relationships are not completely well resolved (Arnason & Widegren 1986; Colbert et al. 1991; Wyss & Flynn 1993; Flynn & Nedbal 1998; Flynn 1998; Arnason et al. 2006; Flynn et al. 2010), with some authors considering that pinnipedes are more closely related to the Mustelida than to Ursidae (Flynn et al. 2005, 2010; Finarelli 2008). As much as four phocoid families (one of them extinct) are distinguished, whereas only two families are included in the Ursoidea: the extant Ursidae Fischer de Waldheim, 1817 and the extinct Hemicyonidae Frick, 1926, the latter having a more primitive and complete dentition than the former (Abella et al. 2014).

Unlike Ursida, the pavorder Mustelida includes a single superfamily Musteloidea Fischer de Waldheim, 1817 with several families (Wolsan 1993; Wyss & Flynn 1993; Bryant 1996; McKenna & Bell 1997; Flynn & Nedbal 1998; Janis et al. 1998; Finarelli 2008; Flynn et al. 2010): Ailuridae Gray, 1843 (red pandas), Mephitidae Bonaparte, 1845 (skunks and badgers), Procyonidae (raccons and coatis), Mustelidae (weasels and allied taxa). The phylogenetic relationships between these musteloid families remain mostly unresolved (Flynn et al. 2010; Morlo & Peigné 2010). Traditionally, mephidids were merely distinguished as a mustelid subfamily (Simpson 1945; McKenna & Bell 1997), but current molecular and morphological features support their distinction at the family rank (Flynn & Nedbal 1998; Flynn et al. 2000, 2005, 2010; Arnason et al. 2007; Finarelli 2008; Hunter 2011). The phylogenetic relationships among the remaining mustelid subfamilies are currently uncertain to a large degree (Hunter 2011), and some of their most basal forms are informally referred to as “paleomustelids” (basal Mustelidae s.l.) or “paleomustelids” (basal mustelids+mephitids), being closer to the Mustelidae than to Procyonidae (Finarelli & Flynn 2006). The latter, in turn, are the most likely sister-taxon of the Mustelidae based on molecular data (Koepfli et al. 2007; Hunter 2011).

Evolutionary history

The past diversity of carnivorans, with about 355 extinct genera, surpasses that of the living representatives of the order (about 129 extant genera; Goswami 2010). In spite of such a relatively profuse fossil record, the origins of the order Carnivora are poorly known. Althought the creodonts were traditionally included in the Carnivora (see above), it currently seems that they evolved independently, perhaps from ancestral insectivores, or from the same basal stock that gave rise to the Primates and Chiroptera (Novacek 1992; Wozencraft 1989; Wyss &Flynn 1993).

The extinct viverravids are the basal-most members of the Carnivora. They were small arboreal animals recorded in from the early Paleocene to the late Eocene of North America, Asia and Europe (McKenna & Bell 1997; Janis et al. 1998; Polly et al. 2006; Barycka 2007). In turn, basal carnivoraforms such as miacids are small and carnivorous, viverrad-like animals recorded from the late Paleocene to the early Eocene (McKenna & Bell 1997; Janis et al. 1998), being characterized by the possession of primitive features (such as a non-ossified tympanic bulla and scaphoid not fused with the lunar; Ginsburg 1961a; Martin 1989; Colbert et al. 1991; Heinrich & Rose 1995, 1997; Anyonge 2001; Kruuk 2001; Wesley-Hunt & Flynn 2005; Heinrich & Houde 2006; Polly et al. 2006; Spaulding & Flynn 2009, 2012). Stem carnivorans reached their maximum diversity during the Eocene, becoming extinct before the Oligocene (Wesley-Hunt & Flynn 2005; Spaulding et al. 2010), with the exeption of nimravids, which are first recorded by the late Eocene of North America and Asia, but spread to Europe during the early Oligocene (Peigné 2003; Spaulding & Flynn 2012). Based on molecular data, the divergence between crown carnivorans (caniforms and feliforms) is dated to the early Eocene (Gaubert & Cordeiro-Estrella 2006; Bininda-Edmonds et al. 1999) or somewhat later, by the middle/late Eocene transition (Yoder et al. 2003; Polly et al. 2006). However, only a few of the extant families, such as Nandiniidae among feliforms, and Canidae, Mustelidae and Ursidae among carniforms, are currently recorded by the Eocene (McKenna & Bell 1997; Munthe 1998; Wesley-Hunt & Flynn 2005; Gaubert & Cordeiro-Estrella 2006; Barycka 2007; Finarelli 2008; Flynn et al. 2010; Spaulding & Flynn 2012).

Nandiinids (including the extant African palm civet) is considered the earliest group to diverge from the remaining feliforms, based on both morphological (Hunter 2011) and molecular (Veron 2010) data. Felids would have been the second feliform family to diverge around the middle to late Eocene (Gaubert & Cordeiro-Estrella 2006; Bininda-

Edmonds et al. 1999), although they are not recorded until the Oligocene of Europe, not dispersing into North America until the early Miocene (Hunt 1998a; Barycka 2007) and attaining their highest diversity during the middle Miocene (Barycka 2007). Viverrids might have also diverged by the middle Eocene (Gaubert & Cordeiro-Estrella 2006), although their oldest record is scarce and fragmentary until the the early Miocene of Asia, suggesting at least an Asian origin during the Oligocene (Bininda-Edmonds et al. 1999; Gaubert & Cordeiro-Estrella 2006; Veron 2010) and later spreading to Africa and Europe (Barycka 2007; Gaubert & Cordeiro-Estrella 2006). Based on molecular data (Gaubert & Cordeiro-Estrella 2006; Barycka 2007; Veron 2010), prionodontids are closely related to felids, having probably diverged by the late Eocene (Gaubert & Cordeiro-Estrella 2006). Hyaenids, in turn, would have diverged by the middle Oligocene (Koepfli et al. 2007) or the Eocene/Oligocene transition (Gaubert & Cordeiro-Estrella 2006) based on molecular data, although they are not recorded until the middle Miocene of Europe (Barycka 2007). Apparently, hyaenids share a common African ancestor with herpestids and euplerids (Yoder et al. 2003; Gaubert & Cordeiro-Estrella 2006; Baricka 2007), which are considered sister taxa (Veron 2010). Based on molecular data, hyaenids, herpestids and euplerids would have diverged sometime during the Oligocene (Bininda-Edmonds et al. 1999; Yoder et al. 2003; Barycka 2007; Gaubert & Cordeiro-Estrella 2006; Veron 2010). However, herpestids are not recorded until the early Miocene of Africa and Europe, not reaching Asia until the late Miocene (Gaubert & Cordeiro-Estrella 2006; Barycka 2007; Hunter 2011). Euplerids are restricted to Madagascar, and although their origins are unclear, they probably originated from an ancestral herpestid-like form that dispersed from Africa into Madagascar (Hunter 2011). Among the extinct feliform families, only the phylogenetic affinities of percrocutids (closely related to hyaenids), recorded from the Miocene up to the Pliocene in Africa and Eurasia (Werdelin & Solounias 1991) are clear. The origin of the false sabertooths of family Barbourofelidae, which are first recorded in Africa by the early Miocene, and subsequentlyd dispersing into Eurasia and North America, is unclear (Robles et al. 2013a). Similarly, Stenoplesictidae include civet-like animals recorded from the late Eocene until the middle Miocene of Africa (Morlo et al. 2007). They might have diverged from viverrids by the Eocene/Oligocene transition (Binninda-Edmonds et al. 1999), although this is far from clear (Morlo et al. 2007).

With regard to caniforms, amphicyonids would have originated by the middle Eocene (Finarelli & Flynn 2006), very close to the divergence between caniforms and feliforms at about the middle/late Eocene transition (Yoder et al. 2003), although they are not recorded until the late Eocene of North America (Hunt 1998c). Regarding crown caniforms, the split between Cynoidea (or Canidae) and Arctoidea is considered to have occurred by the middle Eocene (Finarelli & Flynn 2006; Flynn et al. 2010; Bininda-Edmonds et al. 1999). Earliest canids were restricted to North America until the late Miocene (Munthe 1998; Flynn et al. 2010), when they spread across other continents, thus becoming the most widely distributed caniform family (Munthe 1998; Hunter 2011). Among arctoids, the split between Ursoidea, Phocoidea and Musteloidea would have taken place by the late Eocene (Finarelli & Flynn 2006; Bininda-Edmonds et al. 1999), when ursids are first recorded in North America (Hunt 1998b). However, the relationships between these three clades are unclear, with some authors arguing that phocoids (or pinnipeds) would have diverged from musteloids (Finarelli & Flynn 2006) by the early Miocene (Bininda-Edmonds et al. 1999). Phocoid origins are obscure due to the fragmentary nature of their earliest fossil record, having originated and scarce, being first recorded by the middle Miocene (Berta et al. 1989). Among musteloids, the divergence between “paleomustelids” + ailurids from procyonids + mustelids and allied families is considered to have taken place at least by the late Oligocene (Finarelli & Flynn 2006; Bininda-Edmonds et al. 1999). Ailurids would have diverged by the late Oligocene (Flynn et al. 2010; Morlo & Peigné 2010) or the middle Miocene (Finarelli & Flynn 2006), being first recorded in Europe (Morlo & Peigné 2010). Procyonids, in turn, would have diverged by the early to middle Oligocene (Sato et al. 2003; Finarelli & Flynn 2006; Koeplfi et al. 2008; Hunter 2011), being first recorded in the late Oligocene of Europe (Koepfli et al. 2007, 2008), although they experienced their greatest diversification subsequently in North and South America (Baskin 1998; Koepfli et al. 2007; Hunter 2011). Mephitids would have diverged from mustelids by the early Miocene (Finarelli & Flynn 2006), when they are first recorded in the Europe (Wang et al. 2005a), subsequently spreading across Asia as well as North and South America (Hunter 2011). Finally, mustelids include the most derived caniforms, having originated close to the Oligocene/Miocene transition in Europe (Sato et al. 2003; Finarelli & Flynn 2006; Koepfli et al. 2008), and subsequently spreading to North and South America across Asia during the Miocene (Sato et al. 2003).

1.3. Carnivoran anatomy

Dentition

Most of the main adaptations of carnivorans are reflected in their craniodental anatomy, especially their teeth (Fig. 1.4). Thus, the dentition of carnivorans is quite characteristic of the group, since it generally displays conspicuous adaptations for meat consumption—although with considerable variations depending on each particular group and their respective dietary adaptations. Among the Carnivora we can distinguish various dental patterns reflecting the way in which they kill preys or obtain their food (Kruuk 2001; Holliday & Steppan 2004). Strictly meat-eaters (such as most felids) have a hypercarnivorous dentition, which is characterized by long shearing edges (composed by the trigon of the upper fourth premolar and the trigonid of the lower fist molar), as well as a reduction or loss of the postcarnassial dentition (the second and third lower molars and the first and second upper molars). In contrast, other carnivorans with a less strict meat-eating diet (such as most mustelids, ursids or canids) display a hypocarnivorous dentition, which is characterized by more grinding occlusal surfaces and a non-reduced postcarnassial dentition, which allows them to chew or grind the consumed food.

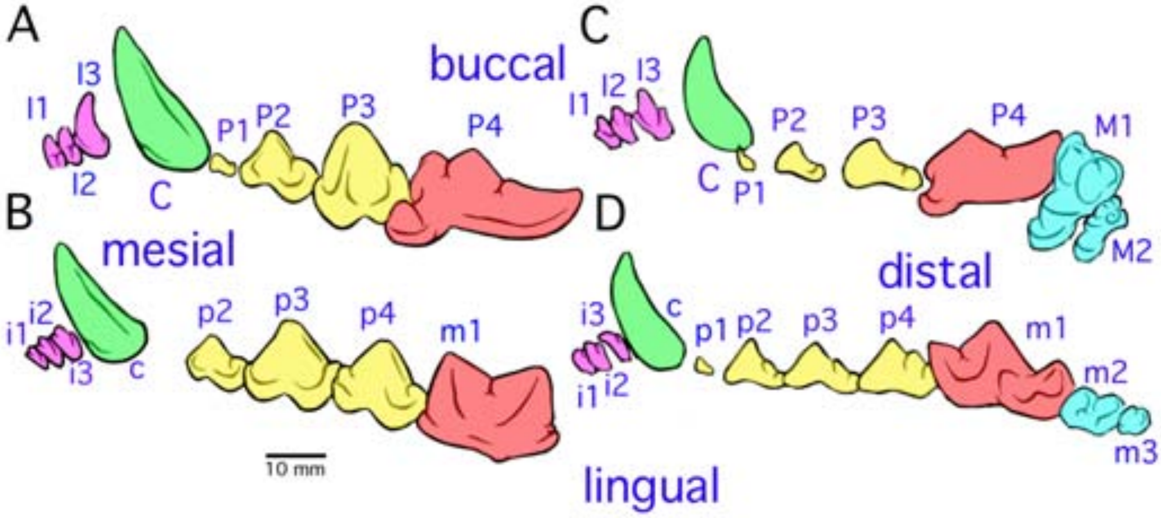

Figure 1.4. The masticatory apparatus of carnivorans. **A.** Upper teeth in Feliformia (*Crocuta crocuta*); **B.** Lower teeth in Feliformia (*Crocuta crocuta*); **C.** Upper teeth in Caniformia (*Canis familiaris*); **D.** Lower teeth in Caniformia (*Canis familiaris*); Color legend: Incisors in magenta; canines in green; premolars in yellow; carnassials in red and non-carnassial molars in blue. Modified from Hillson (2005).

Generalities. The permanent dental formula in extant and extinct carnivorans is generally as follows (Hillson 2005): 3I 1C 2-4P 0-2M / 3i 1c 2-4p 1-3m. Pinnipeds, however, display a slightly different formula (Hillson 2005): 3I 1C 5-6 PC / 2-3i 1c 5pc, since postcanine teeth cannot be distinguished into premolars and molars. In turn, the decidous dental formula is generally as follows (Hillson 2005): 3I 1C 3P / 3i 1c 3-2p. Pinnipeds, however, have a diphyodont dentition, with deciduous teeth being resorbed in utero of just after birth (Hillson 2005).

The carnivoran dentition is characterized by the possession of a shearing blade between the last upper premolar (P4) and the first lower molar (m1) among the permanent dentition, and between the third upper deciduos premolar (dP3) and the last upper deciduous premolar (dp4) among the deciduous denttion. These teeth are referred to as "carnassials" or "carnassial teeth". Their shape depends on the dietary specializations of each group, but generally the P4 displays a triangular occlusal profile, with a well-developed cutting edge constituted by the paracone and the metacone or mestasyle crest, with the protocone reduced or even absent. In the m1, the main cutting edge is formed from high ridges of the protoconid and paraconid; the metaconid is generally reduced, and the talonid remains as a crushing area in most families, being absent in others. The upper and lower carnassials act together as a blade-like structure, by shearing against each another (like a pair of scissors) and thus cutting and crushing throught the meat and skin. This is particularly true for specialized carnivorous taxa, whereas more generalized carnivorous or omnivorous carnivorans (such as ursids and mustelids) display a less specialized dentition, with a well-developed talonid, robust teeth and bunodont cusps, which are mainly used for crushing food items (Ewer 1973; Colbert et al. 1991; MacDonald & Kays 2005). In contrast, the carnivorans most adapted to meat-eating (such as felids and barbourofelids) display a very specialized ("hypercarnivorous") dental morphology, which is characterized by sharper and more blade-like carnassials with a reduced talonid, sharper and taller cusps, and larger upper canines (Hillson 2005; Sanderson & Watson 2011). Other carnivorans display particular dental specializations to their particular dietary regimes, such as insectivory (e.g., the hyeaenid *Proteles cristatus* or the canid *Otocyon megalotis*), resulting in very pointed teeth. Bone-cracking hyaenids, in turn, display very well-developed premolars, which together with other (cranial and digestive) adaptations allow them to crush bones (MacDonald & Kays 2005).

Incisors. The incisors of carnivorans (Fig. 1.4; in magenta) are generally small relative to the remaining teeth (Hillson 2005; Sanderson & Watson 2011) and unicuspid (although frequenly they display accessory mesial and distal cuspules). Most carnivorans possess three permanent incisors on each tooth row (both upper and lower), although with some exception and further being reduced or lost in pinnipeds (Colbert et al. 1991). Commonly, the first incisor is the smallest one, whereas the third one is caniniform, being larger and higher-crowned than the remaining incisors; this is most marked in the upper dentition, although the I3 is still smaller than the canine.

Canines. The canines (Fig. 1.4; in green) are generally large and well-developed, clearly prodruding from the occlusal plane of the postcanine toothrow, although they considerably vary in size and sharpness depending on the taxa (Hillson 2005; Sanderson & Watson 2011). The upper canines are generally slightly separated from the incisors by a small space (diastema). In contrast, the lower canines are juxtaposed to the third incisor. Both the upper and lower canines are unicuspid, high-crowned and elongate, recurved, pointed and sharp, although the crown cross-section from apex to base varies among groups (Hillson 2005; Sanderson & Watson 2011), from round (e.g., felids) to elliptical (e.g., canids; MacDonald & Kays 2005). The canines are generally used to hold and dispatch prey, either by strangulation or by stabbing. In some pinnipeds, the upper canines constitute hypertrophied tusks. The shape of the canine has biomechanical implications, with circular cross-sections being more resistant against stressed from all angles (as in felids), whereas elliptical sections are less resistant against stresses perpendicular to the main cross-sectional crown axis (as in canids). The circular section of felid canines (circular knife-like) allows them to inflict a deep and great damage to the prey, during which stresses across the teeth may come from any direction without danger of breakage. In contrast, the elliptical section of canids allows them to inflict rapid and shallow damage, by applying pressure along the main axis of the elipse section. Among machairodontine felids, barbourofelids and nimravids, the lower canines are smaller than the upper ones, more closely resembling in size the third lower incisor, while the upper canines are desproportionately large. The smaller size of the lower canine allows them to fit well the larger upper canine between the lower dentition without increasing of length of the mandible.

Premolars. In carnivorans, the premolars (Fig. 1.4; in yellow) are usually adapted for cutting and shearing chunks of meat (Hillson 2005; Sanderson & Watson 2011). They are composed by a single main cusp, which is generally situated at about mid-crown length, up to 3 (mesial and distal) accessory cups, the crown being labiolingually compressed and thus suitable for catching and holding prey (Hillson 2005). The upper carnassial (P4) displays a mesiodistally-aligned and labially-situated main cutting edge, constituted by the paracone, the metacone and, in some groups (such as felidae and barbourofelids), even a mestastyle (Hillson 2005). The parastyle is mesiodistally positioned relative to the paracone and is variously protruding (Hillson 2005). In contrast, the P4 protocone is usually an individualized and mesiolingually-situated cusp, which may be absent in some families (e.g., Barbourofelidae). In pinnipeds, the premolars are secondarily simplified to conical and pointed teeth (Colbert et al. 1991). In hyaenids, the lack of molars is compensated by the presence of particularly buttressed precarnassial premolars (MacDonald & Kays 2005).

Molars. The upper molars are situated behind the upper carnassial (P4), but the first lower molar (m1) constitutes the lower carnassial (m1) (Fig. 1.4; carnassials in red and molars in blue). The postcarnassial dentition enables crushing bones and other hard food items in some groups (such as canids, some mustelids and ursids), and further retain hard foods after the hunt against other predators such as voltures and other carnivorans (Colbert et al. 1991; Anyonge 2001; MacDonald & Kays 2005). The upper molars have higher buccal than lingual cusps, although the differences among them vary acccording to their classification (Hillson 2005). Thus, caniforms generally display a continuous cingulum sorrounding the protocone in the upper molars and lack a parastyle in the upper carnassial (Flynn & Galiano 1982; Garrido & Arribas 2008). The trigonid of the lower carnassial is further constituted by an isolated and generally reduced metaconid, which is usually situated at about mid-crown length towards the lingual side (Hillson 2005). Behind the trigonid, most families (such as ursids and hyaenids) display a lower talonid that performs a crushing function, whereas in some other carnivorans (such as felids and barbourofelids) it is considerably reduced or even vestigial. In some groups (such as some canids), there is a single residual postcarnassial lower molar (m2), which may be even absent in some felids and hyaenids.

Skull (cranium and mandible)

As a result of the varied killing and feeding behaviors among extant and extinct taxa, carnivorans not only displayed different dental adaptations, but also significant differences in craniomandibular morphology (including their length, robusticity and weight). Felids, for example, generally display short-snouted (brachycephalic) skulls (Fig. 1.5A), which allow them to focus the bite strenght in the front of their mouth. In contrast, canids display longer (telocephalic) skulls (Fig. 1.5E), which enable them to focus the bite strenght more posteriorly (Turner & Antón 1997; Anyonge 2001; Holliday & Steppan 2004; MacDonald & Kays 2005).

Cranium. The cranium of carnivorans, as in other mammals, is composed by many different bones (Fig. 1.5), some paired and others non-paired, which together constitute an integrated whole that simultaneously performs masticatory and sensory functions (by hosting and protecting the brain and various sense organs). The facial skeleton (splanchnocranium) constitutes the most anterior portion of the cranium (the muzze), serving simultaneously various functions (respiratory, olfactory and masticatory) and being integrated by the paired premaxillae, maxillae, palatines, lacrimals, nasals and zygomatic, and the unpaired vomer. The braincase (neurocranium), which protects the brain, is composed by the unpaired frontal, and the paired parietals, temporals and occipitals. Finally, the basicranium is composed by the unpaired basisphenoid, the unpaired pterygoid, the unpaired occipital bone and the tympanic portion of the temporal bone, which contains the tympanic bulla.

The most hypercarnivorous carnivorans (felids and barbourofelids) generally have brachyocephalic skulls, with very developed sagittal and nuchal crests, coupled with a reduced number of cheek teeth, a reduced pterygoid area, and a deep and large masseteric fossa in the mandible. These adaptations allow them to concentrate the strenght of their bite behind the upper canine for a unique dead bite without lateral movements (Young 1971; Ewer 1973; Anyonge 2001; Turner & Antón 1997; MacDonald & Kays 2005; Sanderson & Watson 2011). Other taxa (such as canids, mustelids or ursids) are characterized by telocephalic skulls with a lesser developed temporalis muscle and non-reduced cheek teeth, which give them a greater shearing power but a less powerful upper canine bite (Sanderson & Watson 2011).

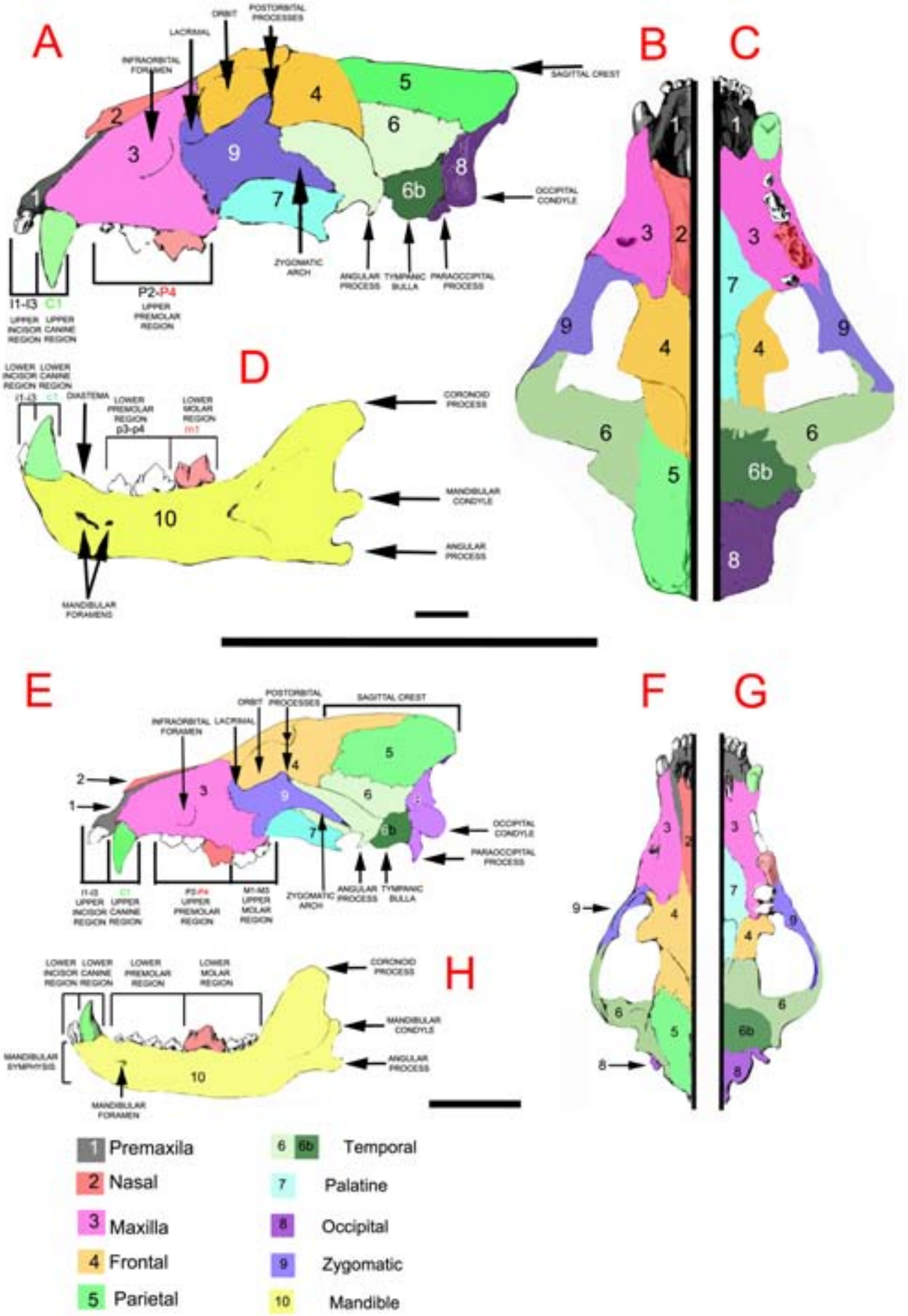

Figure 1.5. Skulls and mandibles of feliforms and carniforms. **A-C**, Skull of an extant feliform (*Panthera leo*), in lateral (A), dorsal (B) and ventral (C) views. **D**, Mandible of an extant feliform (*Panthera leo*), in lateral view; **E-H**, Skull and mandible of an extant caniform (*Canis familiaris*), in lateral (E), dorsal (F) and ventral (G) view. **H.**, Mandible of an extant caniform (*Canis familiaris*), in lateral view. Scale bar equals 5 cm. Modified from Pales & Garcia (1981).

Mandible. The mandible (Fig. 1.5), it is composed by a single bone (the dentary), which is more or lest robust depending on the group. The two dentaries (right and left hemimandibles) are not fused, and anteriorly converge to the more or less verticalized mandibular symphysis. The mandibular bodie host the lower teeth, diverging posteriorly from the symphysis until the angular process. In sabertooth carnivorans, the mandibular corpus may display a genial flange at about the level of the diastema between the lower canine and the first lower premolar, to fit in the upper canine. The mandibular corpus displays near the mandibular symphysis a mental foramen. Each mandibular rami includes a coronoid process (its dorsal-most portion) extending upward and outward, a transversely elongated and sagittally convex mandibular condyle (or articular process), which is part of the temporomandibular joint, and an angular process (the posteroventral portion of the mandible, which constitutes an attachment for the pterygoid and the masseter muscles). On the lateral surface of the ramus, the masseteric fossa serves as the insertion of the masseter muscle, being delimited by the coronoid crest and by the condyloid crest (Evans 1993). In the most hypercarnivorous taxa, the masseteric fossa is very deep and large.

Postcranium

The postcranium includes all the bones situated behind the skull, generically referred to as postcranials. They can be divided into two main regions: the axial skeleton (including the ribs and the vertebral column) and the apendicular skeleton (including the forelimb and the hind limb).

Axial skeleton. The vertebral column, which supports the skull, the rib cage and the limbs, can be subdivided into five regions, which display a different number of vertebrae depending on the taxa; from anterior to posterior, they are the following (Ewer 1973; Evans 1993): cervical (7 vertebrae), thoracic (13-16), lumbar (4-8), sacral (2-6) and caudal (9-34). The rest of the axial skeleton is composed by the ribs, which articulate with the thoracic vertebrae and, much more uncommonly, are also present in the last cervical vertebrae (Evans 1993).

Apendicular skeleton. The forelimb articulates with the vertebral column through the thoracic girdle, which is composed by the scapula. The glenoid fossa of the scapula articulates with the head of the humerus, forming the shoulder joint. Distally, the humeral epiphysis is composed by the trochlea and the capitulum, which respectively articulate with the ulna and radius, forming the elbow joint. Several features of the humerus, such as the development of the deltoid tuberosity, development of the epicondyle, and the articulation axis relative to the ulna, enable the distinction between plantigrade and digitigrade forms (Ginsburg 1961a). The ulna is the longest bone of the carnivoran forelimb, whereas the radius is the main weight-bearing bone of the forearm. These bones articulate with the humerus and with each other proximally, and with the carpus distally. Several of their morphological features, such as the morphology of the olecranon process of the ulna, further enable to distinguish between plantigrade and digitigrade forms. The set of bones including the carpus, metacarpus and phalanges are colectivelly referred to as the forepaw. The carpal bones (scaphholunar, pyramidal, pisiform, trapezoium, magnum and unciform) constitute the wrist joint. One of most distinctive features of crown carnivorans is the fusion between the scaphoid and lunar into a single bone (scapholunar), which articulates with the radius proximally and with other carpals distally, and whose morphology is also distinctive between plantigrades and digitigrades. Unlike the carpals, the metacarpals elongated bones (longer in digitigrades than in plantigrades), situated between the carpus and the phalanges. Generally, five metacarpals are present, although those from rays II to V are the most important one. They articulate with the phalanges though a distinctive trochlear crest present on their distal epiphysis. The phalanges (proximal, middle and distal) , compose the digits. Among carnivorans, the distal phalanx displays a conical and mediolaterally compressed shape, being attached to a horny claw. Finally, several small sesamoid bones are usually present between the metarcapals and the phalanges, serving articulating purposes.

With regard to the hind limb, it articulates with the vertebral column through the pelvic girdle, which is composed by the two os coxae, the sacrum and the first caudal vertebra. Each os coxae is composed by the ilium, ischium and pubis, which together constitute the acetabulum for articulation with the femoral head. The femur is the most massive bone of the carnivoran skeleton, being composed by an hemispherical head for articulation with the acetabulum, separated from the long shaft by a distinct femoral neck, and further characterized by the presence of two (greater and lesser) distinctive trochanters. This bone articulates with the tibia by though two distal condyles, which define a femoral trochlea for articulation with the patella. The shape of the femoral cross-section, as well as the insertion of the gluteus maximums, also serve to distinguish between plantigrade and digitigrade taxa. The tibia, which articulates with the femur proximally and with the tarsus distally, is much stouter than the fibula. The former displays proximally a triangular cross-section, becoming more cylindrical distally, until it articulates with the astragalus. The muscular insertions on its proximal diaphysis are also useful to distinguish between plantigrades and digitigrades. The fibula is much thinner than the tibia. It articulates proximally with the tibia and distally with the astragulus, serving for muscular attachment but supporting little weight. The tarsus, metatarsus and phalanges collectively constitute the hindpaw. Besides the above-mentioned astragalus, and the calcaneus (which is the largest tarsal bones), the tarsus includes several bones (calcaneus, navicular, cuboid and three cuneiforms), which constitute the hock. The cuneiforms and the cuboid articulate with the metatarsals, the shape of the tibiotarsal articulation further being distinctive between plantigrades and digitigrades. The metacarpals are situated between the tarsus and the phalanges, generally resembling in shape but being longer than the metacarpals, from which they can be distinguished by the shape of their proximal articular surface. The phalanges of the hindpaw are also very similar in shape to those from the forepaw.

1.4. Previous research on fossil carnivorans from the Vallès-Penedès Basin

Early studies

Earliest pioneering studies by Bataller. The first report of carnivorans from the Vallès-Penedès Basin corresponds to that of the hyaenid *Hyaenictis graeca* Gaudry, 1862 from Sant Miquel del Taudell in the area of Viladecavalls (Bataller 1921; Fig. 1.6), which was subsequently reassigned to *Hyaenictis almerai* Villalta Comella & Crusafont Pairó, 1948 in the original description of the latter taxon (Villalta Comella & Crusafont Pairó 1948). Shortly afterwards, Bataller (1924) added additional carnivoran species to the faunal list of Miocene mammals from the Vallès-Penedès Basin, such as *Hyaena eximia* Roth & Wagner 1854 [currently *Adcroctua eximia* (Roth & Wagner, 1854), after Werdelin & Solounias (1991)] and *Machairodus ogygius* Zittel 1893 [currently attributed to *Albanosmilus jourdani* (Filhol, 1883) by Robles et al. (2013a)] from Sant Quirze del Vallès (Barcelona).

Crusafont and Villalta during the early postwar period. The Spanish Civil War (1936-1939) represented a serious stagnation of scientific research in Spain. Just after the war, Bataller still published some research on fossil vertebrates from the Vallès-Penedès

Basin, by focusing his work on the Penedès sector of the basin. In particular, Bataller (1924, 1941) reported new discoveries and localities around the areas of Masquefa, els Hostalets de Pierola and Piera (such as Mas Marimon, Gall Mullat, Can Mata de la Garriga and Font d'Ocata). Bataller's (1941) report for each locality included a considerable amount of carnivorans, which were simultaneously described and figured by Villalta Comella & Crusafont Pairó (1941). In fact, these two young paleontologists were the ones that most significantly contributed to the knowledge of Vallès-Penedès fossil vertebrates during the following decades, as a continuation of Bataller's pioneering studies.

Figure 1.6. Lateral view of the holotype of *Hyaenictis almerai* from Sant Miquell del Taudell (Viladecavalls), housed in the Museu de Geologia de Barcelona (MGB). Scale bar equals 5 cm.

Villalta Comella & Crusafont Pairó (1941) provided the first complete compilation of previously-known localities with carnivorans in both the Penedès sector (els Hostalets de Pierola, Masquefa and Piera; see above) and the Vallès sector of the basin. The latter included the following localities: Subsòl de Sabadell, San Quirico de Tarrassa [currently Sant Quirze del Vallès] and Sant Miquel del Taudell in Viladecavalls. Villalta Comella & Crusafont Pairó (1941) also provided the most comprehensive faunal list of carnivorans published until then from the area of els Hostalets de Pierola, with Can Mata 1 as its main fossiliferous site (see below). Moreover, slighly later the same authors (Villalta Comella & Crusafont Pairó 1943a) published a more extensive monograph on carnivorans and insectivores from the Vallès-Penedès Basin. In this publication, these authors revised the remains from the previously reported localities (Villalta Comella & Crusafont Pairó 1941), and further complemented them with newly discovered sites from the same basin. These authors reported a faunal list for each locality, together with the then known stratigraphic range of each taxon from the Early to Late Miocene in the Vallès-Penedès Basin. The most important fossiliferous area mentioned in Villalta Comella & Crusafont Pairó (1943a), as far as carnivorans are concerned, corresponded to els Hostalets de Pierola (in the Penedès sector), and especially to locality Can Mata 1, followed that of Sant Quirze (in the Vallès sector).

Intensive paleontological fieldwork in several areas of the Vallès-Penedès Basin was carried out by Miquel Crusafont and Josep F. de Villalta (e.g., see Crusafont Pairó & Villalta Comella 1952; Villalta Comella & Crusafont Pairó 1944, 1948; Villalta & Crusafont 1952 and Crusafont Pairó 1952). These authors published a complementary appendix (Villalta Comella & Crusafont Pairó 1944) to their previous study (Villalta Comella & Crusafont Pairó 1943a), in which they first reported several carnivoran taxa for the Vallès-Penedès Basin: *Pseudocyon sansaniensis* Lartet, 1851 [currently *Hemicyon goeriachensis* (Toula, 1884), after Ginsburg & Morales (1998)]; *Indarctos vireti* Villalta Comella & Crusafont Pairó, 1943; ?*Agriotherium* sp.; *Herpestes guerini* Villalta Comella & Crusafont Pairó, 1948 [currently *Plioviverrops guerini* (Villalta Comella & Crusafont Pairó 1948), after Werdelin & Solounias (1991)]; *Crocuta eximia* [currently *Adcroctua eximia*]; *Hyaenictis almerai*; ?*Plesictis mutatus* Filhol, 1883 [currently attributed to *Semigenetta sansaniensis*, after Golpe-Posse (1981a); and *Trocharion albanense* Major, 1903. The research by these authors (sometimes in collaboration with other researchers) was further reflected in the erection of new carnivoran taxa (Villalta Comella & Crusafont Pairó 1943a, b, 1945, 1948, 1955; Viret & Crusafont-Pairó 1955; Crusafont Pairó 1950; Crusafont Pairó 1959a): *Indarctos vireti*; *Palaeomeles pachecoi*; *Ictitherium montadai* Villalta Comella & Crusafont Pairó 1943 [currently *Thalassictis montadai* (Villalta Comella & Crusafont Pairó 1943)]; *Hyaenictis almerai* Villalta Comella & Crusafont Pairó, 1948; *Enhydriodon lluecai* Villalta and Crusafont, 1945 [currently *Sivaonyx lluecai* (Villalta Comella & Crusafont Pairó, 1945), after Alcalá et al. (1994)]; *Felis vireti* Crusafont, Villalta and Truyols, 1955 [attributed in part to Viverridae by de Beaumont (1961) and to Felinae indet. by Robles et al. (in prep.)]; *Herpestes guerini* Villalta Comella & Crusafont Pairó, 1948 [currently *Plioviverrops guerini* (Villalta Comella & Crusafont Pairó, 1948)]; *Limnonyx sinerizi* Crusafont Pairó 1950; *Amphicyon* (*Ictiocyon*) *dehmi* Crusafont, Villalta and Truyols 1955 [currently *Ictiocyon socialis* Schlosser, 1904 after Ginsburg (1992)] and *Plesiomeles cajali* Viret and Crusafont Pairó 1955.

The collaboration between Crusafont and Truyols. During the 1950s, Josep Truyols Santoja began to collaborate with Crusafont and Villalta, the former being involved in the establishment of the proper stratigraphic framework for the Miocene localities of the Vallès-Penedès Basin (Crusafont Pairó & Truyols Santoja 1954; Crusafont et al. 1955). Crusafont & Truyols (1954) further published an extensive and updated list of all the then-known Miocene sites from the Vallès-Penedès and Calatayud-Daroca-Teruel basins, with their respective faunal lists. The intensive research activity of Villalta, Crusafont and Truyols during this decade, however, was not only focused on the publication of systematic papers or on the report of new citations and localities. In particular, Crusafont, with the aid of Truyols, further performed more paleobiological researches on the evolution of fissiped carnivorans from a morphometric viewpoint (Crusafont-Pairó 1959b; Crusafont & Truyols 1953; Crusafont-Pairó & Truyols-Santoja 1956, 1957a, b, 1958). These papers represented a very advanced paleontological approach by that time, and might be probably considered the most significant pioneering work on morphometrics applied to paleontology in Spain.

The collaboration between Crusafont and Villalta was interrupted in the late 1950s, and Crusafont's evolutionary studies on feliforms and carniforms, based on morphometric considerations, were interrupted in the early 1960s (his last contribution in this regard corresponding to Crusafont Pairó 1962), more or less coinciding with the attainment of the Paleontology Chair at the Universitat de Barcelona by Crusafont. Systematic studies on Vallès-Penedès carnivorans, however, continued throughout this decade, being mainly devoted to the remains from the locality of Can Llobateres, which had not been subjected to intensive research until Crusafont Pairó (1959a), Crusafont Pairó & Truyols Santoja (1960) and Crusafont Pairó (1964). In the latter study, Crusafont Pairó (1964) also reported an updated faunal list of carnivorans from Sant Quirze.

Modern studies

The contribution by Petter. Throughout the 1960s, many significant advances in the knowledge of Iberian carnivorans are attributable to the work by the French paleontologist Germaine Petter, who published several systematic papers on the mustelids from the Vallès-Penedès and Calatayud Teruel basins (Petter 1963, 1964, 1967). This author updated identifications as well as erected new genera and species, mainly on the basis of previous citations of carnivorans from the Vallès-Penedès (e.g., Villalta Comella

& Crusafont Pairó 1941; Villalta Comella & Crusafont Pairó 1943a; Crusafont Pairó 1950), although further including previously unpublished material from other Vallès-Penedès localities. The new citations of Vallès-Penedès carnivorans provided by Petter include: *Mesomephitis medius* Petter, 1967 and *Martes* aff. *andersoni* Schlosser, 1924 from Can Poncic 1; *Mesomephitis medius* from els Hostalets de Pierola; *Martes melibulla* Petter, 1963, *Proputorius medius* Petter, 1963 [currently *Mesomephitis medius*, after Petter (1967, 1976)], *Sabadellictis crusafonti* Petter, 1963, *Marcetia santigae* Petter, 1967, *Circamustela dechaseauxi* Petter, 1967, *Ischyrictis* sp., *Taxodon* cf. s*ansaniensis* Lartet, 1851 and *Trocharion albanense* from Can Llobateres; and *Promephitis pristinidens* Petter, 1963 from Can Purull.

Subsequently, Petter continued to devote to other carnivorans in collaboration with Miquel Crusafont, jointly publishing a taxonomic revision of the Hyeanidae in the Iberian Peninsula (Crusafont Pairó & Petter 1969). They further revised and updated the record of the genera *Progenetta* (=*Thalassictis*), *Ictitherium* and *Plioviverrops*, including their previous citations from the Vallès-Penedès Basin (Crusafont Pairó 1962, 1964; Villalta Comella & Crusafont Pairó 1943a). By the late 1960s, Crusafont Pairó et al. (1968) further reported a new Miocene locality in the Vallès sector of the basin (Costablanca), in which two unidentified carnivorans were recorded.

The subsequent collaboration between Crusafont and other researchers. Already in the 1970s, Crusafont continued working on the Vallès-Penedès carnivorans, either alone or in collaboration with other researchers. Thus, Crusafont-Pairó (1972) revised the genus *Ischyrictis* in the Miocene, erecting the species *Ischyrictis petteri* Crusafont-Pairó, 1972; based on the material from Can Llobateres previuosly described as *Ischyrictis* sp. by Petter (1963). Crusafont-Pairó (1972) further first reported *Ischyrictis* (*Hoplictis*) *helbingi* Viret, 1951 [currently *Hoplictis helbingi* (Viret, 1951), after Ginsburg (1961b)] from this basin, on the basis of material from Castell de Barberà (then still referred to as Santa Maria de Barberà). Crusafont-Pairó & Aguirre (1972), in turn, described a new genus and species of Felinae, *Steinailurus teilhardi* Crusafont-Pairó & Aguirre, 1972, from the Turolian locality of Piera (in the Penedès sector). In collaboration with Juana M. Golpe Posse, Crusafont further reported new discoveries from Castell de Barberà (Crusafont Pairó & Golpe Posse 1972, 1973a) and erected a new subspecies of *Progenetta montadai* Villalta Comella & Crusafont Pairó, 1943: *P. montadai vallesiensis* Crusafont Pairó & Golpe Posse, 1973 from Sant Quirze [currently considered a junior subjective synonym of the nominotypical subspecies, currently referred to as *Thalassictis montadai*, after Werdelin & Solounias (1991)], from Sant Quirze.

Golpe-Posse (1974) complemented the above-mentioned conributions to Vallès-Penedès carnivorans by publishing updated faunal lists that represented the most complete and updated database for Tertiary sites of the Vallès-Penedès Basin (together with lists for other basins from the Iberian Peninsula and the Balearic Islands). The paleontological localities from the Vallès-Penedès basin with Miocene carnivorans reported by Golpe-Posse (1974) are the following: Barranc Gran, Can Barra, Can Canals, Can Julià, Can Llobateres 1, Can Mata 1, Can Marcet, Ca n'Almirall, Can Poncic 1, Can Purull, Can Vila, Castell de Barberà, Costablanca, El Canyet, La Vinya Vella, LaTarumba 1, Les Cases de la Valenciana, Mas Bernic (=Mas Barnich), Molí Calopa, Sant Mamet, Trinxera del Ferrocarril (Sant Quirze del Vallès), Santiga, Sant Miquel del Taudell, Subsòl de Sabadell and Torrentet de Traginers.

Slightly later, Crusafont Pairó & Kurtén (1976) revised the ursidae and amphicyonid remains from Can Llobateres and Can Poncic 1, thereby updating the faunal lists previously provided by Crusafont Pairó (1964), Petter (1967) and Golpe-Posse (1974). They rected the genus *Protursus* Crusafont & Kurtén, 1976 from Can Llobateres 1, and first reported *Ursavus primaevus*, *Amphicyon* cf. *major* and Canidae indet. from Can Poncic 1. By the same time, Petter (1976) continued the work on smaller carnivorans (Petter 1963, 1964, 1967), thereby adding new taxa to the faunal lists from the Vallès-Penedès and other Iberian basins (such as Calatayud-Teruel and the Tagus area). The new taxa reported from the Vallès-Penedès by Petter (1976) include *Martes* cf. *basilii* Petter, 1964 and two Melinae indet. [currently *Plesiomeles* aff. *cajali*, after Robles et al. (in prep.)] from Can Poncic 1, another Melinae indet. [currently *Plesiomeles* sp., after Robles et al. (in prep.)] from Castell de Barberà, *Trochictis narcisoi* Petter, 1976 and *Semigenetta ripolli* Petter, 1976 from Can Llobateres, and *Martes pusilla* (?) Viret, 1951 [currently *Mesomephitis medius* (Petter, 1963)] from Santiga.

In the late 1970s, Golpe Posse et al. (1979) and Golpe Posse (1979) reported additional carnivoran-bearing Miocene localities (Can Perellada and Can Jofresa) from the area of Terrassa (in the Vallès sector). Finally, Crusafont-Pairó (1979a) also reported new dental remains attributed to *Ischyrictis mustelinus* from Can Mata 1. The research on Vallès-Penedès fossil carnivorans was subsequently continued during the early 1980s by Crusafont & Golpe-Posse, who published several papers in this regard (Crusafont-Pairó & Golpe-Posse 1981; Crusafont Pairó and Golpe-Posse 1982; Golpe-Posse (1981a,b, 1984), soon before Crusafont's decease in 1983 and the subsequent retirement of Golpe-Posse from paleontological research afterwards. Thus, Crusafont-Pairó & Golpe-Posse (1981) erected the species *Semigenetta grandis* Crusafont-Pairó & Golpe-Posse, 1981 from Castell de Barberà, corresponding to the previous citation of Viverridae indet. by Crusafont Pairó & Golpe Posse (1973a). Golpe-Posse (1981a,b) further compared this taxon with the material from other European localities. Crusafont Pairó & Golpe Posse (1982) further published new remains of *Palaeomeles pachecoi* Castell de Barberà, while de Beaumont & Crusafont (1982) revised the presence of *Machairodus aphanistus*, *Sansanosmilus* spp. and even erected the subspecies *S. jourdani vallesiensis* [currently *Albanosmilus jourdani*, after Robles et al. 2013a] in the Vallès-Penedès Basin. These authors reported the presence of *Machairodus* cf. *aphanistus* from Can Llobateres, Can Poncic and Santiga, whereas the barbourofelid remains from Can Poncic, Santiga and Castell de Barberà were attributed to *Albanosmilus jourdani*. Finally, in one of her last papers, Golpe-Posse (1984) provided a complete revision of the Melinae [currently *Plesiomeles* sp., after Robles et al. (in prep.)] and Gulolinae from the Vallès-Penedès Basin (including *Plesiomeles cajali*, *Palaeomeles pachecoi*, *Sabadellictis crusafonti* and *Trochictis narcisoi*).

State of the art

The 1980s and 1990s. Crusafont's death marked a significant inflection point in the study of Miocene carnivorans (and other fossil mammals) from the Vallès-Penedès Basin. Thus, although some contributions were made subsequently, the pace of research in the late 1980s and throughout the 1990s is not comparable with that of previous decades. Among the few contributions regarding carnivorans from this basin, Agustí et al. (1984, 1985) updated some identifications of Vallès-Penedès carnivorans in their revision of some Miocene localities. Probably, the most important contribution from this time corresponds to Pons-Moyà's (1990) revision of fossil carnivorans from the area of Terrassa (MN10). Otherwise, during the following decade, Vallès-Penedès carnivorans were mainly cited in museum catalogs (Gómez-Alba 1997) or in the faunal lists reported from newly-discovered localities of the basin (e.g., Agustí & Galobart 1997; Checa Soler & Rius Font 2000).

The discovery of the Early Miocene (MN4) locality of Els Casots in the late 1990s provided new remains of fossil carnivorans, among many other mammals (Moyà-Solà & Rius Font 1993). However, the study of the carnivorans from Els Casots was never completed and did not result in any publication specifically devoted to this group, unlike with artiodactyls (Alba et al. 2014). An updated list of this site not published by Casanovas-Vilar et al. (2011b,c), without including substantial revision of the carnivoran remains.

Abocador de Can Mata. No significant new finds were done until the beginning late in 2002 of the works of paleontological control at Abocador de Can Mata (MN7+8), in the area of els Hostalets de Pierola (Alba et al. 2006, 2007, 2009, 2010a, 2011b; Carmona et al. 2011; Casanovas-Vilar 2007; Casanovas-Vilar et al. 2006, 2008, 2011a,d). The numerous discoveries at ACM soon evidenced that the Vallès-Penedès carnivorans were in need of revision, so that in-depth studies were required not only for the newly-discovered remains, but also from the classical finds from this basin. Excavations at ACM must be therefore considered the triggering factor that ultimately resulted in the present dissertation, whose author was involved in the fieldwork at ACM almost since the beginning. The study of the newly recovered remains was commissioned by Salvador Moyà-Solà (who was supervising the fieldwork at ACM) to the author of this thesis, under the supervision of David M. Alba (then director of the paleontological works at ACM). Initially, only preliminary identifications of some carnivorns from ACM were published in the faunal lists reported in varous papers on this stratigraphic series (Alba et al. 2006, 2007, 2009, 2010a, 2011b; Casanovas-Vilar 2007; Casanovas-Vilar et al., 2006, 2008, 2011a,d). Subsequently, however, several systematic papers specifically devoted to carnivorans were published in the framework of the present dissertation (Abella et al. 2012; 2014; Robles et al. 2010a,b, 2013a,b).

The revision of Miocene carnivorans from the Vallès-Penedès Basin is still an unfinished task, given the large amount of new remains recovered during the last decade. The list available before the work performed in the framework of this dissertation is updated and summarized in the Discusson (see Tables 9.1 and 9.2).

Chapter 2. Materials and methods

2.1. Sample, anatomical nomenclature and measurements

Studied sample

As explained in the preceding chapter, it is beyond the scope of this dissertation to revise in detail all (or even the most representative) Miocene carnivoran remains from the Vallès-Penedès Basin. Below, the studied sample is succinctly described (see Chapters 5 to 8 for further details). However, in the framework of this dissertation, all public collections with Vallès-Penedès fossil carnivorans were visited. Mainly, the puclicly available carnivoran remains from this basin are housed in the Institut Català de Paleontologia Miquel Crusafont (ICP, Sabadell and Universitat Autònoma de Barcelona), the Museu de Geologia del Seminari Conciliar de Barcelona, and the Museu de Geologia de Barcelona (Museu de Ciències Naturals de Barcelona). Up to 55 species, belonging to 41 genera and 11 families, of carnivorans from the Early to the Late Miocene are considered to be recorded in the Vallès-Penedès Basin, following the work reported in this dissertation (see Chapters 9 and 10 for further details).

This work is mainly focused on craniodental material—including complete and partial skulls, maxillary and mandibular fragments, and isolatd upper and lower cheek teeth. To a lesser extent, postcranial material is also described in detail for some taxa. The emphasis on craniodental over postcranial material in this work is due to several reasons: (1) the mechanical properties of enamel and other dental tissues (Hillson 2005), so that isolated teeth as well as mandibular and maxillary fragments are harder than other bony structures and, hence, more frequently represented in the fossil record; (2) the relatively larger amount of taxonomic information provided by dental and cranial remains compared to postcranial ones, so that the former are usually more easily identifiable to the species level when no associated skeletons are preserved; and (3) the emphasis on the preparation of craniodental elements over isolatd postcranial fossils, for the reasons exposed in the preceding point.

It should be taken into account that many of the fossils studied in this work come from surveys and excavations performed at Abocador de Can Mata (ACM) in the framework of the building works of a landfill. This means that the recovery of fossil remains (funded by the company exploiting the landfill) has been prioritized over the preparation of the remains for its scientific study. The latter process, carried out and funded by the former Institut de Paleontologia Miquel Crusafont, and subsequently by the Institut Català de Paleontologia Miquel Crusafont, has inevitably proceeded at a much slower pace than that of recovery. As a result, for many carnivoran taxa from ACM, only craniodental remains have been prepared, whereas most carnivoran postcranial isolated remains remain unprepared and unidentified. The fact that different, similarly-sized carnivoran taxa, frequently from the same family (e.g., mustelids), are recorded at a single locality (this is particularly dramatic at Can Llobateres) further hinders the identification to the species or even genus level of many isolated postcranial remains. These factors explain why, in this work, postcranial material has been only described for the felid *Machairodus aphanistus* (Chapter 8), which was available from classicial collections of various localities, and which can be readily identified on the basis of size and other morphological details.

Anatomical nomenclature

The dental terminology used in this work mainly follows the general recommendations by Smith & Dodson (2003), as well as those by Ginsburg (1999) and Hillson (2005). With regard to cranial and postcranial anatomy, nomenclature mainly follows Ginsburg (1961a), Schultz et al. (1970), Pales & Garcia (1981), and Evans (1993).

Measurements

Standard dental measurements, such as labiolingual breadth or mesiodistal length, are employed in this work. The measurements of the described material were taken by the authors of the various chapters, or compiled from the literature for the comparative sample. Original measurements were taken with a digital caliper to the nearest 0.1 mm, following the general recommendations provided by Salesa et al. (2012). The definition of other measurements (such as maxium cranial length and width, among others) was taken from Schultz et al. (1970), Salesa et al. (2012) and other sources detailed in each chapter.

2.2. Analytical methods

Taxonomy and comparative anatomy

As already explained in Chapter 1, this dissertation follows the provisions of the *International Code of Zoological Nomenclature* (ICZN 1999), which regulates the nomenclatural usage of species-, genus- and family-group taxa. However, with the exception of the chapters that have been already published in various journals, none of the contents of this dissertation are intended to be considered as a formal publication in the sense of the *Code* (ICZN; 1999: Articles 7, 8, 9). For the reasons further explained in Chapter 1, this work does not use so-called phylogenetic nomenclature, and hence relies on the more traditional (but still most useful) Linnean ranks. This work is more devoted to alpha-taxonomy than to systematics at higher taxonomic levels, the former being the scientific discipline devoted to finding, describing and naming taxa, both extant and extinct (Carroll 1988). However, this work adopts a cladistic viewpoint, according to which the use of paraphyletic taxa should be avoided when possible, at least at suprageneric ranks.

Phylogenetic reconstruction

Besides dealing with alpha-taxonomy, this work is also focused on the phylogenetic relationships of several of the studied carnivoran taxa. Phylogenetic reconstruction is based on a cladistic methodology, which delivers one or several preferred trees (cladograms) depicting sister-taxon relationships, but not ancestor-descendant hypotheses (Felsenstein 2004; Swofford & Sullivan 2009). The preferred cladograms are derived based on the principle of maximum parsimony, according to which the phylogenetic hypotheses requiring least changes in characters are to be preferred over those requiring more character state transitions. It must be always borne in mind that most parsimonious cladograms are just the best hypotheses (those with a higher explanatory power) that can be derived based on currently available features. Therefore, they are merely provisional hypotheses that must be subjected to further testing as more data or analyses become available. Given that this dissertation deals with extinct organisms, cladistic analyses were based on morphological features. Theoretically, there is an infinite number of characters that can be defined for each organisms, and the definition of character states depends to a large extent on the skills of the researcher as a morphologists and taxonomist. Accordingly, there is always some inherent subjectivity in cladistic analyses. However, they have the advantage that analyses are repeatable, because characters are explicitly defined and scored, so that other researchers can subject them to further scrutiny.

From the viewpoint of parsimony, constant characters (with no change in character states) or autapomorphic characters (with only a single taxon with a different state) are parsimony-uninformative, i.e., useless for supporting any phylogenetic hypotheses. Accordingly, cladistic analyses are derived based on synapomorhic (shared-derived) features, which are used to support clades (monophyletic groups of taxa). The polarity of characters (i.e., determining which are primitive and which are derived for each clade) was determined by the outgroup method, either using a theoretical outgroup or an actual one (see Chapters 5–7 for further details). Character statements (character and character state definitions) were taken from previously-published literature, although they were revised and modified based on both recent publications and the studied material. These data are arranged into a character matrix (taxon x character), in which the state of each character for each taxon is scored (or left as missing data if it cannot be ascertained due to lack of proper material). The matrix is then analyzed by means of a computer algorithm using specialized software, which in the case of this dissertation was PAUP* (*Parsimony Analysis Using Parsimony And Other Methods*; Swofford 2003). Given the amount of characters and taxa, it would have been too time consuming to perform exhaustive searches (looking at all the possible combinations). Accordingly, the cladistic analyses performed in this dissertation were performed by using PAUP*'s 'branch-and-bound method' (Henry & Penny 1982; Swofford & Sullivan 2009).

When more than a single most parsimonious cladogram is found by the analysis, it means that all the phylogenetic hypotheses depicted by these cladograms have the same explanatory power. Accordingly, the analysis cannot resolve certain clades, which is shown based on the strict consensus tree. The latter shows those clades recovered by all maximum parsimonious cladograms, and collapses the rest. It should be taken into account, however, that not all the clades recovered by the maximum parsimonious tree(s) are equally stable, which is assessed based on metrics of clade stability. In particular, this work employed Bremer's indices (which measure the number of additional steps, or character transitions, required to collapse each tree; Bremer 1994) as well as bootstrap analysis. The latter is a method of resampling that delivers a probability that measures how frequently a particular clade is recovered (Farris 1983; Felsenstein 1983, 1985, 2004; Soltis

& Soltis 2003); only clades with a bootstrap percentage of 50% or more are retained in the so called bootstrap 50% majority rule consensus tree.

Finally, it is necessary to remark that, in cladistic studies, homoplasy (false homology, i.e., similarities due to independent evolution instead of community of descent) is not evaluated a priori, but a posteriori, according to the topology or branching order among the various taxa based on the most parsimonious tree(s). Normally, homoplasy levels are quite high. This is evaluated by means of several metrics (Farris 1989a,b, Klassen et al. 1991, Williams 2007): the Consistency Index (CI), the Retention Index (RI) and the Homoplasy Index (HI). These metrics can be computed for individual characters or whole cladograms (in the latter case, as a summatory for all the characters), based on the following formulae: $\mathrm{CI} = m / s$; $\mathrm{HI} = 1 - \mathrm{CI}$; and $\mathrm{RI} = (M - s) / (M - m)$; where m is the minimum number of steps, s the observed number of steps, and M the maximum conceivable number of steps. CI scales total homoplasy relative to minimum necessary change (thus reflecting the fit of characters to the most parsimonious cladogram), ranging from 1 (no homoplasy) towards 0 (as homoplasy increases). RI scales total homoplasy relative to maximum possible homoplasy for the data.

Computed tomography

This dissertatin mostly relies on the study of the external morphology of fossil remains. However, in particular cases, it was necessary to further assess the internal cranial anatomy of some taxa. This was donce by means of computed tomography (CT) scans. This is a non-invasive technique based on X-ray radiation that enables obtaining internal sections of specific areas of the scanned fossil. A digital geometry processing software is used to generate a three-dimensional image of the internal parts of the fossil, by using a large series of two-dimensional radiographic images (Herman 2009). CT-scans of some of the studied fossil remains were performed at the Hospital Mútua de Terrassa (Barcelona, Spain) with a medical tomograph Siemens Sensations 16. The technical details on the performed scans are specified in the relevant chapter (Chapter 6). Images were processed using the software MIMICS (Materialise, Belgium).

Chapter 3. Geology of the Vallès-Penedès Basin

3.1 An introduction to the Vallès-Penedès Basin

Geographic situation

The Vallès-Penedès Basin is located in the NE Iberian Peninsula (Fig. 3.1), in the Catalan shires (*comarques*) of l'Alt Penedès, l'Anoia, el Baix Llobregat, el Baix Penedès, el Vallès Oriental and el Vallès Occidental (province of Barcelona, Catalonia, Spain). The most important Miocene vertebrate fossiliferous sites are located in the municipalities of Subirats (l'Alt Penedès), els Hostalets de Pierola and Piera (l'Anoia), in the Penedès sector of the basin, and Barberà del Vallès, Rubí, Sabadell, Sant Cugat del Vallès, Sant Quirze, Terrassa and Viladecavalls (el Vallès Occidental) and Martorell (Baix Llobregat) in the Vallès sector (Fig. 3.2).

Figure 3.1. Geographic map of the Iberian Peninsula (top left) showing the position of Catalonia (in red), containing the geographic position of the Vallès-Penedès Basin (in grey).

Tectonosedimentary history

The Vallès-Penedès Basin is a half-graben of NNE-SSW orientation, about 100 km in length and 12-14 km in breadth (depending on the area). It is situated along the Catalan continental margin (the NW margin of the Valencia Trought, see below), being limited by the two (Littoral and Pre-littoral) Catalan Coastal Ranges.

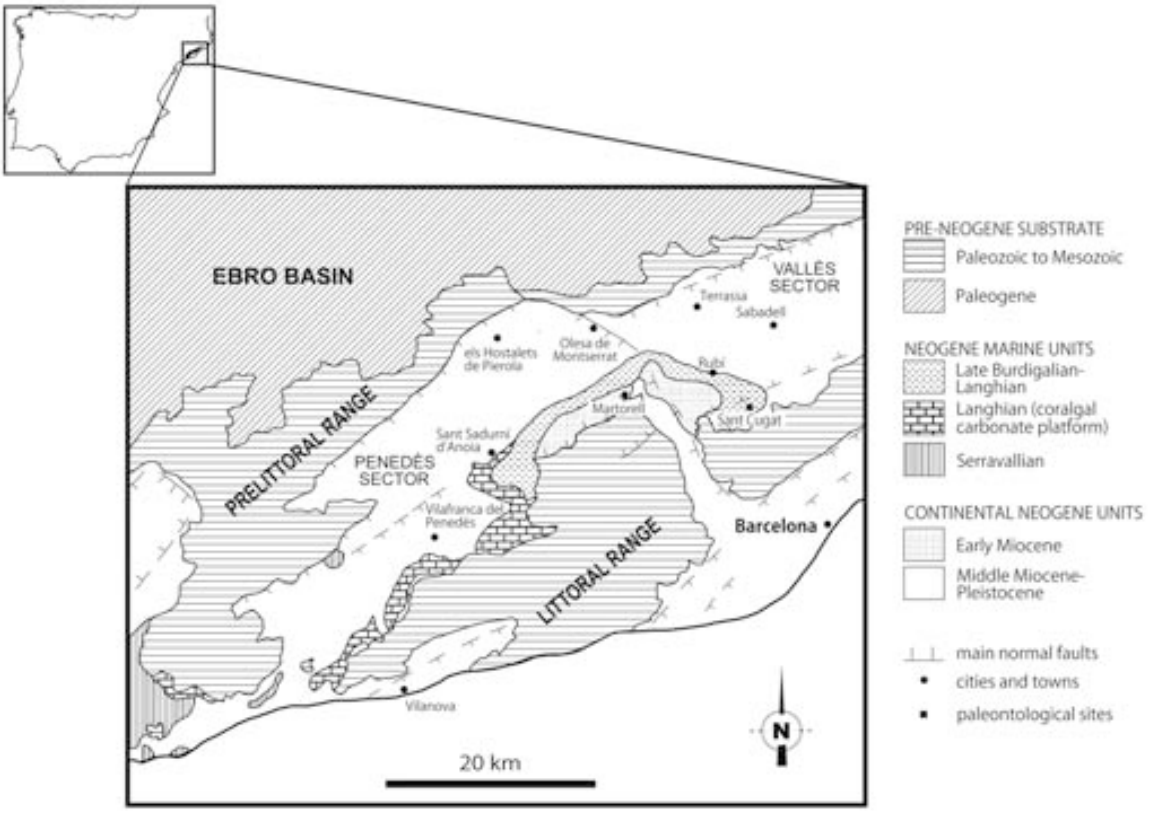

Figure 3.2. Schematic geological map of the Vallès-Penedès Basin, showing the main geological units. Modified from Robles et al. (2013a).

The progressive collision between Europe and Africa during the Mesozoic and the Tertiary generated several marginal basins as a result of an indirect subduction processes that occurred in eastern areas of the Western Mediterranean. The Catalan-Balearic Basin is one of these marginal basins, which commonly displays several compressive structures in the SE of the margin, related to the Alpine thrust belt. In contrast, in the NW of the Catalan-Balearic Basin, the extensional structures are predominant, giving rise to distensional areas, such as the Valencia Trought, extending aproximately 60 km in width along the Catalan coastline. All of these distensional faults of the basement, which were NE-SW to NNE-SSW oriented (Roca & Guimerà 1992; Bartrina et al. 1992; de Gibert & Casanovas-Vilar 2011), reactivated during the Oligocene-Miocene transition, or even before (such as in some other small grabens like the Barcelona Plain or the Campins Basin, which initiated their infilling during the late Oligocene). Shortly afterwards, during the lastest Oligocene-Early Miocene, a first phase of rifting and half-graben generation started in the Catalan continental margin, and the sediment infilling of those half-grabens (one of them corresponding to the Vallès-Penedès Basin) began. After this distensional event, a cortical cooling in this area enabled the beginning of a phase of thermal subsidence during the middle and late Early Miocene (Casanovas-Vilar et al. 2011a). The sediment infilling of the Vallès-Penedès Basin thus started during the Early Miocene (20 to 17 Ma), and was irregular, depending on the subsidence and the amount of sediment coming from the source areas.

Main stratigraphic units of the Vallès-Penedès Basin

The Miocene deposits of the Vallès-Penedès Basin have been classically subdivided into three or four stratigraphic units (Agustí Ballester & Cabrera 1980; Agustí et al. 1985; Casanovas-Vilar et al. 2011a; de Gibert & Casanovas-Vilar 2011). The morphology of these units is asymetrical, depending on the area of the basin, reaching a maximun thickness (over 2,500 m) in the Pre-littoral Range and less than 1,000-2,000 m near the Littoral Range (Agustí et al. 1985). These units are the following (Agustí et al. 1985; Cabrera & Calvet 1990; Casanovas-Vilar 2007; Casanovas-Vilar et al. 2011a,c; de Gibert & Casanovas-Vilar 2011):

Basal Unit of Breccias. The sedimentation of the Basal Unit of Breccias started during the Early Miocene (20-17 Ma) and ended by the Middle Miocene (14.8 Ma; Agustí et al. 1985; Casanovas-Vilar 2011a,d). This unit is mainly composed by breccias of clays and conglomerates (Agustí et al. 1985) and apparently corresponds to proximal facies of alluvial fans. It is restricted to the proximal margins of the Littoral and Pre-littoral Catalan Coastal Ranges. The presence of continental fossil localities are restricted to the locality of Turó de les Forques (TDF).

Lower Continental Complexes. These complexes were deposited from the Early Burdigalian (Ramblian; Early Miocene) to the Early Langhian (earliest Aragonian; Early Miocene). The thickness of these deposits is about 1.5 km in some areas such as Martorell (Agustí et al. 1985). They are characterized by mostly reddish terrigenous litologies, such as conglomerates, which correspond to proximal, medium and distal facies of alluvial fans. In some areas, however, these complexes are composed of lutites, which are barely interbedded with gypsums and lignite desposits that correspond to distal alluvial fan facies (Agustí et al. 1985; Casanovas-Vilar et al. 2011a). The Lower Continental Complexes can be observed in the southern margins of the basin, and they contain some important paleontological site in the municipalities of Sant Cugat del Vallès, Martorell and Subirats

(Agustí Ballester & Cabrera 1980; Agustí et al. 1985; Casanovas-Vilar 2007; Casanovas-Vilar et al. 2011a, c). The deposits of the Lower Continental Complexes can be further subdivided into three distinct units (Casanovas-Vilar et al. 2011c):

a) Lower Detritic Unit (LDU): It is the lower unit of these complexes, being composed by coarse-grained, class-supported red breccias. These materials are covered by channel deposits, consisting in red conglomerates and sands interbedded with dark-red lutites, which are interpreted as proximal to medial facies of alluvial fans.

b) Detritic-Carbonated Unit (DCU): This is a discontinuous unit which crops out at different points of the basin, such Molí de Can Calopa (MC), El Canyet (EC), Can Canals (CC), Les Cases de la Valenciana (LCV), Costablanca (CBL), Els Casots (CS), Torrent de Vilaroc (TV), La Vinya Vella (VV), Can Julià (CJ) and Sant Andreu de la Barca (SB), reaching a maximum thickness of about 150 m. The lithology of this unit consists in a succession of carbonate and clay layers with abundant invertebrate fossils, punctually interbedded with thin gypsum layers. All these lithologies describe a marked cyclicity (there is a recurrent pattern in the alternation of clay and carbonate layers).

c) Upper Detritic Unit (UDU): It is composed by red-orange conglomerates, sands and lutites, reaching a maximum thickness of about 450-580 m, with a great lateral continuity. The top of this unit includes fossils of marine mollusks within conglomerates, showing processess of reworking in a transitional environment.

Marine and Transitional Complexes. These deposits are related to the marine transgressions that took place from the late Burdigalian to the Langhian (Early Miocene to Middle Miocene transition; Agustí et al. 1985; Casanovas-Vilar 2007; Casanovas-Vilar et al. 2011a). The lithology of these complexes varies depending on the sector of the basin (Vallès or Penedès) as well as its particular local depositional conditions. These trangressions came from the southwestern margin of the basin in different events, differing in intensity and in range, and reaching a maximum trangressional level at the current cities of Sant Cugat and Cerdanyola in the Vallès sector. By the late Burdigalian (earliest Aragonian), some evaporitic formations developed in restricted areas of el Baix Penedès (Vilobí Gypsums) in the Penedès sector, due to presence of residual lagoons (Casanovas-Vilar 2007; de Gibert & Casanovas-Vilar 2011). By the latest Burdigalian to early Serravallian (early-late Aragonian), during the maximum extension of sea water over the basin, the sedimentation became siliciclastic, creating terrigenous and terrigenous/carbonate platform-bay deposits in some areas such El Penedès and El Camp areas, together with developed reefs, only present in protected and isolated areas from the siliciclastic sources (from the Litoral and Pre-Litoral ranges), such Sant Pau d'Ordal or Sant Sadurní d'Anoia (Agustí et al. 1985; Navas et al. 1994; Casanovas-Vilar 2007). Because of the marine transgressions and the lack of continental sedimentation during this time span, the presence of continental fossil sites are restricted to the single locality of Ca n'Almirall (CAL).

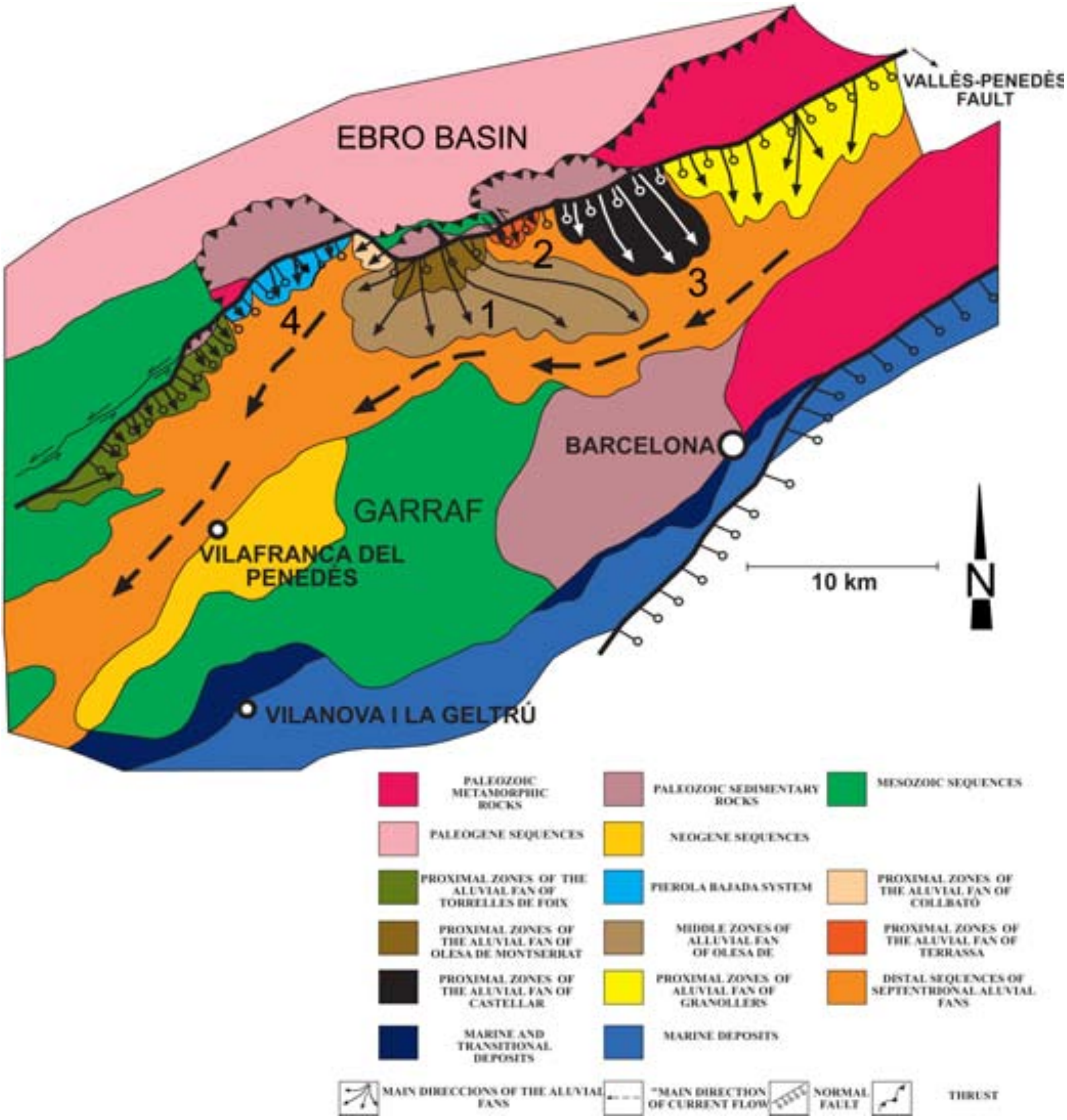

Figure 3.3. Paleobiogeographic map of the Vallès-Penedès Basin during the late Aragonian and early Vallesian. The main alluvial fan systems are indicated with numbers as follow: 1. Olesa-Les Fonts System; 2. Terrassa-Vialdecavalls System; 3. Castellar del Vallès System and 4. Hostales de Pierola System.

Upper Continental Complexes. Their sedimentation started by the Langhian and finished during the latest Tortonian (early Aragonian-middle Turolian). These deposits reach a maximum thickness greater than 1,000 m (Agustí et al. 1985). The lithology of these complexes is very similar in composition to that of the Lower Continental Complexes. However, unlike the latter, the Upper Continental Complexes did not originate exclusevily from the northern source areas, and the color of their sediments is not exclusively reddish, but also yellowish, grayish or ocher. Among the various alluvial fan systems that can be discerned within these complexes (Cabrera & Calvet 1990; Garcés Crespo 1995), four of them must be higlighted on the basis of their significance for vertebrate fossil localities of this basin. They are the following (the first three mostly correspond to the Vallès sector, and the last one to the Penedès sector; see Fig. 3.3):

1) Olesa-Les Fonts System: This system is a long-radius alluvial fan of about 14 km, sourced from the NE of the Vallès-Penedès Basin. This alluvial fan system also includes part of the Penedès area, although its most important paleontological localities are located in the Vallès sector. Its proximal facies are situated in the sourroundings of Olesa de Montserrat, reaching the southern margin of the basin with its distal facies. This system is interbedded with the Terrasa-Viladecavalls system in the northeastern margin of the basin. The huge catchments of the former include a variety of metamorphic Paleozoic clasts and sedimentary Mesozoic, Triassic and Paleogene rocks (Agustí et al. 1997; Casanovas-Vilar 2007). The distal parts of this alluvial fan contain the main fossiliferous sites such as Creu Conill (CCN), Autovia Orbital de Barcelona B-40 stretch Olesa de Montserrat-Viladecavalls (B40OV), Can Perallada (CPE), Can Poncic (CP), Creu Conill (CCN), Sant Miquel del Taudell (SMT), Trinxera Sud Autopista (TSA) and Viladecavalls (VL) (Fig. 3.4).

2) Terrassa-Viladecavalls System: This system developed synchronously with that of the Olesa-Les Fonts system, although the former is smaller, reaching a long radius of less than 10 km (Agustí et al. 1997). Its proximal facies are very close to Viladecavalls and Terrassa, being mainly composed by polygenetic breccias of Paleozoic clasts (Casanovas-Vilar 2007). As in the above-mentioned alluvial fan, the distal facies of the Terrassa-Vialdecavalls System also contains its main fossiliferous sites, such Can Missert (CMS), La Tarumba (LTR), Torrent de Febulines (TF) and Trinxera Nord Autopista (TNA) (Fig. 3.4).

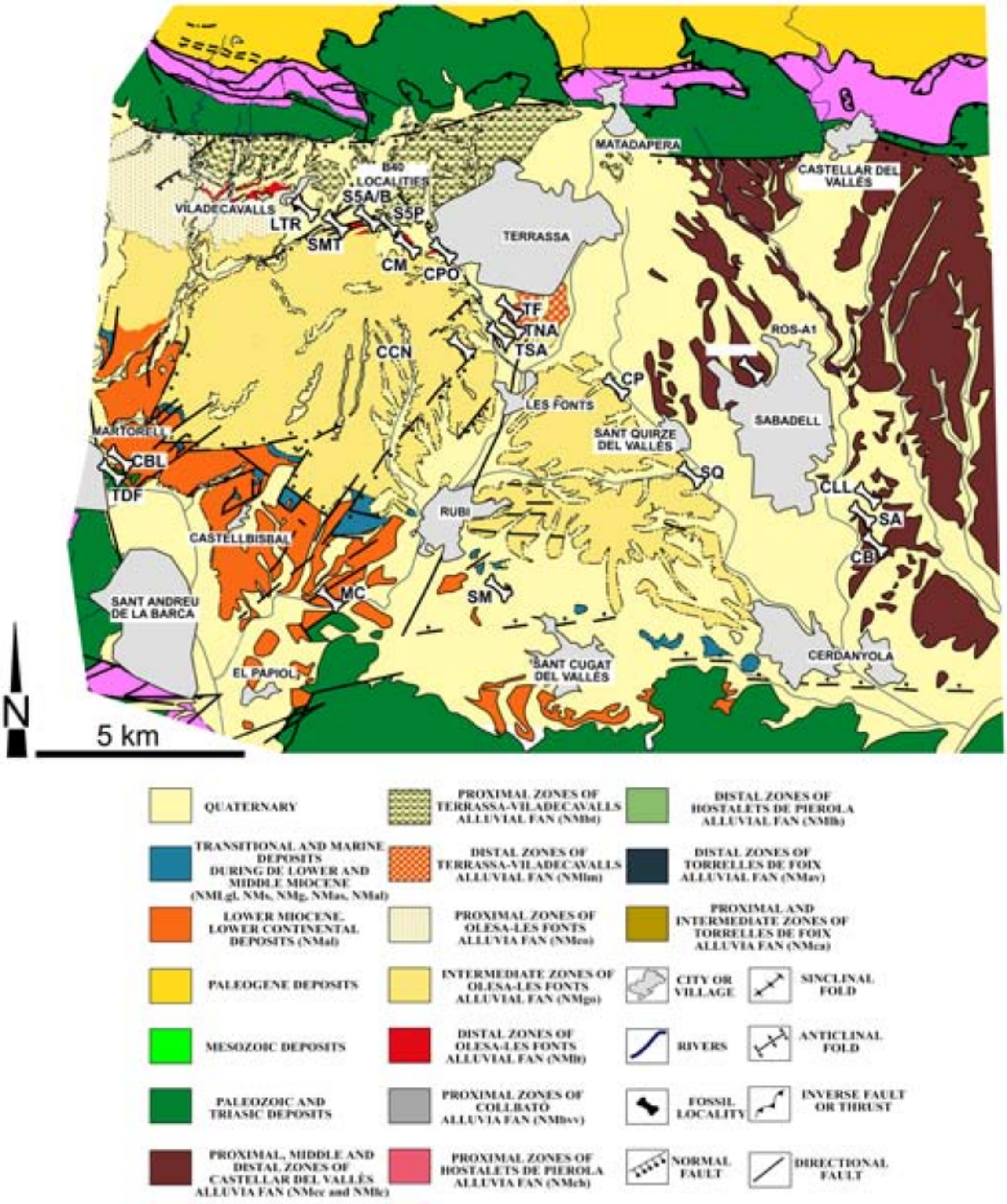

Figure 3.4. Geological map of the Vallès sector, showing the main geological units and its main fossiliferous Miocene localities. Abbreviations: B40OV, Autovia Orbital de Barcelona B-40 stretch Olesa de Montserrat – Viladecavalls; S5A, S5B and S5P, B40OV sectors; CB, Castell de Barberà; CBL, Costablanca; CLL, Can Llobateres; CM, Can Missert; CCN, Creu Conill; CP, Can Poncic; CPO, Can Poal; LTR, La Tarumba; MC, Molí Calopa; ROS, Ronda Oest de Sabadell; A1 and D6, ROS sectors; SA, Santiga; SM, Sant Mamet; SMT, Sant Miquel del Taudell; SQ, Sant Quirze; TDF, Turó de les Forques; TF, Torrent de Febulines; TNA, Trinxera Nord Autopista; TSA, Trinxera Sud Autopista. Modified from Garcés Crespo (1995) and Casanovas-Vilar et al. (2011a).

3) Castellar del Vallès System: This system was synchronously deposited with those of the Olesa de Montserrat-Les Fonts and Terrassa-Viladecavalls. Like the Olesa de Montserrat-Les Fonts System, the Castellar del Vallès one is a long-radius system that reaches the sourthern parts of the margin of the basin, its source areas being situated near Castellar del Vallès and Matadepera. Its deposits are mainly composed by Paleozoic clasts, as well as more commonly grayish and ocher lutites towards its distals facies (Casanovas-Vilar 2007). Its main fossiliferous sites include Can Llobateres (CLL), Castell de Barberà (CB), Ronda Oest de Sabadell (ROS), Santiga (SA) and Sant Quirze (SQ) (Fig. 3.4).

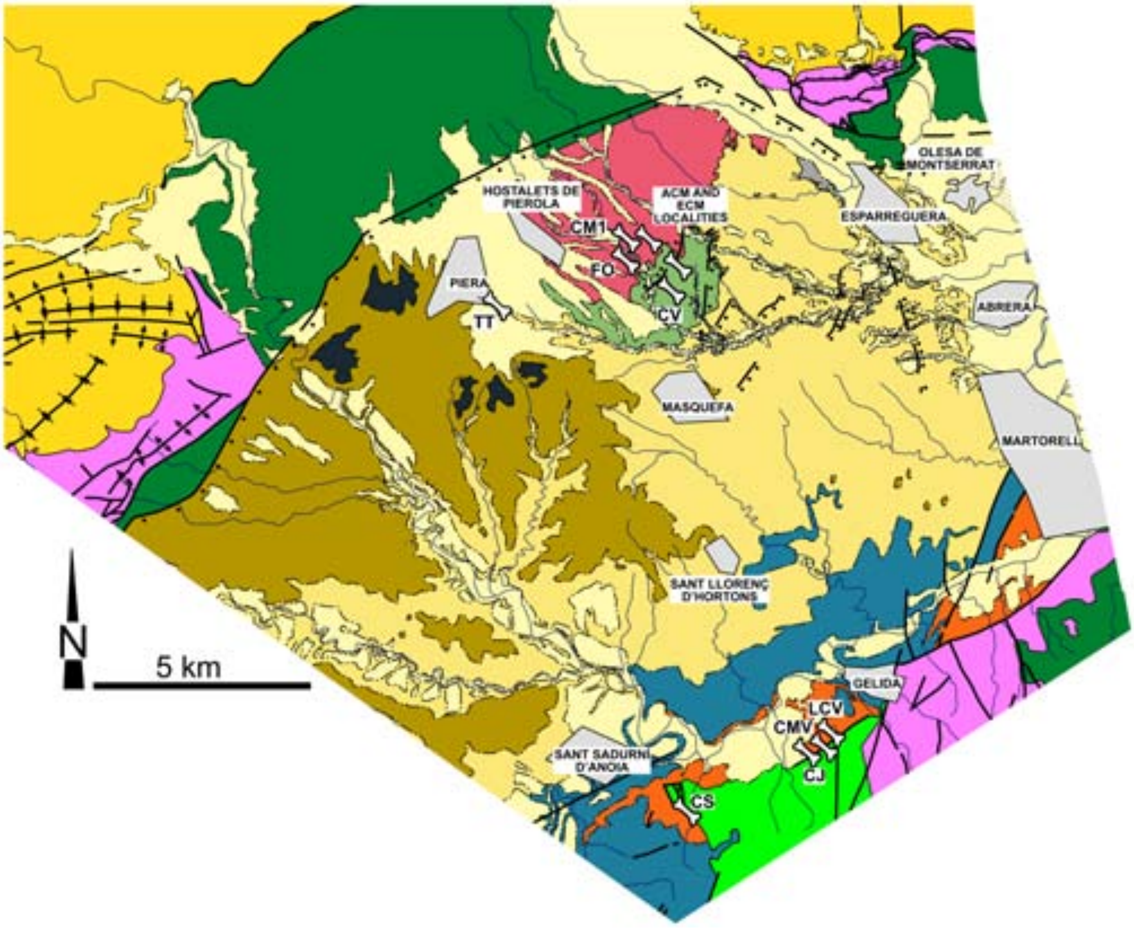

Figure 3.5. Geological map of the Penedès sector, showing the main geological units and its main fossiliferous Miocene localities. Abbreviations: ACM, Abocador de Can Mata; CM1, Can Mata 1; CM3, Can Mata 3; CMV, Can Martí Vell; CS, Els Casots; CV, Can Vila; ECM, Ecoparc de Can Mata; FO, Font d'Ocata, LCV, Les Cases de la Valenciana; TT, Torrentet de Traginers. Redrawn from maps 1:25.000 and 1:50.000 of Institut Cartogràfic i Geològic de Catalunya.

4) Els Hostalets de Pierola System: It is a short-radius alluvial fan system, sourced from the NW margin of the basin (thus originating from the Pre-littoral Range), and located in the sourroundings of els Hostalets de Pierola. This system is characterized by sedimentary sequences from the Middle to Late Miocene that cover the late Aragonian/early Vallesian tansition. They include the late Aragonian and early Vallesian fossil localities from the Abocador de Can Mata (ACM) and Ecoparc de Can Mata (ECM), as well as classical localitites from els Hostalets de Pierola, such as Can Mata 1 (CM1) and Can Vila (CV), further extending to the Turolian in Piera, wich localities such as Torrentet de Traginers (TT) and Torrent del Gall Mullat (TGM). This system is interbedded with the Olesa-Les Fonts system, and includes metamorphic Paleozoic clasts, brown mudstones, sandstones, breccias and conglomerates, although it is dominated by reddish-brown, grayish mottled and pale yellowish mudstones (Casanovas-Vilar 2007; Moyà-Solà et al. 2009; Alba et al. 2011a) (Fig. 3.5).

3.2 The vertebrate fossil record from the Vallès-Penedès Basin

The continental vertebrate fossil record from the Vallès-Penedès basin ranges in age from the Ramblian (Early Miocene) to the Turolian (Late Miocene), being partly interrupted by marine and transitional sediments from the early Aragonian (early Middle Miocene).

Early Miocene (MN3; Ramblian; early and middle Burdigalian). The deposits infilling the Vallès-Penedès Basin are composed by basal breccias. These deposits have provided several fossil remains from the sites of Turó de les Forques (TDF), Sant Andreu de la Barca (SB) and Molí Calopa (MC), which have delivered taxa such as *Procervulus* (Crusafont Pairó et al. 1968), *Anchitherium* (Rotgers et al. 2011) and *Gomphotherium* (Agustí & Galobart 1997). These sites are dated to the Ramblian (MN3) based on the presence of micromammals (*Pseudotheridomys*, *Ligerimys*, *Melissiodon*, *Simplomys* and *Armantomys*), allowing their correlation with localities of this age from other Iberian basins such as Calatayud-Daroca (Casanovas-Vilar et al. 2011a).

Late Early Miocene (MN4; early Aragonian; late Burdigalian). Latest Early Miocene localities from the Vallès-Penedès Basin, such San Mamet (SM), Can Martí Vell (CMV), Les Cases de la Valenciana (LCV), Can Julià (CJ), or Els Casots (CS), have provided characteristic micromammals associations including *Democricetodon hispanicus*, *Megacricetodon minor primitivus* and *Eumyarion weinfurteri* (Agustí 1983; Agustí et al.

1985; Casanovas-Vilar et al. 2011a,b,c), coupled with macromammals such as *Prodeinotherium*, *Listriodon*, *Dorcatherium crassum* and *Bunolistriodon lockharti*, which overall indicate an MN4 age between 17 Ma and 16 Ma (Casanovas-Vilar et al. 2011a).

Middle Miocene (MN5-MN6; early to middle Aragonian; Langhian and early to middle Serravallian). During the early and middle Aragonian, and because of the marine trangressions, the continental vertebrate localities in the Vallès-Penedès during this time interval are very few ones: Vilobí (VI), Ca n'Almirall (CAL) and Les Conilleres (LCC). The scarce fossil remains recovered from these sites, including *Megacricetodon crusafonti* and *Democricetodon*, together with *Muscardinus*, *Cricetodon*, and *Eumyarion medium*, enable the correlation of these localities with MN5, MN6, but also with MN7+8. Therefore, a detailed study of thes micromammals from these localities would be required to provide a more precise dating (Casanovas-Vilar et al. 2011a).

Middle to Late Miocene (MN7+8; late Aragonian; late Serravallian and early Tortonian). The Vallès-Penedès fossil vertebrate localities correlated to the MN7+8 correspond to the basal-most part of the Upper Continental Complexes (see above). In the Vallès sector, the fossiliferous outcrops of this age are scarce and restricted to the Castellar del Vallès System. Several localities from Sant Quirze (SQ) have been classically attributed to the late Aragonian (MN7+8), based on biostratigraphy, since there are no magnetostratigraphic data available (Crusafont Pairó & Golpe Posse 1973a; Crusafont-Pairó & Golpe-Posse 1981, 1982; Golpe-Posse 1974; Petter 1976; Aguilar et al. 1979; Casanovas-Vilar 2007; Robles et al. 2010a; Casanovas-Vilar et al. 2011a; Rotgers & Alba 2011; Alba et al. 2011a; Almécija et al. 2012). The rodent assemblages correspond to the *Megacricetodon ibericus* + *Democricetodon crusafonti* local biozone (Alba et al. 2006; Casanovas-Vilar 2007), which corresponds to the latest Aragonian (late MN7+8, or MN8 sensu Mein & Ginsburg 2002), which would be close the Middle/Late Miocene transition at 11.6 Ma. The main biostratigraphic problem of the Aragonian/Vallesian transition is that the first appearance datum of hipparionin horses (dated to 11.1 Ma in the Vallès-Penedès Basin; Garcés et al. 1997) is not accompanied by conspicuous concomitant changes in the rodent faunas (Agustí et al. 2001), since the typically Vallesian genus *Cricetulodon* does not immediately become a common element.

In the Penedès sector, all the early Aragonian to early Vallesian localities correspond to the area els els Hostalets de Pierola, which belong to the Hostalets the Pierola System. The fossiliferous localities from this area have long been documented (Bataller Calatayud 1938; Bataller 1941; Crusafont & Truyols 1954; Golpe-Posse 1974; Agustí et al. 1985; Alba et al. 2006, 2007, 2009, 2011a; Carmona et al. 2011). The classical localities from els Hostalets de Pierola were traditionally grouped into Hostalets Inferior (late Aragonian) and Hostalets Superior (late Vallesian) (e.g., Agustí et al. 1985), mostly based on the absence/presence of hipparionins. Unfortunally, as noted by Alba et al. (2006), most of these localities (with the exception of Can Mata 1) are not paleontological localities in a strict sense (i.e., corresponding to a single fossiliferous layer), but loosely defined areas. The exact location of many of these localities is unknown, which coupled with the lack of stratigraphic data, makes their age somewhat uncertain. This situation contrasts with the detailed stratigraphic control of the local series of Abocador de Can Mata (ACM) and Ecoparc de Can Mata (ECM), which together with some classical localities from that area constitute the series of Can Mata (Alba et al. 2011a, 2012). The Can Mata series includes the Middle/Late Miocene boundary (11.6 Ma) as well as the Aragonian/Vallesian transition (11.1), although the ACM series is exclusively late Aragonian in age. The latter includes more than 250 formally-defined localities, which are scattered along a composite series of about 300 m in thickness, which span a time interval of about one million years, from 12.5 to 11.5 Ma (Alba et al. 2006, 2007, 2009, 2011a; Moyà-Solà et al. 2009; Casanovas-Vilar et al. 2011d). Initially, based on certain cricetid taxa, Alba et al. (2006) divided the ACM stratigraphic series into three local biozones, with the lowest portion corresponding the MN6, although subsequent findings have shown that an alternative correlation to the MN7+8 of the whole series is more likely (Alba et al. 2011a). Currently, the upper portion of the ACM sequence is correlated to the *Megacricetodon ibericus* + *Democricetodon crusafonti* local biozone (Alba et al. 2011a; Casanovas-Vilar et al. 2011a,d), and hence to the late MN7+8 (or MN8 sensu Mein & Ginsburg 2002). The lower portion, in contrast, is corelated to the *M. ibericus* + *D. larteti* biozone (Alba et al. 2011a; Casanovas-Vilar et al. 2011d), and hance to the early MN7+8 (or MN7 sensu Mein & Ginsburg 2002). The limit between these two biozones is correlated to subchron C5r.3r, with an estimated age of 11.9-11.8 Ma (Alba et al. 2011a; Casanovas-Vilar et al. 2011c).

Late Miocene (MN9-MN10; Vallesian; middle Tortonian). The Vallès-Penedès fossiliferous localities dated from the Vallesian (MN9-MN10) correspond to the middle portion of the Upper Continental Complexes. In the Vallès sector, these localities are concentrated on the distal deposits of several alluvial fan systems. They include the Olesa-

Les Fonts System, with sites such as those from Autovia Orbital de Barcelona B-40 stretch Olesa de Montserrat – Viladecavalls (B40OV), Can Poncic (CP), Can Perallada (CPE), Creu Conill (CCN), Sant Miquel del Taudell (SMT), Trinxera Sud Autopista (TSA) and Viladecavalls (VL). The oldest locality of this time span corresponds to one of the Creu Conill (CCN) localities, which represents the first appearance datum of *Hippotherium* (marking the beginning of the Vallesian) in the Vallès-Penedès Basin, dated at 11.1 Ma (Garcés Crespo 1995; Garcés et al. 1996, 1997; Casanovas-Vilar 2007; Casanovas-Vilar et al. 2011a). The presence of *Cricetulodon hartenbergeri* in Autovia Orbital de Barcelona B-40 stretch Olesa de Montserrat – Viladecavalls (B40OV), Can Poncic (CP) and Viladecavalls (VL), togheter with *Hippotherium*, indicates for these localities an early Vallesian (MN9) age of ca. 10.4–9.9 Ma (Alba et al. 2010b; Casanovas-Vilar et al. 2011a; Pineda-Muñoz et al. 2011). Regarding to the late Vallesian; the co-existence of *Progonomys* and *Rotundomys montisrotundis* with *Rotundomys bressanus* in the locality of Trinxera Sud Autopista (TSA), togheter with the first appearance of carnivorans such as *Hyaenictis almerai* from Sant Miquel del Taudell (SMT), indicates a late Vallesian (MN10) age of 9.2–9.0 Ma (Casanovas-Vilar 2007; Casanovas-Vilar & Agustí 2007; Casanovas-Vilar et al. 2011a; Pineda-Muñoz 2011).

Regarding to the Terrassa-Viladecavalls System, it includes the localities of Can Missert (CMS), Can Poal (CPO), La Tarumba (LTR), Torrent de Febulines (TF) and Trinxera Nord Autopista (TNA). The locality of Can Missert has been traditionally attributed to the latest Aragonian (Agustí et al. 1985, 1997, 2001, 2005; Moyà-Solà & Agustí 1990; Aldana Carrasco 1992; Casanovas-Vilar et al. 2006; Casanovas-Vilar 2007) based on the absence of *Hippotherium*, thus being correlated to the local biozone *Megacricetodon ibericus* + *Democricetodon crusafonti* (Agustí et al. 1985, 2005). However, this association is is also found in the earliest Vallesian (Agustí et al. 1997, 2001; Casanovas-Vilar et al. 2006), and given the proximity of Vallesian levels with *Hippotherium* in Autovia Orbital de Barcelona B-40 stretch Olesa de Montserrat – Viladecavalls (B40OV) as well as Can Poal (Alba et al. 2010a; Tomàs et al. 2010; Robles et al. 2011; Pineda-Muñoz et al. 2011), it seems much more likely that Can Missert is early Vallesian (MN9) in age (Robles et al. 2011) despite the lack of *Hippotherium*. The faunal association of La Tarumba (LTR) and Trinxera Sud Autopista (TNA), corresponding to the local biozone *Progonomys* + *Rotundomys montisrotundis*, indicates a late Vallesian age (MN10) of 9.7–9.4 Ma (Alba et al. 2010a; Casanovas-Vilar et al. 2011a). These localities record the first appearance of some macromammals, such as *Cremohipparion* *mediterraneum*, *Tragoportax gaudryi* and cf. *Promegantereon ogygia*, as well as the last appearance of others, such as the crouzeliid *Egarapithecus narcisoi* (Moyà-Solà 1983; Moyà-Solà et al. 2001; Casanovas-Vilar et al. 2011a).

Finally the Castellar del Vallès System, encompasses Castell de Barberà (CB), Can Llobateres 1 (CLL1) and Can Llobateres 2 (CLL2), Ronda Oest de Sabadell (ROS; sectors A and D) and Santiga (SA). The locality of Castell de Barberà, given the lack of magnetostratigraphic data, has the same dating problems as Can Missert (Almécija et al. 2012; Alba & Moyà-Solà 2012). The rodent assemblage from this locality would correspond to the *Megacricetodon ibericus* + *Democricetodon crusafonti* local biozone (Alba et al. 2006; Casanovas-Vilar 2007). Therefore, in the past, most authors attributed Castell de Barberà to the late Aragonian (late MN7+8; e.g., Crusafont Pairó & Golpe Posse 1973a; Crusafont-Pairó & Golpe-Posse 1981, 1982; Golpe-Posse 1974; Petter 1976; Aguilar et al. 1979; Agustí et al. 1985, 2001; Begun 2002; Robles et al. 2010a), and only a few authors attributed it to the early Vallesian (MN9; e.g., Andrews et al. 1996). The correlation of Castell de Barberà to the MN9 apparently stems from De Bruijn et al. (1992), given the faunal similarities of the rodent assemblage (Aguilar et al. 1979) with that of Can Llobateres. Neverthelss, Crusafont-Pairó & Golpe-Posse (1974) reported the find of a *Hippotherium* remain from some level that could be at most situated a few meters above the main fossilifereous layer of Castell de Barberà, and Rotgers & Alba (2011) also reported a *Hippotherium* molar from the site among the collections of the Institut Català de Paleontologia Miquel Crusafont (Alba & Moyà-Solà 2012), thereby favoring an MN9 age for this site. Regarding Can Llobateres 1 (CLL1), an early Vallesian age is consistent with the presence of *Cricetulodon sabadellensis* (Agustí et al. 1996; Casanovas-Vilar et al. 2011a; Alba et al. 2011b), whereas at Can Llobateres 2 (CLL2), the association of *Cricetulodon sabadellensis* with *Progonomys* and *Rotundomys* cf. *montisrotundi* (I. Casanovas-Vilar, pers. com.) enables a correlation with the late Vallesian *Rotundomys montisrotundi* + *Progonomys* biozone (Agustí et al. 1996; Casanovas-Vilar 2007; Casanovas-Vilar et al. 2011a; Pineda-Muñoz 2011; Alba et al. 2011b). Moreover, magnostratigraphic data reveal an inverse polarirty in the lower part of the stratigraphic section of Can Llobateres, indicating a correlation of Can Llobateres 1 (CLL1) to subchron C4Ar.3r and that of Can Llobateres 2 (CLL2) to the base of chron C4Ar.2r, with estimated interpolated ages of 9.72 Ma and 9.65 Ma, respectively (Garcés Crespo 1995; Agustí et al. 1996; Alba et al. 2011b; Casanovas-Vilar et al. 2011d).

In the Penedès sector, all the Vallesian localities correspond to the Hostalets the Pierola System, in the area of els Hostalets de Pierola. As explained above, the classical localities with *Hippotherium*, and hence correlated to the Vallesian, were traditionally grouped into Hostalets Superior (HPS) (e.g., Agustí et al. 1985). Unfortunally, due to the lack of the proper stratigraphic context and uncertainties in their exact location, in most instances the age of these localities cannot be further specified. There are however some exceptions to this: Can Mata 1 (CM1), without *Hippotherium*, has been traditionally considered to be latest Aragonian in age, whereas the nearly locality of Can Mata 3 (CM3), situated a few meters stratigraphically above the former, would be the first one recording the entry of *Hippotherium* in this area (Moyà-Solà et al. 2009; Alba et al. 2011a). The Ecoparc de Can Mata stratigraphic series (ECM), including 10 formally-defined localities distributed along a composite series of 170 m in thickness, is stratigraphically situated above Can Mata 1 (CM1) and 3 (CM3), and hence considered earliest Vallesian in age (Alba et al. 2011a, 2012; Carmona et al. 2011). This is confirmed by magnetostratigraphic data (Alba et al. 2012), indicating that the whole ECM series corresponds to the long normal chron C5n from the earliest Vallesian, as well as by some micrommamal data (Alba et al. 2012), thus contrasting with the lack of hipparionin remains from the whole series. The case of ECM thus most clearly shows that the lack of hipparionins is not a reliable dating criterion, so that additional biostratigraphic and magnetostratigraphic data are required to accurately date early Late Miocene localities close to the Aragonian/Vallesian boundary.

Late Miocene (MN11-MN12; early and middle Turolian; late Tortonian and early Messinian). In the Vallès sector, the stratigraphic series of Ronda Oest de Sabadell (ROS) encompasses at least three localities from two different that overall cover the MN10-MN11 transition (see above regarding the MN10 sector ROS-D). The joint record of *Huerzelerimys vireti*, *Kowlaskia fahlbuschi* and *Hispanomys* cf. *peralensis* in sector ROS-A indicates an MN11 age, being correlated to zone K of the Teruel basin, with an estimated age of 8.7–8.0 Ma (I. Casanovas-Vilar, pers. com.).

With regard to the Penedès sector, there are several fossiliferous localities (such as Torrentet de Traginers and Torrent del Gall Mullat) from the area of Piera that correspond to the transition between the Tortonian and Messinian (Late Miocene), being restricted to the Hostalets de Pierola System. The mammalian association from these localities, with the carnivorans *Stenailurus* and *Adcrocuta*, the artiodactyls *Tragoportax* and *Birgerbohlinia*, and the rodent *Occitanomys* (Casanovas-Vilar 2007) indicate a Turolian age, but there is no geological background or magnetostratigraphic correlation for them. Classically, the localitites from Piera were thus attributed to the MN11, but most recently they have been re-assigned to the MN12 based on the small mammals assemblage from Torrentet de Traginers (I. Casanovas-Vilar, pers. com.).

RESULTS

Chapter 4. Updated chronology for the Miocene hominoid radiation in Western Eurasia

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Updated chronology for the Miocene hominoid radiation in Western Eurasia

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Extant apes (Primates: Hominoidea) are the relics of a group that was much more diverse in the past. They originated in Africa around the Oligocene/Miocene boundary, but by the beginning of the Middle Miocene they expanded their range into Eurasia, where they experienced a far-reaching evolutionary radiation. A Eurasian origin of the great ape and human clade (Hominidae) has been favored by several authors, but the assessment of this hypothesis has been hampered by the lack of accurate datings for many Western Eurasian hominoids. Here we provide an updated chronology that incorporates recently discovered Iberian taxa and further reevaluates the age of many previously known sites on the basis of local biostratigraphic scales and magnetostratigraphic data. Our results show that identifiable Eurasian kenyapithecins (*Griphopithecus* and *Kenyapithecus*) are much younger than previously thought (*ca*. 14 Ma instead of 16 Ma), which casts serious doubts on the attribution of the hominoid tooth from Engelswies (16.3–16.5 Ma) to cf. *Griphopithecus*. This evidence is further consistent with an alternative scenario, according to which the Eurasian pongines and African hominines might have independently evolved in their respective continents from similar kenyapithecin ancestors, resulting from an early Middle Miocene intercontinental range extension followed by vicariance. This hypothesis, which would imply an independent origin of orthogrady in pongines and hominines, deserves further testing by accurately inferring the phylogenetic position of European dryopithecins, which might be stem pongines rather than stem hominines.

paleoprimatology | biostratigraphy | magnetostratigraphy

Inferring the phylogeny of both living and extinct taxa is essential for understanding the evolutionary history of any particular clade. In this regard, chronostratigraphic data are of utmost significance, not only for testing paleobiogeographic scenarios but even for testing phylogenetic hypotheses (1). Current evidence indicates that hominoids originated in Africa, where they experienced an impressive early radiation during the Early Miocene (2, 3). During the Middle and Late Miocene, however, hominoids are also known from Eurasia, where they are recorded by a plethora of new forms, coinciding with a likely decline in hominoid diversity recorded in Africa. This Eurasian radiation partly reflects the acquisition of diverging adaptative strategies along several lineages in response to new habitats and changing environmental conditions through time (4–6), although geographic isolation followed by vicariance probably also played a significant role (7–9). Our understanding of the Miocene hominoid radiation in Eurasia and its implications for the origin of the great ape and human clade has been seriously hampered by the lack of a robust chronostratigraphic background and accurate datings for many sites. Here we provide an updated chronology for the Miocene hominoid sites of Western Eurasia (Europe, Turkey, and Georgia) which incorporates Iberian sites where several new hominoid taxa have recently been described. Particular emphasis is placed on those localities for which controversial and uncertain ages have been previously reported, and their implications for hominoid evolution are further discussed.

Results and Discussion

Oldest Eurasian Hominoid? A partial upper third molar from Engelswies (Bavarian Molasse Basin, Germany), previously tentatively attributed to *Griphopithecus* (a discussion of the taxonomy of Miocene Eurasian hominoids is provided in *SI Appendix*, *Text 1*), has been considered to be the oldest Eurasian hominoid (10) (Fig. 1). An age of *ca*. 17 Ma was favored for Engelswies on the basis of associated mammals and lithostratigraphic correlation with the main units of the Bavarian Molasse (10) (see *SI Appendix*, *Text 2* for more details on the regional chronological systems units and Dataset S1 for additional data on the chronology of the Miocene hominoid sites of Western Eurasia). Preliminary magnetostratigraphic data (11) enabled a correlation of the short (less than 5 m) Engelswies section to longer magnetostratigraphic profiles of the Bavarian Molasse (12, 13), resulting in a correlation to geomagnetic polarity chron C5Cr (17.235–16.721 Ma) that confirmed previous age estimates. On biostratigraphic grounds, Engelswies can be correlated to the *Keramidomys–Megacricetodon bavaricus* Overlap zone of the Swiss Molasse, which ranges from 16.2 to 16.7 Ma (14). The Middle Miocene biozonations for the Swiss and the Bavarian Molasse are identical but for an age discrepancy (diachrony) regarding the boundaries of the different units, so that older ages are usually proposed based on the Bavarian Molasse succession (14). Such discrepancy is attributable to the fact that the Bavarian Molasse magnetostratigraphic sections record too few geomagnetic reversals, which precludes an unambiguous correlation to the geomagnetic polarity timescale (GPTS). Therefore, correlations for the Bavarian Molasse frequently rely on second- and even third-order lithostratigraphic correlations, together with the occurrence of radiometrically dated bentonites within the successions (12, 13). If the higher-resolution record of the Swiss Molasse is considered, the reversed magnetozone of the Engelswies section best correlates either to chron C5Cn.1r (16.303–16.268 Ma) or C5Cn.2r (16.543–16.472 Ma), that is, immediately before the Langhian. Hence, if the exact stratigraphic provenance of the hominoid teeth is accurately recorded (10), hominoids would have dispersed into Eurasia by the latest Early Miocene. This earliest occurrence is, however, very surprising, because it predates the other oldest Eurasian sites by at least 1.3–1.5 Myr (see below). Even more surprising is that hominoids have not been recorded from Sandelzhausen, a temporally equivalent locality from the Bavarian Molasse that after decades of excavation has delivered more than 50,000 identifiable specimens (15).

Middle Miocene Sites. After Engelswies, the oldest hominoid sites of Western Eurasia are Paşalar and Çandir in Turkey. Both record *Griphopithecus alpani*, and recently a second hominoid, *Kenyapi-*

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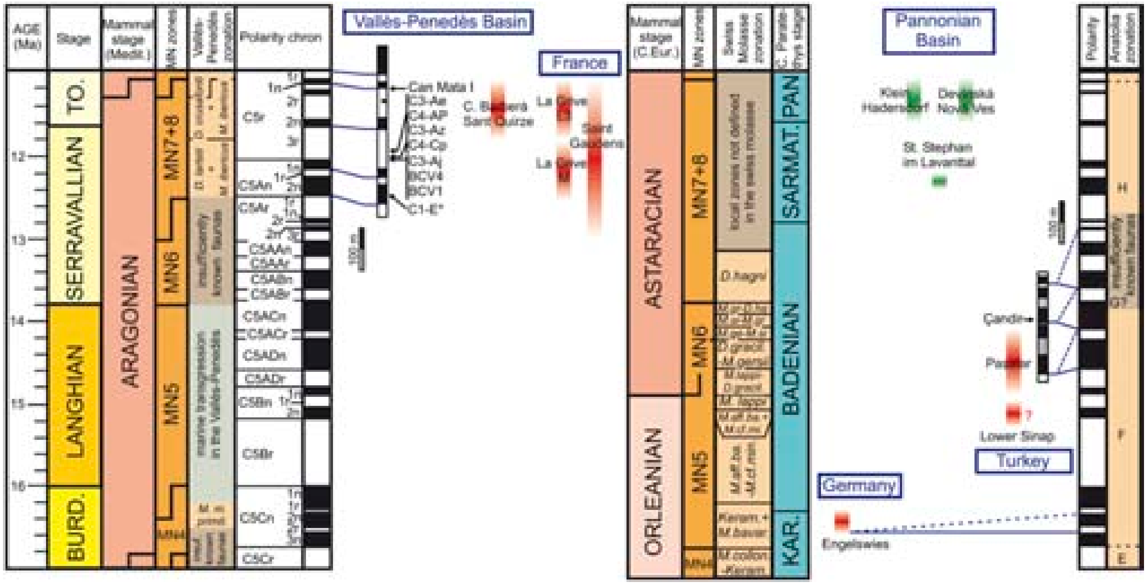

Fig. 1. Early and Middle Miocene hominoid localities of Western Eurasia and their correlation to the geological timescale. Three different regional chronological systems are included (from left to right): for the Iberian Peninsula and France, for Central and Eastern Europe, and for Turkey. Preferred magnetostratigraphic correlations are indicated by solid blue lines and alternative correlations with dashed blue lines. The scale is the same for all of the magnetostratigraphic sections. Red bars indicate biostratigraphic correlations based on mammal faunas, the length of the bar referring to the uncertainty in this correlation. Correlations based in marine/freshwater stages are indicated with a green bar, and the length of this bar also refers to the uncertainty in the correlation. A question mark indicates a highly uncertain correlation because of lack of data. For additional details regarding the local/regional chronological systems used, see *SI Appendix, Text 2*; for more data on the age of a particular site, see Dataset S1.

thecus kizili, was reported from Paşalar (16). On biostratigraphic grounds, Çandir can be correlated to either Mammal Neogene Zone 5(MN5) or MN6 (17, 18). Unfortunately, magnetostratigraphic results (19) do not allow an unambiguous correlation to the GPTS; three correlations are possible: C5ACn (14.095–13.734 Ma), C5ABn (13.605–13.369 Ma), or C5Cn (16.721–15.974 Ma). Although the latter correlation requires assuming large sedimentary and/or tectonic hiatuses in the Çandir section, it has been favored by some (20). Based on biostratigraphy, Çandir was initially correlated to the MN6 (18) and subsequently to the MN5 (17). The presence of *Megacricetodon collongensis* argues against the former correlation, because this taxon is last recorded in the MN4 in Central Europe and in the MN5 in Spain. However, because the disappearance of this rodent appears to be highly diachronic, an alternative correlation to the MN6 and chron C5ACn or C5ABn, as favored by Krijgsman (19), is supported by the rest of the fauna, resulting in an estimated age of *ca*. 13.4–14.1 Ma. Regarding Paşalar, the correlation must entirely rely on biostratigraphy. The rodent fauna suggests a correlation to the MN6 (21) or to the equivalent Turkish Zone F (22). Therefore, as further suggested by the macrofauna (23), Paşalar would be close in age to Çandir, although slightly older. A hominoid tooth from the Lower Sinap Member (24) in Turkey might be somewhat older, although the exact situation of this ancient find is unknown. On the basis of the associated fauna, this find has been correlated to the locality of Inönü with an estimated age of *ca*. 15 Ma (25, 26) (Dataset S1). Be that as it may, this earliest occurrence is much younger than customarily assumed by most paleoprimatologists (4, 5, 20), and postdates by at least 1.3 Myr the earliest Eurasian occurrence of hominoids as documented by Engelswies.

Regarding the hominoid sites from Slovakia (Devínská Nóva Ves) and Austria (Klein Hadersdorf), they include several teeth and postcranials attributed to *Griphopithecus suessi* (=*G. darwini*; *SI Appendix, Text 1*). These localities occur in transitional facies that delivered a mixed assemblage of terrestrial vertebrates with both MN6 and MN7+8 elements (27). Planktonic foraminifera from the same facies allow a correlation to zones MMi9/MMi13 (28), whereas nannoplankton indicates an MNN6/MNN7 age (29), suggesting an age not older than 11.6 Ma. Similarly, the clay pit of St. Stefan im Lavanttal (Austria), the type locality of the nominal taxon *Dryopithecus fontani carinthiacus* (here considered a junior synonym of *D. fontani*), can be correlated to the Central Paratethys stages. The mollusk fauna from this site indicates a Late Sarmatian (Upper *Ervilia* Zone) age (30), which is congruent with the results provided by the rodent fauna indicating an MN7+8 age (31).

The densest Middle Miocene hominoid record occurs at the Vallès-Penedès Basin (Catalonia, Spain) (see *SI Appendix, Text 3* for an updated synthesis of the biostratigraphy and magnetostratigraphy of the Vallès-Penedès record). Comprehensive fieldwork in the 250-m-thick Abocador de Can Mata (ACM) local stratigraphic series (els Hostalets de Pierola) has recently led to the description of two new genera and species, *Pierolapithecus catalaunicus* (32) and *Anoiapithecus brevirostris* (33), as well as to the recovery of new material of *D. fontani* (34) and some fragmentary hominoid remains yet to be described. High-resolution magnetostratigraphic studies at the ACM series allow an unambiguous correlation to the GPTS (34). The series spans from *ca*. 12.5 to 11.4 Ma and includes more than 150 mammal localities, enabling a detailed local biozonation. The oldest hominoid occurrence corresponds to locality ACM/C1-E*, with an estimated age of 12.2–12.3 Ma, whereas the youngest occurrence is a single tooth from Can Mata I (35), which would be close to 11.2–11.1 Ma. The remaining ACM hominoid sites cluster in a tight interval of less than 0.2 Myr (11.8–11.9 Ma). The holotype of "*Sivapithecus*" *occidentalis* (nomen dubium) has an uncertain stratigraphic provenance, so that an estimated age spanning the whole ACM series (12.5–11.4 Ma) cannot be further specified.

On biostratigraphic grounds, other hominoid sites from the Vallès-Penedès Basin can be correlated to the ACM series. Thus, Castell de Barberà and Sant Quirze correspond to the *Democricetodon crusafonti* + *Megacricetodon ibericus* Concurrent range zone and would be somewhat younger than most of the ACM hominoid sites. This local biozonation can also be recognized in France, which allows refining the age of some ancient localities, including the fissure fillings from La Grive-Saint-Alban (Dataset S1 and *SI Appendix, Text 3*). *D. fontani* has been reported from La Grive fissures M and L3 (or L5) (Dataset S1). La Grive M is correlated to the Vallès-Penedès *D. larteti* + *M. ibericus* Concurrent range zone (*ca*. 12.4–11.8 Ma), whereas La Grive L3 and L5 sites are correlated to the *D. crusafonti* + *M. ibericus* Concurrent range zone (11.8–11.2 Ma). Finally, the karstic site of Saint Gaudens, the type locality of *Dryopithecus fontani*, has delivered a poor macromammal assemblage that merely suggests an MN7+8 correlation (*ca*. 12.5–11.1 Ma), not allowing further accuracy.

Late Miocene Sites. During the early Vallesian (earliest Late Miocene), hominoids are still diverse and widespread across Western Eurasia. In the Iberian Peninsula, most hominoids occur in the Vallès-Penedès Basin, where they are represented by *Hispanopithecus laietanus* and *H. crusafonti*. This genus occurs at several early Vallesian sites (i.e., Can Poncic, Can Llobateres 1) but becomes rarer during the late Vallesian, being last recorded at La Tarumba 1. The range of *Hispanopithecus* in the Vallès-Penedès Basin can be constrained between 11.1 and 9.5 Ma, thanks to the detailed bio- and magnetostratigraphic data available for most of the sites (Fig. 2) (*SI Appendix*, *Text 3*). Regarding the mandible of cf. *H. crusafonti* from Teuleria del Firal (36, 37), in the small intra-Pyrenean Seu d'Urgell Basin, such detailed information is not available. This locality delivered a macromammal assemblage that includes *Hippotherium primigenium*, indicating a Vallesian age. The location of this site in the lithostratigraphic unit of Bellestar enables further refinement of this age, on the basis of two micromammal sites (38) from the same unit. These localities can be correlated to the *Cricetulodon hartenbergeri* Local range zone of the Vallès-Penedès, indicating an age close to that of Can Poncic (10.4–9.9 Ma), which is the type locality of *H. crusafonti*.

In Germany, isolated hominoid molars have been recovered from a series of fissure fillings and from Wissberg and Eppelsheim. These sites are located within the well-known Dinotheriensande Formation, which ranges from the early Vallesian to the early Turolian, and consists of an alternation of conglomerates and sands of fluvial origin. Part of the assemblage may be reworked, because some fossils show signs of abrasion (39). The fauna associated to the as yet undescribed material from Eppelsheim (40) clearly points to an early Vallesian age (MN9). On the other hand, the fauna from Wissberg is a mixture of predominantly Vallesian elements with Astaracian (*Prodeinotherium bavaricum*, *Anchitherium aurelianense*) and Turolian ones (cf. *Mesopithecus pentelicus*). Regarding the karstic sites, Salmendingen, the type locality of *Neopithecus brancoi* (nomen dubium), deserves special attention. The poor fauna from Salmendingen includes a few taxa that may indicate a Vallesian age as well as the beaver *Dipoides*, which dispersed into Europe from North America during the early Turolian (MN11) (41). Hence, Salmendingen has been assigned to either the MN9/MN10 (37) or the MN11 (27), and it is likely that the fauna represents a mixture of Vallesian and Turolian elements, as it is frequent in karstic sites. The same situation may apply to Melchingen, which apparently mixes Vallesian and Turolian elements, including *Dipoides*. The remaining German karstic sites, Ebingen and Trochtelfingen, have not delivered additional material to the few primate teeth, so nothing can be said about their age.

The chronology of Götzendorf and Mariathal, in the Vienna Basin (Austria), is more firmly established because they are located in fluvial and lacustrine sediments related to Lake Pannon. The successions of the Vienna Basin have been intensively studied and a highly detailed biostratigraphy based on molluskan faunas is available (42). On this basis, Götzendorf can be correlated to the late Pannonian Zone F2 (i.e., latest early Vallesian) (43). Mariathal is correlated to the early to middle Pannonian age (zones C or D) (44), indicating a slightly older Vallesian age. All these finds are very fragmentary and contrast with the much more complete material recovered from Rudabánya (Hungary) attributed to *Hispanopithecus hungaricus*. This site, located within lacustrine sediments of Lake Pannon, delivered an extremely rich fossil assemblage that suggests an MN9 age (45). Nevertheless, the occurrence of *Hippotherium intrans*, a derived member of the *Hippotherium primigenium* lineage, may indicate an age of 10.0–9.8 Ma, closer to the early/late Vallesian boundary (46).

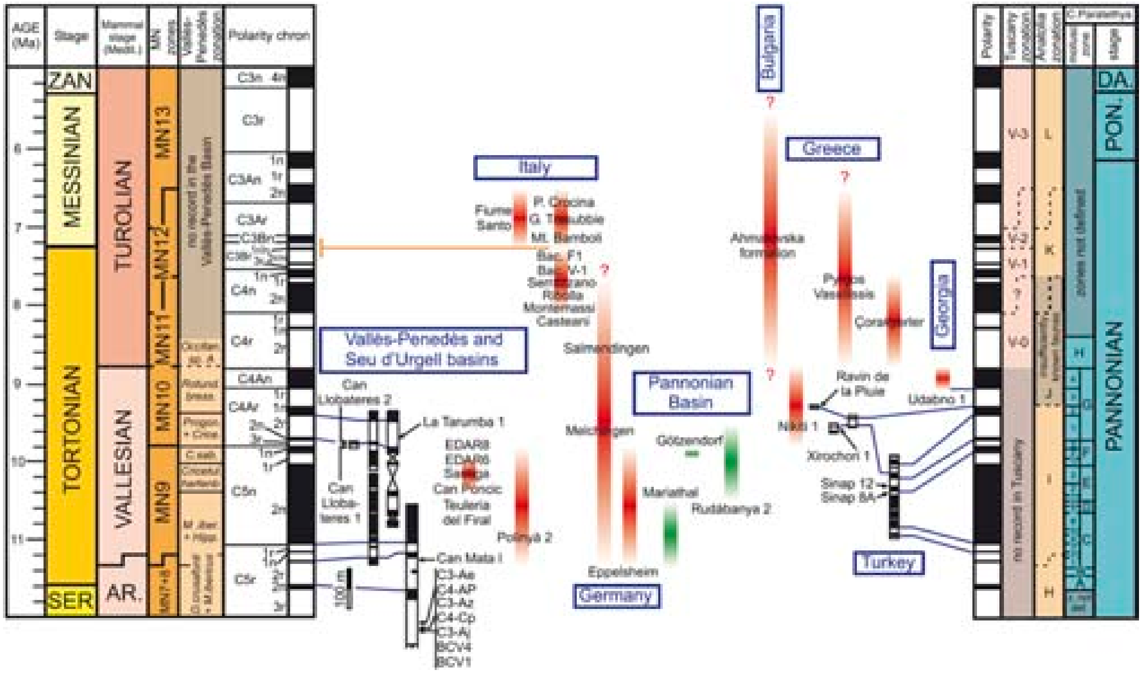

Fig. 2. Late Miocene hominoid localities of Western Eurasia and their correlation to the geological timescale. For the regional chronological systems used and conventional symbols, see Fig. 1. For the Italian sites, the red line refers to a radiometrically dated tuff layer within the Baccinello succession (see text for details). For additional details regarding the local/regional chronological systems used, see *SI Appendix*, *Text 2*; for more data on the age of a particular site, see Dataset S1.

During the Vallesian, two additional distinct hominoid genera are recorded in the Eastern Mediterranean: *Ankarapithecus* in Turkey and *Ouranopithecus* in Greece. The former is known from the densely sampled Sinap Formation, and its age is well-constrained by the means of bio-, litho-, and magnetostratigraphy (25, 26). The specimens, including postcranial and cranial remains, have been recovered from the similarly aged localities 8A and 12. Locality 8A is correlated to chron C5n.1r (9.987–9.934 Ma), whereas locality 12 can be correlated either to chron C5n.1n (9.934–9.779 Ma) or to C4Ar.2n (9.717–9.656 Ma) (26). Therefore, the age of the specimens would lie close to the early/late Vallesian boundary, being very close in time (if not synchronous) to the specimens of Can Llobateres 1 (9.7 Ma) and/or Rudabánya (10.0–9.8 Ma). On the other hand, *O. macedoniensis* is recorded from Nikiti 1, Xirochori 1, and Ravin de la Pluie. All these Greek localities have delivered a rich mammal assemblage, which at Ravin de la Pluie includes both micro- and macromammals that clearly indicate a late Vallesian (MN10) age (47). Typical MN10 large mammal faunas also occur at Xirochori 1 and Nikiti 1. However, at Nikiti 1, a few early Turolian (MN11) taxa are recorded (*Oioceros*, *Helladotherium*) which suggest a slightly younger age (47). The magnetostratigraphic survey of the Late Miocene mammal succession of the Lower Axios Valley (48) has allowed further refining the age of these sites, even though the studied sections are too short to provide an independent correlation to the GPTS. Ravin de la Pluie is correlated to chron C4Ar.1n (9.409–9.312 Ma), and the somewhat older site of Xirochori 1 is correlated to chron C4Ar.2n (9.717–9.656 Ma). Nikiti 1 is supposed to be slightly younger than Xirochori 1 but still late Vallesian (MN10) in age (47), like the other localities.

Latest Hominoids from Western Eurasia. Hominoids are last recorded from the Vallès-Penedès Basin at 9.5 Ma, whereas their youngest unambiguous record from Central Europe is that of Rudabánya *ca*. 10.0–9.8 Ma. Nevertheless, they clearly persist longer in the Eastern Mediterranean, so that many Late Miocene hominoid sites of that area have been assigned to the Turolian, even though available data do not always support such age. These latest hominoid occurrences comprise that of *Graecopithecus freybergi* (nomen vanum) from Pyrgos Vassilissis in Greece. The mammal fauna from this site is too fragmentary to reach sound chronological conclusions (47), although several taxa (*Tragoportax amalthea*, *Gazella deperdita*) indicate a Turolian age (MN11-MN12; i.e., 8.7–6.8 Ma).

A maxillary fragment attributed to ?*Udabnopithecus garedziensis*, from the Shiraki Formation close to Udabno (Georgia), has also been assigned to the Turolian (49). The Shiraki Formation is a 300-m-thick clay succession with two mammal localities (Udabno 1 and 2). The primate remains were found 40 m above Udabno 1 (49), which yielded a rich mammal assemblage indicating a late Vallesian (MN10) age. Udabno 1 yielded a normal polarity that is correlated to chron C4An (9.098–8.769 Ma) (50). Therefore, ?*Udabnopithecus* would be a late Vallesian taxon roughly contemporaneous to *Ouranopithecus macedoniensis*, although maybe slightly older.

Furthermore, another species of *Ouranopithecus*, *O. turkae*, has been described from Çorakyerler in Turkey (51). This site delivered a rich assemblage including small and large mammals. The rodent fauna is dominated by the murid *Hansdebruijnia*, exclusively known from this site (52), but further includes two species of *Byzantinia* and a species of *Pseudomeriones*. These elements suggest a correlation to the Turkish zones J or K (MN9–MN12) (22), although a tentative correlation to the MN11 (8.7–7.9/7.5 Ma) has been favored (52). The macromammal fauna also suggests an MN11 age, although certain ruminants (*Pliocervus* sp., *Miotragocerus valenciennesi*, *Oioceros rothi*) would alternatively favor an MN12 age (7.9/7.5–6.8 Ma). On this basis, a somewhat younger age (MN12) cannot be discarded for *O. turkae*. Regarding the hominoid dental material from the Ahmatovska Formation in Bulgaria (53), although additional faunal data would be required, a Turolian age (8.7–4.9 Ma) is suggested by the presence of *Protragelaphus* and *Anancus*.

Finally, the latest Western Eurasian hominoid is *Oreopithecus*, which evolved under insularity conditions in the Tusco-Sardinian paleobioprovince during the Late Miocene (54). The dating of the so-called *Oreopithecus* faunas has always been problematic because of their endemism. The Baccinello-Cinigiano Basin succession from Tuscany has been divided into four different biochronological units, V-0 to V-3 (55). Unlike V-1 and V-2, the V-0 and V-3 faunas are not completely endemic and can be correlated to the MN11 and MN13, respectively (55). Therefore, the *Oreopithecus* faunas were short-lived, spanning from about 8.5/8 Ma to 7/6.5 Ma. This fully agrees with a radiometric dating of 7.5 ± 0.03 Ma for a volcanic layer within the Baccinello succession (56). Thus, *Oreopithecus* was contemporary with other Turolian hominoids from the Eastern Mediterranean, but may have survived until slightly later, probably becoming extinct when the Tusco-Sardinian archipelago became connected to the mainland at *ca*. 7 Ma (57).

Conclusions

If the stratigraphic provenance of the Engelswies tooth is correctly recorded, hominoids must have first dispersed into Eurasia shortly before the Langhian transgression (Fig. 3), that is, before 16.3 Ma. The partial molar from this locality, however, offers very limited morphologic information, other than indicating an attribution to a thick-enameled undetermined hominoid. The previous assignment of this tooth to cf. *Griphopithecus* (10) was largely based on similarly old previous age estimates for the Turkish localities where this taxon has been securely recorded. Here we show that, on the contrary, these localities are much younger (*ca*. 14 Ma). This considerable temporal gap therefore casts serious doubts on the attribution of the Engelswies hominoid to *Griphopithecus*, so that a phylogenetic link with kenya-

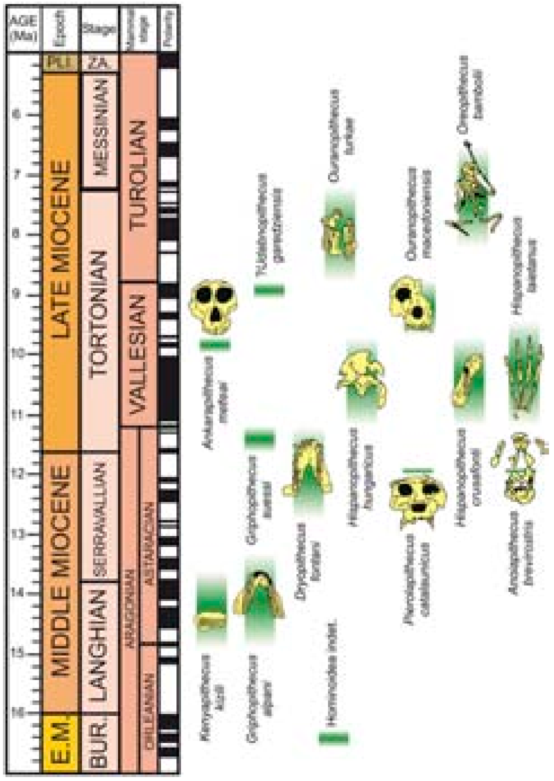

Fig. 3. Range chart for Miocene hominoids of Western Eurasia. For details on the taxonomy, see *SI Appendix*, *Text 1*; for details on the age of particular sites, see *SI Appendix*, *Text 2* and Dataset S1.

pithecins remains to be established. On the basis of currently available evidence, it can only be confidently concluded that, after the Langhian transgression, a group of hominoids of African origin, the pronograde kenyapithecins (2, 3, 5, 58, 59), extended their geographic range into Eurasia, being first recorded in Turkey by both *Griphopithecus* (Eurasia) and *Kenyapithecus* (Eurasia and Africa). The retention of kenyapithecin features in the late Middle Miocene Iberian dryopithecins (33) at *ca*. 12 Ma suggests that the Eurasian hominoid radiation might have originated from some kenyapithecin ancestor, but it remains to be ascertained whether this radiation gave origin exclusively to extant pongines or to both pongines and hominines.

During the last decade, some authors have favored a Eurasian origin of the great ape and human clade (Hominidae) followed by a later back-into-Africa dispersal of the Homininae (4, 9, 37, 60). This biogeographic scenario is dismissed by the recent description of putative hominines from the African Late Miocene (61, 62), as well as by phylogenetic uncertainties surrounding *Hispanopithecus* and *Ouranopithecus*, interpreted either as hominines (2, 37, 60, 63) or as pongines (64–66). Deciphering the phylogenetic status of Middle Miocene European dryopithecins, previously considered stem hominids (32–34), is of much higher significance for testing this scenario, because undoubted pongines are almost simultaneously recorded in Asia *ca*. 12.5 Ma (67). This is consistent with an initial far-reaching range extension of kenyapithecins throughout Eurasia between 14 and 12.5 Ma, followed by vicariance processes giving rise to pongins in Eastern Eurasia and dryopithecins in Western Eurasia. If correct, this would indicate an independent evolution of pongines (including dryopithecins) and hominines in their respective continents from similar pronograde kenyapithecin ancestors, that is, that orthogrady is homoplastic among crown hominids.

Such a high degree of homoplasy is not as unlikely as it might seem at first sight (68–70), particularly given global paleoenvironmental changes that could have prompted similar adaptive responses in both groups. In particular, the climatic deterioration initiated at 14 Ma (71) apparently acted as a trigger of the hominoid Eurasian radiation, as reflected by the wide geographic range, and increased taxonomic and ecological diversity shown by hominoids until the early Vallesian. After the late Vallesian (*ca*. 9.5 Ma), however, hominoids are no longer recorded in Western and Central Europe—with the exception of *Oreopithecus*, which survived until *ca*. 7 Ma on its insular refuge. This probably reflects a true regional extinction event (the so-called Vallesian Crisis) (72–74), resulting from the crossing of some paleoenvironmental threshold that hominoids were unable to manage. Only in the Eastern Mediterranean did hominoids survive somewhat longer (until *ca*. 8.0–7.5 Ma), probably thanks to the preexisting adaptations of ouranopithecins to the environmental conditions of the Greco-Iranian biome. Ultimately, however, the paleoenvironmental changes associated with increased aridification and seasonality (75, 76) completely wiped out hominoids from Western Eurasia during the Turolian, further leading to their progressive diversity decline and geographic range restriction in Asia throughout the Plio-Pleistocene (77, 78). This heavily contrasts with the evolutionary response of hominoids to climatic change in Africa where, coinciding with the extinction of European hominoids, purportedly bipedal hominins are already recorded during the Late Miocene [*ca*. 7–6 Ma by *Sahelanthropus* and *Orrorin* (79, 80)] and during the latest Miocene (5.8–5.2 Ma) and earliest Pliocene (4.4 Ma) by *Ardipithecus* (81, 82).

Materials and Methods

Chronological Framework: Regional Timescales and Correlation. For decades, the chronology of European Neogene sites has relied extensively on the use of MN zones. This biochronological system, introduced during the 1970s (83), takes into account the first and last appearances of selected taxa as well as the characteristic association of taxa within a particular unit. Furthermore, a reference fauna is attached to each unit. The system was immediately accepted and applied to all European regions, and even to Asia and Africa. Since then, MN zones have gone through successive reviews and updates and, at the same time, have witnessed the development of more refined regional biochronological and biostratigraphic scales. Recently, the system has been criticized because its accuracy and applicability across Europe is strongly affected by the provinciality of the faunas and the diachrony of first and last appearances (84, 85). Furthermore, the diachrony of important faunal events has been clearly shown (85), implying discrepancies in MN-zone boundaries sometimes exceeding 1 Myr. In the present work, we favor the use of regional chronological scales together with the correlation of magnetostratigraphic sections to the GPTS (86) (*SI Appendix*, *Text 2*). As such, we have only relied on the MN-zone system for rough, long-distance correlations when other relevant data are not available. In these cases, a certain error margin that can be of ±0.5–1.0 Myr has to be assumed.

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1. Finarelli JA, Clyde WC (2004) Reassessing hominoid phylogeny: Evaluating congruence in the morphological and temporal data. *Paleobiology* 30:614–651.
2. Begun DR (2007) *Handbook of Paleoanthropology*, eds Henke W, Tattersall I (Springer, Heidelberg), pp 921–977.
3. Harrison T (2010) *Cenozoic Mammals of Africa*, eds Werdelin L, Sanders WJ (University of California Press, Berkeley), pp 429–469.
4. Begun DR (2003) Planet of the apes. *Sci Am* 289:74–83.
5. Andrews P, Kelley J (2007) Middle Miocene dispersals of apes. *Folia Primatol (Basel)* 78:328–343.
6. Ward C (2007) *Handbook of Paleoanthropology*, eds Henke W, Tattersall I (Springer, Heidelberg), pp 1011–1030.
7. Agustí J, et al. (1996) Can Llobateres: The pattern and timing of the Vallesian hominoid radiation reconsidered. *J Hum Evol* 31:143–165.
8. Andrews P, Bernor RL (1999) *Hominoid Evolution and Environmental Change in the Neogene of Europe*, eds Agustí J, Rook L, Andrews P (Cambridge Univ Press, Cambridge, UK), Vol 1, pp 454–487.
9. Begun DR (2004) *Sivapithecus* is east and *Dryopithecus* is west, and never the twain shall meet. *Anthropol Sci* 113:53–64.
10. Heizmann EP, Begun DR (2001) The oldest Eurasian hominoid. *J Hum Evol* 41:463–481.
11. Böhme M, Abdul Aziz H, Prieto J, Bachtadse V (2008) *Giornate de Paleontologia VIII Edizione—Simposio della Società Paleontologica Italiana*, eds Mazzei R, Fondi R, Foresi L, Riforgiato F, Verducci M (Accademia dei Fisiocritici, Siena, Italy), pp 120–121.
12. Abdul Aziz H, et al. (2008) Integrated stratigraphy and 39Ar/40Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in Eastern Bavaria (Germany). *Int J Earth Sci* 97:115–134.
13. Abdul Aziz H, et al. (2010) Integrated stratigraphy and 39Ar/40Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in Western Bavaria (Germany). *Int J Earth Sci* 99:1859–1886.
14. Kälin D, Kempf O (2009) High-resolution stratigraphy from the continental record of the Middle Miocene Northern Alpine Foreland Basin of Switzerland. *N Jb Geol Paläont Abh* 254:177–235.
15. Moser M, Rössner GE, Göhlich UB, Böhme M, Fahlbusch V (2009) The fossil lagestätte Sandelzhausen (Miocene; Southern Germany): History of investigation, geology, fauna and age. *Paläont Z* 83:7–23.
16. Kelley J, Andrews P, Alpagut B (2008) A new hominoid species from the Middle Miocene site of Paşalar, Turkey. *J Hum Evol* 54:455–479.
17. De Bruijn H, et al. (2003) Rodents, lagomorphs and insectivores from the Middle Miocene hominoid locality of Çandir (Turkey). *Cour Forsch-Inst Senckenberg* 240:51–87.
18. De Bruijn H, et al. (1992) Report of the RCMNS Working Group on fossil mammals, Reisenburg 1990. *Newls Stratigr* 26:65–118.
19. Krijgsman W (2003) Magnetostratigraphic dating of the Çandir fossil locality (Middle Miocene, Turkey). *Cour Forsch-Inst Senckenberg* 240:41–49.
20. Begun DR, Güleç E, Geraads D (2003) The Çandir hominoid locality: Implications for the timing and pattern of hominoid dispersal events. *Cour Forsch-Inst Senckenberg* 240:240–265.
21. Peláez-Campomanes P, Daams R (2002) Middle Miocene rodents from Paşalar, Anatolia, Turkey. *Acta Palaeontol Pol* 47:125–132.
22. Ünay E, De Bruijn H, Saraç G (2003) A preliminary zonation of the continental Neogene of Anatolia based on rodents. *Deinsea* 10:539–547.

23. Bernor RL, Tobien H (1990) The mammalian geochronology and biogeography of Paşalar, Turkey. *J Hum Evol* 19:551–568.
24. Ozansoy F (1965) Study of the continental sites and the mammals from the Cenozoic of Turkey. *Mem Soc Geol F* 44:1–92.
25. Kappelman J, et al. (2003) *Geology and Paleontology of the Miocene Sinap Formation, Turkey*, eds Fortelius M, Kappelman J, Sen S, Bernor RL (Columbia Univ Press, New York), pp 41–66.
26. Kappelman J, et al. (2003) *Geology and Paleontology of the Miocene Sinap Formation, Turkey*, eds Fortelius M, Kappelman J, Sen S, Bernor RL (Columbia Univ Press, New York), pp 90–124.
27. Mein P (1986) *Primate Evolution*, eds Else JG, Lee PC (Cambridge Univ Press, Cambridge, UK), pp 58–70.
28. Blow WH (1969) *Proceedings of the First International Conference on Planktonic Microfossils, Geneva 1967*, eds Bronnimann R, Renz HH (E.J. Brill, Leiden, The Netherlands), Vol 1, pp 199–422.
29. Martini E (1971) in *Second Planktonic Conference, Roma*, ed Farinaci A (Editioni Tecnoscienza, Rome), pp 739–785.
30. Harzhauser M, Gross M, Binder H (2008) Biostratigraphy of Middle Miocene (Sarmatian) wetland systems in an Eastern Alpine intramontane basin (Gratkorn Basin, Austria): The terrestrial gastropod approach. *Geol Carpathica* 59:45–58.
31. Daxner-Höck G (2010) Sciuridae, Gliridae and Eomyidae (Rodentia, Mammalia) from the Middle Miocene of St. Stefan in the Gratkorn Basin (Styria, Austria). *Ann Naturhist Mus Wien A* 112:507–536.
32. Moyà-Solà S, Köhler M, Alba DM, Casanovas-Vilar I, Galindo J (2004) *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. *Science* 306:1339–1344.
33. Moyà-Solà S, et al. (2009) A unique Middle Miocene European hominoid and the origins of the great ape and human clade. *Proc Natl Acad Sci USA* 106:9601–9606.
34. Moyà-Solà S, et al. (2009) First partial face and upper dentition of the Middle Miocene hominoid *Dryopithecus fontani* from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, NE Spain): Taxonomic and phylogenetic implications. *Am J Phys Anthropol* 139:126–145.
35. Crusafont-Pairó M, Golpe-Posse JM (1973) New pongids from the Miocene of Vallès Penedès Basin (Catalonia, Spain). *J Hum Evol* 2:17–23.
36. Begun DR (1992) *Dryopithecus crusafonti* sp. nov., a new Miocene hominid species from Can Ponsic (Northeastern Spain). *Am J Phys Anthropol* 87:291–310.
37. Begun DR (2002) *The Primate Fossil Record*, ed Hartwig WC (Cambridge Univ Press, Cambridge, UK), pp 339–368.
38. Agustí J, Gibert J, Moyà-Solà S, Cabrera L (1979) Rodents and insectivores (Mammalia) from the Late Miocene of la Seu d'Urgell (Catalonia, Spain). *Acta Geol Hisp* 14: 362–369.
39. Franzen JL, Storch G (1999) *Hominoid Evolution and Environmental Change in the Neogene of Europe*, eds Agustí J, Rook L, Andrews P (Cambridge Univ Press, Cambridge, UK), Vol 1, pp 165–190.
40. Franzen JL, Fejfar O, Storch G, Wilde V (2003) Eppelsheim 2000—New discoveries at a classic locality. *Deinsea* 10:217–234.
41. Hugueney M (1999) *The Miocene Land Mammals of Europe*, eds Rössner GE, Heissig K (Verlag Dr. Friedrich Pfeil, Munich), pp 281–300.
42. Papp A (1951) The Pannonian of the Vienna Basin. *Mitt Geol Gessell Wien* 39–41: 99–193.
43. Harzhauser M, Daxner-Höck G, Piller WE (2004) An integrated stratigraphy of the Pannonian (Late Miocene) in the Vienna Basin. *Aust J Earth Sci* 95/96:6–19.
44. Steininger F (1986) *Primate Evolution*, eds Else JG, Lee PC (Cambridge Univ Press, Cambridge, UK), pp 71–84.
45. Bernor RL, et al. (2004) Recent advances on multidisciplinary research at Rudabánya, Late Miocene (MN9), Hungary: A compendium. *Palaeontogr Ital* 89:3–36.
46. Bernor RL, Armour-Chelu M, Kaiser TM, Scott RS (2003) An evaluation of the Late MN9 (Late Miocene, Vallesian age), *Hipparion* assemblage from Rudabánya (Hungary): Systematic background, functional anatomy and paleoecology. *Colloq Paleontol* 1(Ext):35–45.
47. Koufos GD (2006) The Neogene mammal localities of Greece: Faunas, chronology and biostratigraphy. *Hell J Geosc* 41:183–214.
48. Sen S, Koufos G, Kondopoulou D, De Bonis L (2000) Magnetostratigraphy of the Late Miocene continental deposits of the Lower Axios Valley, Macedonia, Greece. *Bull Geol Soc Greece*, Special Publication no. 9, pp 197–206.
49. Gabunia L, Gabashvili E, Vekua A, Lordkipanidze D (2001) *Hominoid Evolution and Environmental Change in the Neogene of Europe*, eds De Bonis L, Koufos G, Andrews P (Cambridge Univ Press, Cambridge, UK), Vol 2, pp 316–325.
50. Sen S (1997) Magnetostratigraphic calibration of the European Neogene mammal chronology. *Palaeogeogr Palaeoclimatol Palaeoecol* 133:181–204.
51. Güleç ES, Sevim A, Pehlevan C, Kaya F (2007) A new great ape from the Late Miocene of Turkey. *Anthropol Sci* 115:153–158.
52. Ünay E, De Bruijn H, Suata-Alpaslan F (2006) Rodents from the Upper Miocene hominoid locality Çorakyerler (Anatolia). *Beitr Paläont* 30:453–467.
53. Spassov N, Geraads D (2008) The latest prehumans of Europe: Discovery of a Late Miocene hominoid in Bulgaria of about 7 Ma. *Bulg Acad Sci News* 54:2–4.
54. Hürzeler J, Engesser B (1976) The Neogene mammal faunas of the Baccinello Basin (Grosseto, Italy). *C R Acad Sci Paris* 283:333–336.
55. Rook L, Harrison T, Engesser B (1996) The taxonomic status and biochronological implications of new finds of *Oreopithecus* from Baccinello (Tuscany, Italy). *J Hum Evol* 30:3–27.
56. Rook L, Renne P, Benvenuti M, Papini M (2000) Geochronology of *Oreopithecus* -bearing succession at Baccinello (Italy) and the extinction pattern of European Miocene hominoids. *J Hum Evol* 39:577–582.
57. Rook L, Gallai G, Torre D (2006) Lands and endemic mammals in the Late Miocene of Italy: Constrains for palaeogeographic outlines of Thyrrenian area. *Palaeogeogr Palaeoclimatol Palaeoecol* 238:263–269.
58. Begun DR (1992) Phyletic diversity and locomotion in primitive European hominids. *Am J Phys Anthropol* 87:311–340.
59. Ersoy A, Kelley J, Andrews P, Alpagut B (2008) Hominoid phalanges from the Middle Miocene site of Paşalar, Turkey. *J Hum Evol* 54:518–529.
60. Begun DR, Güleç E, Geraads D (2003) Dispersal patterns of Eurasian hominoids: Implications from Turkey. *Deinsea* 10:23–39.
61. Suwa G, Kono RT, Katoh S, Asfaw B, Beyene Y (2007) A new species of great ape from the Late Miocene epoch in Ethiopia. *Nature* 448:921–924.
62. Kunimatsu Y, et al. (2007) A new Late Miocene great ape from Kenya and its implications for the origins of African great apes and humans. *Proc Natl Acad Sci USA* 104:19220–19225.
63. Begun DR, Ward CV, Rose MD (1997) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptation*, eds Begun DR, Ward CV, Rose MD (Plenum, New York), pp 389–415.
64. Solà SM, Köhler M (1993) Recent discoveries of *Dryopithecus* shed new light on evolution of great apes. *Nature* 365:543–545.
65. Moyà-Solà S, Köhler M (1995) New partial cranium of *Dryopithecus* Lartet, 1863 (Hominoidea, Primates) from the Upper Miocene of Can Llobateres, Barcelona, Spain. *J Hum Evol* 29:101–139.
66. Köhler M, Moyà-Solà S, Alba DM (2001) *Hominoid Evolution and Environmental Change in the Neogene of Europe, Vol 2. Phylogeny of the Neogene Hominoid Primates of Eurasia*, eds De Bonis L, Koufos G, Andrews P (Cambridge Univ Press, Cambridge, UK), pp 192–212.
67. Kappelman J, et al. (1991) The earliest occurrence of *Sivapithecus* from the Middle Miocene Chinji Formation of Pakistan. *J Hum Evol* 21:61–73.
68. Larson SG (1998) Parallel evolution in the hominoid trunk and forelimb. *Evol Anthropol* 6:87–99.
69. Young NM (2003) A reassessment of living hominoid postcranial variability: Implications for ape evolution. *J Hum Evol* 45:441–464.
70. Begun DR (2007) How to identify (as opposed to define) a homoplasy: Examples from fossil and living great apes. *J Hum Evol* 52:559–572.
71. Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686–693.
72. Agustí J, Moyà-Solà S (1990) Mammal extinctions in the Vallesian (Upper Miocene). *Lect Notes Earth Sci* 30:425–432.
73. Fortelius M, Hokkanen A (2001) *Hominoid Evolution and Environmental Change in the Neogene of Europe*, eds De Bonis L, Koufos G, Andrews P (Cambridge Univ Press, Cambridge, UK), Vol 2, pp 19–47.
74. Casanovas-Vilar I, García-Paredes I, Alba DM, Van den Hoek Ostende L, Moyà-Solà S (2010) The European Far West: Miocene mammal isolation, diversity and turnover in the Iberian Peninsula. *J Biogeogr* 37:1079–1093.
75. Van Dam JA (2006) Geographic and temporal patterns in the late Neogene (12–3 Ma) aridification of Europe: The use of small mammals as paleoprecipitation proxies. *Palaeogeogr Palaeoclimatol Palaeoecol* 238:190–218.
76. Strömberg CAE, Werdelin L, Friis EM, Saraç G (2007) The spread of grass-dominated habitats in Turkey and surrounding areas during the Cenozoic: Phytolith evidence. *Palaeogeogr Palaeoclimatol Palaeoecol* 250:18–49.
77. Eronen JT, Rook L (2004) The Mio-Pliocene European primate fossil record: Dynamics and habitat tracking. *J Hum Evol* 47:323–341.
78. Nelson SV (2003) *The Extinction of Sivapithecus* (Brill Academic, Boston).
79. Senut B, et al. (2001) First hominid from the Miocene (Lukeino Formation, Kenya). *C R Acad Sci Paris* 332:127–144.
80. Brunet M, et al. (2002) A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* 418:145–151.
81. Haile-Selassie Y (2001) Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* 412:178–181.
82. White TD, et al. (2009) *Ardipithecus ramidus* and the paleobiology of early hominids. *Science* 326:75–86.
83. Mein P (1975) in *Report on Activity of RCMNS Working Groups. VI Congress of the Regional Committee of Mediterranean Neogene Stratigraphy Proceedings 1*, ed Sénes J (Regional Committee of Mediterranean Neogene Stratigraphy, Bratislava, Slovakia), pp 78–81.
84. Van Dam JA, et al. (2001) The Upper Miocene mammal record from the Teruel-Alfambra region (Spain): The MN system and continental stage/age concepts discussed. *J Vertebr Paleontol* 21:367–385.
85. Van der Meulen AJ, et al. Biostratigraphy or biochronology? Lessons from the Early and Middle Miocene small mammal events in Europe. *Geobios*, 10.1016/j.geobios.2010.11.004.
86. Ogg JG, Smith AG (2004) *A Geologic Time Scale 2004*, eds Gradstein FM, Ogg JG, Smith AG (Cambridge Univ Press, Cambridge, UK), pp 63–87.

SI Appendix for

An updated chronology for the Miocene hominoid radiation in Western Eurasia

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Contents

Text 1. Systematics of Western Eurasian hominoids

In Table S1 we provide a taxonomy of the fossil hominoids discussed in this paper. Given the scope of this paper, it is not intended to give a broad taxonomic review of the group, but rather to discuss the most contentious taxonomic and phylogenetic issues regarding the taxa treated in the paper. As such, the following discussion is restricted to extinct hominoids from Western Eurasia.

Following ref. 1 (their SI Text and Table 2), the concept of Hominoidea employed here is a broad one, i.e. including the Proconsulidae and Afropithecidae, in recognition of the likely status of these taxa as stem hominoids (2–9). This contrasts with the alternative systematic schemes of some authors, which employ a narrower definition of the Hominoidea (10–12), by distinguishing a separate superfamily Proconsuloidea. Despite lacking orthogrady-related features, proconsulids already share some facial (5) and several postcranial (6–7, 13) synapomorphies with crown hominoids, such the lack of external tail—documented in both *Proconsul* and *Nacholapithecus* (6, 8, 13–15). As such, they can be considered stem hominoids. Moreover, we see no need for a new family-group name other than the superfamily Hominoidea for designating the total group that includes both crown hominoids and stem taxa more closely related to them than to cercopithecoids (contra ref. 12, where the magnafamily Hominidea was employed to include both Proconsuloidea and Hominoidea).

At the family, subfamily and tribe level, the taxonomy employed here also follows ref. 1 (their SI Text and Table S1) to a large extent, although with some significant differences, which are explained in greater detail below. We follow ref. 1 by employing a broad definition of the Hominidae that includes Ponginae, Homininae, and all extinct taxa more closely related to them than to the Hylobatidae (see also refs. 12, 16–17). Moreover, according to this scheme, afropithecids are considered a distinct family with two subfamilies, Afropithecinae and Kenyapithecinae, the latter being subdivided into the tribes Equatorini for *Equatorius* and *Nacholapithecus*, and Kenyapithecini for *Kenyapithecus* and *Griphopithecus*. Over the last decade, some authors have transferred the Kenyapithecini (as the subfamily level, Kenyapithecinae) (11, 18–19), or even all the Afropithecidae (as a subfamily, Afropithecidae) (9, 20), into the Hominidae. This is however problematic for several reasons. The presence of kenyapithecin features in the Middle Miocene dryopithecins from Spain (1), usually considered to be stem hominids preceding the divergence of pongines and hominines (1, 21–22) (but see later), might be certainly indicative of a close phylogenetic link between kenyapithecins and hominids. If so, as noted previously (1), the Afropithecidae as conceived here might be paraphyletic. This, however, depends on the relative branching order between hylobatids, afropithecids and hominids. An early divergence of hylobatids would imply that some or all afropithecids would be more closely related to hominids as conceived here, but given uncertainties regarding the the phylogenetic relationships of the former, it is preferably to provisionally retain afropithecids as a separate family.

Given the fact that the nomina for both afropithecid subfamilies were erected simultaneously as two distinct tribes (Kenyapithecini and Afropithecini) in the same publication (2), some uncertainties arise regarding which of them has priority at the family level. Delson and Andrews (20) first employed the nominal taxon Kenyapithecinae for referring simultaneously to both Afropithecini and Kenyapithecini. As such, it might be argued (E. Delson, pers. comm. to SMS) that these authors established the priority of the former on the basis of the Principle of the First Reviser (ref. 23: Article 24.2.1), irrespective of whether this taxon is elevated to family rank or not. According to this reasoning, the nomen for referring simultaneously to these taxa would be Kenyapithecidae instead of Afropithecidae (contra ref. 1). Although such priority, as determined by the Principle of the First Reviser, would certainly apply if *Afropithecus* and *Kenyapithecus* were included into the same tribe, regarding the proper family-group name at higher ranks there are other articles of the Code must be taken into account. In particular, Article 35.5 (ref. 23) asserts that “If after 1999 a name in use for a family-group taxon (e.g. for a subfamily) is found to be older than a name in prevailing usage for a taxon at higher rank in the same family-group taxon (e.g. for the family within which the older name is the name of a subfamily) the older name is not to displace the younger name.” On the basis of the Principle of the First Reviser, the nomina Kenyapithecini would take priority over Afropithecini. However, given that, at the family rank, only Afropithecidae has been employed (1, 17-19, 22-24), whereas (to our knowledge) the nomen Kenyapithecidae has not been employed by any author, Kenyapithecinae is not to displace Afropithecidae at the family level. This contention is further stressed by the fact that the Principle of Priority is “to be used to promote stability and it is not intended to be used to upset a long-accepted name in its accustomed meaning by the introduction of a name that it is its senior synonym" (ref. 23: Article 23.2).

Besides the uncertainties regarding the phylogenetic position and the systematic status of the tribe including *Kenyapithecus* and *Griphopithecus* (here included in the Kenyapithecini, following ref. 1), there are also some nomenclatural issues that deserve discussion. These two genera were classified into the subfamily Kenyapithecinae (within the family Hominidae) by some authors (9, 18). On the contrary, other authors distinguished a distinct subfamily Griphopithecinae (within the Afropithecidae) for *Griphopithecus* (17), or even a distinct family Griphopithecidae, either for *Griphopithecus* and *Afropithecus* (25), or for *Griphopithecus* and *Kenyapithecus* (16). Most recently, Begun (26) included *Griphopithecus*, *Equatorius*, *Nacholapithecus* and *Kenyapithecus* (i.e., the Kenyapithecinae as conceived here and in ref. 1) into a distinct subfamily Griphopithecinae (within the Hominidae). As previously noted (ref. 1: their SI Text), this is contrary to the principle of Priority, so that both Kenyapithecini and Kenyapithecinae must be adopted instead of Griphopithecini and Griphopithecinae. To our knowledge, Begun (25) was the first author to employ a family-group nominal taxon with *Griphopithecus* (Griphopithecidae) in 2001 (25), whereas both Afropithecini and Kenyapithecini had been previously erected by Andrews in 1992 (2). It has been previously argued that the nominal taxon Griphopithecini would be still available for a family-group taxon including *Griphopithecus*, if neither *Kenyapithecus* nor *Afropithecus* were included in it (1). This is however contrary to the Code (ref. 23: Article 16), because after 1999 it is mandatory that new nominal taxa are explicitly indicated as intentionally new (Article 16.1), and also that the type genus is cited for new family-group names (Article 16.2). These provisions were not fulfilled by Begun either in 2001 (25) or in 2002 (16). In the latter paper, it was merely specified that the nomina Griphopithecidae and Griphopithecinae were employed with "new rank" (16), but no reference was provided as to who might have previously erected a putative tribe Griphopithecini (ref. 17 also failed to specify the authorship for the Griphopithecinae). If the authorship of these family-group nominal taxa based on *Griphopithecus*, such as Griphopithecini, is to be attributed to Begun, 2001, then they all must be deemed as nomina nuda, because their erection failed to fulfill the requirements of Article 16.2 and also because new names published after 1950 with anonymous authorship are not available according to the Code (ref. 23: Article 14).

Additional nomenclatural problems arise regarding the correct binomen for the European species of *Griphopithecus*. Two nominal species were originally erected on the basis of two different holotype dental specimens from the same type locality (Devínská Nová Ves, in Slovakia) by Abel (26): *Griphopithecus suessi* and *Dryopithecus darwini*. Both taxa were subsenquently considered synonymous (27–28), and after a complicated nomenclatural and taxonomic history (29–30), the genus *Griphopithecus* was finally resurrected (31) for the two Slovakian species and material from Turkey (*Griphopithecus alpani*). Remane (27) apparently acted as the First Reviser (30, contra ref. 29) in 1921, by selecting the nomen *Dryopithecus darwini*, which he considered more suitable as a type species than *Griphopithecus suessi* due to the information provided by their respective holotypes (even though the latter binomen had page priority). This notwithstanding, the combination *Griphopithecus darwini* employed by modern authors (16, 30–31) is incorrect (29), because the two nominal species erected on the basis of the Slovakian material are not merely considered congeneric, but conspecific. Given that *Griphopithecus suessi* is the type species of the genus by original designation (ref. 23: Article 68.2.1), this binomen is to be preferred if *Griphopithecus* is considered a valid genus. In other words, since the priority of *G. darwini* over *G. suessi* was determined on the basis of the principle of the First Reviser (29–30), and given that this action is nullified when unnecessary if subsequently shown that the precedence of names can be objectively determined (ref. 23: Article 24.2.5), we concur with ref. 29 that the correct binomen is *Griphopithecus suessi* instead of *G. darwini*.

With regard to the postcranial material from Klein Hadersdorf, originally two different species were erected in 1938 (32) on the basis of two different holotype specimens: *Austriacopithecus weinfurteri* and *A. abeli*. The former nominal taxon was subsequently used for both specimens for some time (33–34). However, after the recognition of the potential affinities of this material with *Griphopithecus* (35), both nominal species were finally synonymized with *Griphopithecus darwini* (16, 31). Given the arguments provided above regarding the validity of this binomen, here the two nominal species erected on the basis of the Klein Hadersdorf material are formally considered junior subjective synonyms of *Griphopithecus suessi*, and *Austriacopithecus* is considered a junior subjective synonym of *Griphopithecus*. Finally, the partial tooth from Engelswies—variously attributed to ?*Griphopithecus* sp. (31), cf. *Griphopithecus* sp. (36) and aff. *Griphopithecus* (16)—is here attributed to Hominoidea indet. Besides the thick enamel, the information provided by this particular specimen is insufficient to warrant an attribution at the genus level. The main justification for tentatively attributing it to *Griphopithecus* was the supposed similarity in age to the Turkish and Central European localities where this genus is recognized. Given that this argument no longer applies, Engelswies predating by a substantial amount of time the remaining localities (see main text), we think it is more conservative to leave it without a formal taxonomic attribution.

The systematic position of the tribe Dryopithecini and the taxonomy of the species included in it are even more controversial. The nominal taxon Dryopithecini was employed by Begun (16) as a distinct tribe within the Homininae, including both *Dryopithecus* s.l. and *Ouranopithecus*. After the proposal that *Dryopithecus* should be restricted to Middle Miocene taxa (22), some authors (1) restricted the Dryopithecini to Middle Miocene putative stem hominids from Europe (*Dryopithecus* s.s., *Pierolapithecus* and *Anoiapithecus*), whereas Begun (37–38) continued to include Late Miocene European genera into the Dryopithecini. This issue is not only complicated by disagreements on the phylogeny of these taxa, but also by opposite taxonomic opinions among several authors regarding the validity of the several proposed genera. Here we follow ref. 1 by considering that *Pierolapithecus*, *Anoiapithecus* and *Dryopithecus* s.s. are distinct dryopithecin genera. On the contrary, Begun and co-authors (12, 39–40) suggested that *Pierolapithecus catalaunicus* might be a junior synonym of *Dryopithecus fontani* (the type species of the genus *Dryopithecus*), and more recently he formally concluded that both *Pierolapithecus* and *Anoiapithecus* are junior subjective synonyms of *Dryopithecus*, at least at the genus level (38). However, given the striking cranial differences between the three above-mentioned genera, on the basis of the original descriptions of *Pierolapithecus* and *Anoiapithecus* (1, 21) and the newly-recovered cranial material of *D. fontani* (22), we cannot accept such synonymy (22, 24).

Furthermore, although the phylogenetic relationships of the above-mentioned genera certainly deserve further inspection, we consider unconvincing the arguments proposed to date to suggest that they are stem hominines (37–38). Instead, we consider more likely that they are stem hominids (1, 21–22). As such, instead of leaving the tribe Dryopithecini as incertae sedis at the subfamily level (1), we have elevated this taxon to subfamily rank, as previously done by other authors (18, 41). As conceived here, the Dryopithecinae include the tribes Dryopithecini, Hispanopithecini and Ouranopithecini (see later). It is currently uncertain whether dryopithecines are paraphyletic or represents a clade of stem hominids (1), and it is even conceivable that some or all of them might ultimately be more closely related to the Pongini (the tribe including extant orangutans, as well as *Ankarapithecus* and other Asian genera more closely related to *Pongo*, such as *Sivapithecus*). If this was the case, the dryopithecine tribes recognized here would be better classified into the Ponginae, but given current phylogenetic uncertainties we refrain from formally adopting this view here.

The Dryopithecinae as employed here resembles Begun's (38) concept of the Dryopithecini, which includes both Middle and Late Miocene genera, distributed into two distinct subtribes (Dryopithecina and Ouranopithecina). We, however, employ higher ranks for each of these groups, and further distinguish a third group, the Hispanopithecini. According to Begun (38), both the subtribe Dryopithecina and the genus *Dryopithecus* (according to his emended diagnosis) would be characterized by thin-enamelled teeth and large maxillary sinuses. These features, however, are not shared by either *Pierolapithecus* or *Anoiapithecus*, which display thick enamel (24) and restricted maxillary sinuses (1). Among other traits (1, 22), these features indicate that these nominal taxa should not be synonymized with *Dryopithecus*. It must be further noted that, as conceived here, the genus *Dryopithecus* is monotypic, i.e. it only includes the type species *D. fontani*. This is because *D. carinthiacus*—originally erected as a subspecies of *D. fontani* on the basis of the St. Stefan mandible (42)—is here merely considered a junior subjective synonym of the latter species, as previously recognized by other authors (16, 22, 43). More recently, this taxon was recognized as a distinct *Dryopithecus* species (38), but since no further explanation was provided, we do not follow this taxonomic opinion.

At least, some agreement has been recently reached regarding the need to restrict *Dryopithecus* to Middle Miocene taxa (1, 22, 24, 37–38, 40), after the initial resurrection of *Hispanopithecus* by ref. 22. The latter differs from previous proposals to resurrect *Hispanopithecus*, which were restricted to the Spanish material but still included the Hungarian species into *Dryopithecus* (44). However, some disagreements still persist regarding the taxonomy of *Hispanopithecus*: while some authors recently restricted this genus to the Spanish taxa (*H. laietanus* and *H. crusafonti*) and included the Hungarian species into a distinct genus *Rudapithecus* (37–38), others included all these species into *Hispanopithecus* and considered *Rudapithecus* as a junior synonym of the latter (22, 45). Here we take an intermediate view, by considering that *Rudapithecus* and *Hispanopithecus* warrant a distinction at the subgenus level, although this taxonomic opinion should be subjected to further careful scrutiny in the future.

An agreement has also been apparently reached regarding the species nomen that must be employed for the Hungarian species (irrespective of the preferred genus nomen). Until recently, this species was attributed to *Dryopithecus brancoi*, after the nomen *Neopithecus brancoi*, erected on the basis of an isolated molar from Salmendingen and with a very restricted hypodigm. For some years, this fossil material was considered conspecific with the hominoid from Rudabánya (12, 16, 46–47). Later on, however, this nominal taxon was considered a nomen dubium (22), given the limited information provided by the material from the type locality. Most recently, Begun (38) considered that *Neopithecus brancoi* is most similar to the material from Rudabánya but that insufficient anatomy is preserved to justify the synonymy. This is precisely the reason why we ratify here our opinion that both *Neopithecus* and *N. brancoi* should be considered a nomina dubia until their taxonomic identity can be further clarified. Contrary to nomina nuda, nomina dubia are nomenclaturally valid, but of doubtful taxonomic application according to available knowledge—although they might finally prove to be valid (either as a distinct taxon, or as a senior or junior synonym of another taxon) through the study of the type specimens or new material (48). These circumstances further apply to *“Sivapithecus” occidentalis*, originally erected on the basis of two lower molars from Can Vila (of uncertain stratigraphic provenance) (47), and of currently uncertain generic attribution. Over the years, this nominal taxon was considered a synonym of *“Dryopithecus” brancoi* (46), of *Hispanopithecus laietanus* (50–51) and of *“Dryopithecus” laietanus* (31, 52). More recently, however, *“Sivapithecus” occidentalis* was considered a nomen dubium (21), although on the basis of additional material or more detailed studies it might be finally shown to be a senior subjective synonym of some other taxon in the future.

Regarding the Late Miocene European genera here provisionally attributed to the Dryopithecinae, as already mentioned above, the systematic scheme employed in this paper classifies *Hispanopithecus* and *Ouranopithecus* into two distinct tribes (Hispanopithecini and Ouranopithecini, respectively). Regarding the latter, both the nomina Graecopithecini Cameron, 1997 (18, 44) and Ouranopithecini Begun, 2009 (38) are available, and determining the correct nominal taxon to be preferred is further complicated by the taxonomic uncertainties regarding the validity of *Graecopithecus*. *Ouranopithecus macedoniensis* and *Graecopithecus freybergi* have been frequently considered synonyms (31, 44, 55), and if so, the latter should be preferred on the basis of priority. Nevertheless, this synonymy is far from clear, because *Graecopithecus* is only known from a very damaged mandible from the type locality (Pyrgos). The presence of several morphologic differences between the holotype of *Graecopithecus* and the female mandibles attributed *Ouranopithecus*, together with the age differences between Pyrgos and the known chronostratigraphic range recorded for the latter genus, have led several researchers to consider that these nominal taxa represent two different species (18) or genera (16, 38, 56). In fact, the holotype of *Graecopithecus freybergi* is so damaged as to be inadequate for providing an acurate diagnosis, so that it is here considered here a nomen vanum (48).

This has important nomenclatural implications for the validity of family-group nomina derived from *Ouranopithecus* or *Graecopithecus*. Begun (38) erected a subtribe Ouranopithecina within the Dryopithecini for including *Ouranopithecus*, *Graecopithecus* and the hominoid from Çorakyerler (currently attributed to *Ouranopithecus turkae*, see ref. 57). Given the inclusion of *Graecopithecus*, the Ouranopithecina as originally conceived by Begun (38) must be considered a junior objective synonym of Graecopithecina Cameron, 1997, because the type genus of the latter family-group was considered to be a valid at that time (ref. 23: Article 13.2). Even if *Graecopithecus* was considered to be a junior synonym of *Ouranopithecus*, which cannot be the case—unless a reversal of priority is ruled by the International Commission on Zoological Nomenclature—, the priority of Graecopithecini over Ouranopithecini (at any family-group rank) should be maintained (ref. 23: Article 40.1). However, if *Graecopithecus* is not included into the same family-group name as *Ouranopithecus*—as in the systematic scheme employed here—then Ouranopithecini is no longer a junior synonym of Graecopithecini, and the former name must be employed for *Ouranopithecus*.

Oreopithecus, finally, is here restricted to a monotypic tribe Oreopithecini, which is left as incertae sedis at the subfamily level. It might be warranted to united *Oreopithecus* and *Hispanopithecus* into a single tribe, Oreopithecini, in recognition of the close phylogenetic link that has been hypothesized for these taxa (19, 53). Nevertheless, this supposed link strongly contrasts with the phylogenetic hypotheses favored by other authors (3). A family-group nominal taxon based on *Oreopithecus* was previously employed by several authors, either with a family (33, 54), subfamily (16, 18) and/or tribe (18–19) rank. In some instances, such nominal taxa were used to refer only to *Oreopithecus* (18–19, 46) or to *Oreopithecus* plus *Nyanzapithecus* (54), although the latter genus is currently considered a proconsulid (11). If *Oreopithecus* and *Hispanopithecus* were to be included into a single tribe, Oreopithecini Schwalbe, 1915 would take priority over Hispanopithecini Cameron, 1997 (44). Similarly, if the Oreopithecini were to be included into the same subfamily than the Dryopithecini, then Oreopithecinae Schwalbe, 1915 would also take priority over Dryoptihecinae Gregory and Hellman, 1939.

Table S1. Systematic classification of extinct Hominoidea discussed in this paper.

- Superfamily **Hominoidea** Gray, 1825
  - Family **Afropithecidae** Andrews, 1992
    - Subfamily **Kenyapithecinae** Andrews, 1992
      - Tribe **Kenyapithecini** Andrews, 1992
        - Genus ***Kenyapithecus*** L.S.B. Leakey, 1962
          - ***Kenyapithecus kizili*** Kelley, Andrews & Alpagut, 2008
        - Genus ***Griphopithecus*** Abel, 1902
          - ***Griphopithecus alpani*** (Tekkaya, 1974)
          - ***Griphopithecus suessi*** Abel, 1902
  - Family **Hominidae** Gray, 1825
    - Subfamily **Dryopithecinae** Gregory & Hellman, 1939
      - Tribe **Dryopithecini** Gregory & Hellman, 1939
        - Genus ***Dryopithecus*** Lartet, 1856
          - ***Dryopithecus fontani*** Lartet, 1856
        - Genus ***Pierolapithecus*** Moyà-Solà, Köhler, et al., 2004
          - ***Pierolapithecus catalaunicus*** Moyà-Solà, Köhler, et al., 2004
        - Genus ***Anoiapithecus*** Moyà-Solà, Alba, et al., 2009
          - ***Anoiapithecus brevirostris*** Moyà-Solà, Alba, et al., 2009
      - Tribe **Hispanopithecini** Cameron, 2004
        - Genus ***Hispanopithecus*** Villalta & Crusafont, 1944
          - Subgenus ***Hispanopithecus*** Villalta & Crusafont, 1944
            - ***Hispanopithecus (Hispanopithecus) laietanus*** Villalta & Crusafont, 1944
            - ***Hispanopithecus (Hispanopithecus) crusafonti*** (Begun, 1992)
          - Subgenus ***Rudapithecus*** Kretzoi, 1969
            - ***Hispanopithecus (Rudapithecus) hungaricus*** (Kretzoi, 1969)
      - Tribe **Ouranopithecini** Begun, 2009
        - Genus ***Ouranopithecus*** de Bonis & Melentis, 1977
          - ***Ouranopithecus macedoniensis*** (de Bonis & Melentis, 1974)
    - Subfamily **Ponginae** Elliot, 1913
      - Tribe **Pongini** Elliot, 1913
        - Genus ***Ankarapithecus*** Ozansoy, 1957
          - ***Ankarapithecus meteai*** Ozansoy, 1965
    - Subfamily **incertae sedis**
      - Tribe **Oreopithecini** Schwalbe, 1915
        - Genus ***Oreopithecus*** Gervais, 1872
          - ***Oreopithecus bambolii*** Gervais, 1872
      - Tribe **incertae sedis**
        - Genus ?***Udabnopithecus*** Burtschak-Abramovich & Gabachvili, 1950
          - ***?Ubadnopithecus garedziensis*** Burtschak-Abramovich & Gabachvili, 1950
        - Genus ***Graecopithecus*** von Koenigswald, 1982 nomen vanum
          - ***Graecopithecus freybergi*** von Koenigswald, 1982 nomen vanum
        - Genus ***Neopithecus*** Abel, 1902 nomen dubium
          - ***Neopithecus brancoi*** (Schlosser, 1901) nomen dubium
        - Genus **incertae sedis**
          - ***"Sivapithecus" occidentalis*** Villalta & Crusafont, 1994 nomen dubium

Text 2. Regional chronological systems

For a few areas of Western Eurasia, a high-resolution chronology resulting from the combination of a huge amount of litho-, magneto- and biostratigraphic data is available. These include some Spanish basins (Calatayud-Daroca, Teruel and the Vallès-Penedès Basin) (22, 58–61), the Swiss Molasse Basin (62) and the Turkish Sinap Formation (63–65). For these areas, magnetostratigraphic sections are long enough to allow an unambiguous direct correlation to the GPTS. In other areas, such as the Bavarian Molasse Basin in Germany (66–67) and the Axios Valley (68) in Greece, similar efforts have been conducted but the studied sections are too short to provide unique correlations to the GPTS. Magnetostratigraphic ages from these regions are strongly dependent on other, biostratigraphic or radiometric, constrains.

When no magnetostratigraphic or radiometric data are available, our correlations rely on regional biostratigraphy. Fortunately, high-resolution biozones derived from certain basins can be easily extended to nearby areas, thus enabling the refinement of the chronology of many sites. To this regard, the Vallès-Penedès biozonation for the late Aragonian and Vallesian can be recognized in nearby Spanish basins as well as in France (22, 69). Regarding the alpine region, it is worth noting that the chronostratigraphy of the Bavarian and Swiss Molasse sequences have provided a consistent biozonation, but with different magnetostratigraphy-based ages. Given that the magnetostratigraphic framework of the Bavarian molasse is relatively less robust, the Swiss Molasse chronology (62) can be extended into the Bavarian Molasse Basin by means of biostratigraphic correlation. For Turkey, a preliminary local zonation for central Anatolia has been proposed and tentatively correlated to the European MN zones (70). Unfortunately, the Anatolian local zonation does not allow a higher resolution than the MN zonation, so our correlations regarding the Turkish record emphasize magnetostratigraphic data. Finally, regarding the insular Late Miocene faunas of Tuscany, a useful local biozonation was proposed by Lorenz (71) for the faunas of the Baccinello basin, and subsequent studies have allowed the correlation of these endemic faunas to the MN zones (72–73).

Last but not least, marine-continental correlations have been taken into account for the localities from the Pannonian basin. This basin, which covers all of Hungary and Slovakia as well as part of nearby countries, connected to the Paratethys during the Middle and Late Miocene (74–75). Since many hominoid sites occur in transitional facies or interbedded with marine sediments, their age can be directly tied to marine chronostratigraphic scales, based either on planktonic foraminifera, nannoplankton or molluscs.

Text 3. The Miocene record of the Vallès-Penedès Basin: biostratigraphy and magnetostratigraphy

The Vallès-Penedès Basin (Catalonia, Spain) is a small half-graben parallel to the Catalan coastline that originated during the latest Oligocene as a result of extensional processes related to the opening of the western Mediterranean (76). The sedimentary sequences of the basin cover most of the Miocene and consist mainly of alluvial fan units. During the Middle Miocene a large part of the basin was covered by a shallow sea (76–78) as a result of the Langhian transgression (ca. 15 Ma). The continental sediments of the Vallès-Penedès Basin have been intensively surveyed for almost 70 years and have become a classical area for the study of the Miocene mammal faunas of Europe. More than 200 mammal-bearing sites have been discovered to date which make this are one of the most densely-sampled of Eurasia. Furthermore, magnetostratigraphic studies have been carried at the most important sections further refining the correlations and age estimates (22, 58–59). Here we summarize and update the results of previous works (59, 79–83) and further refine the biozonation of the Vallès-Penedès Basin.

The Early Miocene. A dozen of localities are known from the Early Miocene sediments, some of them (els Casots, Molí de Calopa) yielding very rich assemblages. Two distinct biozones can be distinguished on the basis of the rodent fauna (79). The first biozone (*ibericus* zone of ref. 79) is characterized by the presence of the glirid *Pseudodyromys ibericus*, the muroid *Melissiodon* cf. *dominans* and the equid *Anchitherium* sp. The faunas are insufficiently known but this zone probably correlates to zone A (late Ramblian) of the Calatayud-Daroca Basin (east-central Spain) (60), thus covering the late MN3 (ca. 18-17 Ma), although somewhat younger ages (MN4) cannot be discarded. The second biozone is the *Megacricetodon minor primitivus* + *Ligerimys ellipticus* Concurrent range zone which records the first appearance of the cricetodontids *Democricetodon*, *Megacricetodon* and *Eumyarion*. This biozone is correlated to zone C (early Aragonian, later part of MN4) of the Calatayud-Daroca Basin (60), ranging from about 16.5 to 16 Ma. Primates are not recorded during the Early Miocene in the Vallès-Penedès Basin.

The Middle Miocene. During the Langhian transgression, a few mammal localities (i.e. Ca n'Almirall) are recorded in transitional facies (80) and have been correlated to the MN6. However, these faunas have yet to be studied in detail. Other localities which may correlate to the MN6 in the Vallès-Penedès Basin include Les Conilleres and a few micromammal sites from the lower part of the Abocador de Can Mata (ACM) series (22, 81-82). These localities have delivered a very poor micromammal fauna and have been correlated by the means of magnetostratigraphy to chron C5Ar.1r (12.730-12.415 Ma). Clearly more sampling is needed to adequately characterize the time interval that follows the end of the Langhian transgression until ca. 12.5 Ma in the Vallès-Penedès.

The densely sampled ACM series (81-82) has allowed the subdivision of the Late Aragonian record into two distinct biozones according to the cricetodontid species present: the *Democricetodon larteti* + *Megacricetodon ibericus* Concurrent range zone and the *Democricetodon crusafonti* + *Megacricetodon ibericus* Concurrent range zone (69, 83). The *D. larteti* + *M. ibericus* zone is further characterized by the occurrence of a diverse rodent fauna in many sites that includes two *Hispanomys* species (*H. decedens* and *H.* cf. *aguirrei*) and several glirids (of the genera *Glirudinus*, *Myoglis*, *Muscardinus*, *Paraglis*, *Microdyromys* and *Paraglirulus*) although this family is not abundant. The eomyids (*Eomyops*, *Keramidomys*) and pteromyines (flying squirrels of the genera *Miopetaurista* and *Albanensia*) may occur occasionally. This biozone ranges begins at chron C5An.2n (12.415-12.207 Ma) and ends within chron C5r.3r (12.014-11.614) so we estimate an age of 11.8 Ma for the upper boundary of this biozone. Hominoids are first recorded within this biozone in the Vallès-Penedès Basin at locality C1-E* (estimated age 12.2-12.3 Ma see SI Dataset). The *D. crusafonti* + *M. ibericus* zone begins within chron C5.3r and ends at chron C5r.1n (11.154-11.118 Ma). Since many primate finds of the ACM series occur within chron C5r.3r, but these sites have not always delivered a rich rodent sample, it is not possible to this biozone or to the previous one. The *D. crusafonti* + *M. ibericus* zone is characterized by the presence of *D. crusafonti*, although its ancestor *D. larteti* still is recorded at some sites, where it is very rare. The rodent fauna does not show many changes except for the replacement of some cricetodontid species (*D. brevis brevis*, *M. minor minor*) by their putative descendants (*D. brevis nemoralis*, *M. minor debruijni*). The genus *Hispanomys* is represented by three new species (*H. lavocati*, *H. decedens*, *H. daamsi*). The beavers occur at some sites where they can be very common. To the top of this biozone the rodent fauna becomes impoverished by the temporal disappearance of many glirid species, the eomyids and the flying squirrels, which may indicate a shift towards dryer environments. This local zonation can be recognized in other Iberian basins such as Calatayud-Daroca (83) and can be further extended to France (69, 83) allowing to constrain the age of certain sites such as La Grive fissure fillings.

The Late Miocene. The Late Miocene record ends abruptly because of a pronounced marine regression by the Messinian (middle Turolian, ca. 7.2 Ma) which implied the prevalence of erosional processes over sedimentation. The beginning of the Late Miocene is particularly well represented in the basin, so a land mammal stage, the Vallesian, was erected on the basis of the Vallès-Penedès mammal successions (84). The Vallesian has been intensively sampled and the main Vallesian sites have been situated in a magnetostratigraphic framework (58–59). The lower boundary of the Vallesian is marked by the dispersal into the Old World of the hipparionine horses, of North American origin. In the Vallès-Penedès Basin, these equids are first recorded at the lower part of chron C5r.1n, which would imply and age of 11.154 Ma (58, 85). This age is congruent with the radiometric dating of key sites of Central Europe (86) but it is somewhat older than other age estimates for this event in other areas (Calatayud-Daroca Basin, Sinap Formation, Siwaliks) which range from 10.8 to 10.3 Ma (64, 87–89). The presence of *Hipparion* sensu lato characterizes the *Hipparion* s.l. + *M. ibericus* Concurrent range zone (59). Amongst the macromammals, the first occurrence of the felid *Machairodus* is also recorded (59), but the rodent fauna does not show significant differences compared to that of the latter part of the *D. crusafonti* + *M. ibericus* zone. The upper boundary of the *Hipparion* s.l. + *M. ibericus* zone is located within chron C5n.2n (11.040-9.987 Ma) with an estimated age of about 10.4 Ma (59).

Agustí and co-workers (59) defined the *Cricetulodon* zone for the rest of the early Vallesian, which is here divided into two different biozones: *Cricetulodon hartenbergeri* Local range zone and *Cricetulodon sabadellensis* Local range zone. These two biozones are distinguished on the basis of the species of the cricetid *Cricetulodon*, which is a very common component of the rodent faunas. The rodent assemblage in both zones is very diverse and many of the glirid genera that were absent since the upper half *D. crusafonti* + *M. ibericus* zone reappear in the record together with the eomyids and flying squirrels which may be recorded at certain sites. Nevertheless, all these rodent taxa are not abundant. Amongst the muroids, *M. ibericus* and *D. crusafonti* are not longer present, while the genera *Eumyarion* and *Megacricetodon* are last recorded in the *C. sabadellensis* zone. The primates are represented by the genus *Hispanopithecus* at many sites. The *C. hartenbergeri* zone covers the second half of chron C5n.2n with an estimated age of 10.4 Ma for the lower boundary and of 9.9 Ma for the upper one. This biozone comprises important sites such as Can Ponsic or Santiga and can also be recognized in the Seu d'Urgell Basin (Catalan Pyrenees). In its turn, the *C. sabadellensis* zone ranges from the base of chron C5r.1r to the top of chron C4Ar.3r, that is from 9.987 to 9.717 Ma. Since *C. sabadellensis* is endemic of the Vallès-Penedès Basin, this biozone cannot be extended to other areas. Major localities correlated to this biozone include Can Llobateres 1.

At the top of the *C. sabadellensis* zone, the first occurrence of murids (*Progonomys*) in Western Europe is recorded. This rodent family is first scarcely represented but become very abundant soon afterwards, so they characterize the first biozone of the late Vallesian, the *Cricetulodon* + *Progonomys* Interval zone. The lower boundary of this zone is not characterized by the entry of *Progonomys* but by its common occurrence. This murid first appeared in the Indian subcontinent at about 12 Ma (90) and dispersed into western Eurasia during the Vallesian, being first recorded in Turkey at about 10.135 Ma (64) and arriving into the Iberian Peninsula at about 9.7 Ma. Recently, Aguilar and co-workers (91) suggested a much older age for the *Progonomys* dispersal and the Aragonian/Vallesian boundary. According to these authors, *Progonomys* would have been already present by about 11.4 Ma, so that it would not have taken two million years to reach Western Europe from Asia. These authors reinterpret several sections where *Hipparion* s.l. and *Progonomys* co-occur, including the Can Llobateres section (see Fig. 2), and conclude that these may be nearly two million years older, since the presence of these two taxa is also congruent with this dating. Therefore, these authors ignore the composite bio-magnetostratigraphic context of the Vallés sequence and propose a new correlation of Can Llobateres to chron C5r.2n (see Fig. 2), resulting in an age estimate of 11.5 Ma for Can Llobateres 1. Such surprising results are based on the interpretation of the short (10 m-thick) Ecotet section (France), in which two mammal sites are associated with transitional marine facies that have yielded calcareous nannoplankton and planktonik foraminifera indicating a late Middle Miocene age. The very poor mammal sites have not delivered *Progonomys* or *Hipparion* s.l., but are attributed to the early Vallesian (MN9) on the basis of the presence of *D. brevis* cf. *nemoralis* and *M. minor debruijni*. These taxa, however, were already present in the late Aragonian (in our *D. crusafonti* + *M. ibericus* zone), and do not suggest an MN9 age for these sites or add any new information concerning the dispersal of *Progonomys*.

The *Cricetulodon* + *Progonomys* zone is characterized by the disappearance of many mammal taxa, an extinction event which has been termed the Vallesian Crisis (92). Amongst the rodents, many glirids and all the eomyids became very rare until finally disappearing during the next biozone. The flying squirrels and the beavers also became rarer than during the early Vallesian. Regarding the macromammals, the suids *Listriodon* and *Parachleuastochoerus,* the bovid *Miotragocerus*, and amphicyonid and nimravid carnivorans all disappear in this biozone. Finally, hominids (*Hispanopithecus laietanus*) are last recorded within this biozone at the site of La Tarumba 1. On the other hand, this biozone records a number of new occurrences, including the hypsodont cricetid *Rotundomys montisrotundi*, the suids *Microstonyx* and *Schizochoerus* and the large hyaenid *Adcrocuta*. This biozone ranges from chron C4Ar.2n to chron C4Ar.2r, that is, from 9.717 to 9.409 Ma. Important sites include Can Llobateres 2 and La Tarumba 1.

Finally, the last zone of the Vallesian is the *Rotundomys bressanus* Local range zone (59). This biozone is characterized by the presence of this hypsodont cricetid (first recorded at the base of chron C4Ar.1, that is 9.409 Ma) together with the murids of the genus *Progonomys*; unlike in other Iberian basins (such as the Teruel Basin in east-central Spain) (93), these murids are not very abundant. Amongst the macromammals, some species characteristic of Turolian faunas are first recorded, including the bovid *Tragoportax gaudryi* and the felid *Paramachairodus orientalis*. Pliopithecids are last recorded within this biozone at Torrent de Febulines, where they are represented by the crouzeline *Egarapithecus narcisoi* (94). The upper boundary of this zone coincides with the Vallesian/Turolian boundary and is presumably placed within chron C4An (9.098-8.769 Ma). Important sites within this biozone include Torrent de Febulines, Ceràmiques Viladecavalls, Trinxera Nord Autopista and Trinxera Sud Autopista.

References

1. Moyà-Solà S, et al. (2009) A unique Middle Miocene European hominoid and the origins of the great ape and human clade. *Proc Natl Acad Sci USA* 106:9601-9606.
2. Andrews P (1992) Evolution and environment in the Hominoidea. *Nature* 360:641–646.
3. Begun DR, Ward CV, Rose MD (1997) in *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptation*, eds Begun DR, Ward CV, Rose MD (Plenum Press, New York), pp 389–415.
4. Fleagle JG (1999) *Primate Adaptation and Evolution*. 2nd Ed., (Academic Press, San Diego), 608 pp.
5. Rae TC (1999) Mosaic evolution in the origin of the Hominoidea. *Folia Primatol* 70:125–135.
6. Kelley J (1997) in *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptation*, eds Begun DR, Ward CV, Rose MD (Plenum Press, New York), pp 173–208.
7. Rose MD (1997) in *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptation*, eds Begun DR, Ward CV, Rose MD (Plenum Press, New York), pp 79–100.
8. Ward CV (1997) in *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptation*, eds Begun DR, Ward CV, Rose MD (Plenum Press, New York), pp 101–130.
9. Ward SC, Duren DL (2002) in *The Primate Fossil Record*, ed Hartwig WC (Cambridge University Press, Cambridge), pp 385–397.
10. Harrison T (2002) in *The Primate Fossil Record*, ed Hartwig WC (Cambridge University Press, Cambridge), pp 311–338.
11. Harrison T (2010) in *Cenozoic Mammals of Africa*, ed Werdelin L & Sanders WJ (University of California Press, Berkeley), pp 429–469.
12. Begun DR (2007) in *Handbook of Paleoanthropology*, eds Henke W & Tattersall I (Springer Verlag, Heidelberg), pp 921–977.
13. Ward CV, Walker A, Teaford MF (1991). *Proconsul* did not have a tail. *J Hum Evol* 21:215–220.
14. Nakatsukasa M et al. (2004) Tail loss in *Proconsul heseloni*. *J Hum Evol* 46:777–784.
15. Nakatsukasa M et al. (2003) Definitive evidence for tail loss in *Nacholapithecus*, an East African Miocene hominoid. *J Hum Evol* 45:179–186.
16. Begun DR (2002) in *The Primate Fossil Record*, ed Hartwig WC (Cambridge University Press, Cambridge), pp 339–368.
17. Kelley J (2002) in *The Primate Fossil Record*, ed Hartwig WC (Cambridge University Press, Cambridge), pp 369–384.
18. Cameron DW (2004) *Hominid Adaptations and Extinctions* (University of New South Wales Press, Sydney), 235 pp.
19. Harrison T, Rook L (1997) in *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptation*, eds Begun DR, Ward CV, Rose MD (Plenum Press, New York), pp 327–362.
20. Delson P, Andrews P (2000) in *Encyclopedia of Human Evolution and Prehistory*, eds Delson E, Tattersall I, Van Couvering JA, Brooks AS (Garland, New York), p 362.
21. Moyà-Solà S, et al. (2004) *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. *Science* 306:1339–1344.
22. Moyà-Solà S, et al. (2009) First partial face and upper dentition of the Middle Miocene hominoid *Dryopithecus fontani* from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, NE Spain): taxonomic and phylogenetic implications. *Am J Phys Anthropol* 139: 26–145.
23. International Commission on Zoological Nomenclature (1999) *International Code of Zoological Nomenclature. Fourth Edition* (International Trust for Zoological Nomenclature, London).
24. Alba DM, Fortuny J, Moyà-Solà S (2010) Enamel thickness in Middle Miocene great apes *Anoiapithecus*, *Pierolapithecus* and *Dryopithecus*. *Proc. R. Soc. B* 277:2237–2245.
25. Begun DR (2001) in *Hominoid Evolution and Environmental Change in the Neogene of Europe. Volume 2. Phylogeny of the Neogene Hominoid Primates of Eurasia,* eds Bonis L de, Koufos G, Andrews P (Cambridge University Press, Cambridge), pp 231–268.
26. Abel O. (1902) Two new great apes from the Leitha limestone formations of the Vienna Basin. *S Akad Wiss Wien Math Wiss Kl* 111:1171–1207. [in German]
27. Remane A (1921) A review of fossil anthropoids. *Zbl Min Geol Paleontol* 11:335–339. [in German]

28. Glaessner MF (1931) New teeth of apes from the Miocene of the Vienna Basin. *Ann Naturhist Mus Wien* 46:15–27. [in German]
29. Holec P, Emry RJ (2003) Another molar of the Miocene hominid *Griphopithecus suessi* from the type locality at Sandberg, Slovakia. *Bull Am Mus Nat Hist* 279:625–631.
30. Güleç E, Begun DR (2003) Functional morphology and affinities of the hominoid mandible fron Çandir. *Cour Forsch-Inst Senckenberg* 240 89–111.
31. Andrews P, et al. (1996) in *The Evolution of Western Eurasian Neogene Mammal Faunas*, eds Bernor RL, Fahlbusch V, Mittmann H-W (Columbia University Press, New York), pp 168–207.
32. Ehrensberg K (1938) *Austriacopithecus*, a new ape-like primate from the Miocene of Klein-Hadersdorf near Poysdorf in Lower Austria (Nieder-Donau). *S Kön Bay Akad Wiss Mün* 147:71–110. [in German]
33. Thenius E (1954) The significance of *Austriacopithecus* Ehrensberg for the *phylogeny of the* Hominoidea. *Osterr Akad Wiss math-nat Kl Wien* 13:191–196. [in German]
34. Zapfe H (1960) The primate remains from the Miocene fissure filling of Neudorf an der March (Devinská Nová Ves), Czechoslovakia. *Schweiz Paleontol Abh* 78:1–293. [in German]
35. Begun DR (1992) Phyletic diversity and locomotion in primitive European hominids. *Am J Phys Anthropol* 87:311–340.
36. Heizmann EPJ, Begun DR (2001). The oldest Eurasian hominoid. *J Hum Evol* 41:463–481.
37. Begun DR (2010) Miocene hominids and the origins of the African apes and humans. *Ann Rev Anthropol* 39:67–84.
38. Begun DR (2009). Dryopithecins, Darwin, de Bonis, and the European origin of the African apes and human clade. *Geodiversitas* 31:789–816.
39. Begun DR (2006) Revision of the Dryopithecini. *J Vert Paleontol* 26:40A.
40. Begun DR, Nargolwalla M, Kordos L (2008) Revision of the Dryopithecinae: phylogenetic and paleobiogeographic implications. *Am J Phys Anthropol* S46:66.
41. Delson E, Andrews P (2000) in *Encyclopedia of Human Evolution and Prehistory*, eds Delson E, Tattersall I, Van Couvering JA, Brooks AS (Garland, New York), p 221–222.
42. Mottl M (1957) Report on the new apes finds of Austria, from St. Stefan in the Lavant valley, Carinthia. *Carinthia II, Mitt. Naturwiss. Ver. Kärnten* 67:39–84. [in German]
43. Begun DR, Nargolwalla MC, Hutchison MP (2006) Primate diversity in the Pannonian Basin: In situ evolution, dispersals, or both? *Beitr Paläontol* 30:43–56.
44. Cameron DW (1997) A revised systematic scheme for the Eurasian Miocene fossil Hominidae. *J Hum Evol* 33:449–477.
45. Alba DM (2010) Cognitive inferences in fossil apes (Primates: Hominoidea): does encephalization reflect intelligence? *J Anthropol Sci* 88:11–48.
46. Szalay FS, Delson E (1979) *Evolutionary History of the Primates* (Academic Press, San Diego).
47. Begun DR, Kordos L (1993) Revision of *Dryopithecus brancoi* Schlosser, 1901, based on the fossil hominoid material from Rudabánya. *J Hum Evol* 25:271–285.
48. Mones A (1989) Nomen dubium vs. nomen vanum. *J Vert Paleontol* 9:232–234.
49. Villalta Comella JF de, Crusafont Pairó M (1944) Two new apes from the Spanish Miocene and their situation within the moder systematics of the simiids. *Not Com Inst Geol Min Esp* 13:1–51. [in Spanish]
50. Golpe Posse JM (1982) The hispanopiths (Primates, Pongidae) from the sites of the Vallès Penedès (Catalonia - Spain). I: Already-described material. *Butll Inf Inst Paleontol Sabadell* 14:63–69. [in Spanish]
51. Golpe Posse JM (1993) The hispanopiths (Primates, Pongidae) from the sites of the Vallès-Penedès (Catalonia, Spain). II: Description of the material from the Instituto de Paleontología in Sabadell. *Paleontol Evol* 26-27:151–224. [in Spanish]
52. Begun DR, Moyá-Sola S, Kohler M (1990) New Miocene hominoid specimens from Can Llobateres (Vallès Penedès, Spain) and their geological and paleoecological context. *J Hum Evol* 19:255–268.
53. Moyà Solà S, Köhler M (1997) The phylogenetic relationships of *Oreopithecus bambolii* Gervais, 1872. *C R Acad Sci Paris* 324:141–148.
54. Harrison T (1986) New fossil anthropoids from the middle Miocene of East Africa and their bearing on the origin of the Oreopithecidae. *Am J Phys Anthropol* 71:265–284.
55. Martin L, Andrews P (1984) The phyletic position of *Graecopithecus freybergi* Koenigswald. *Cour Forsch-inst Senckenberg* 69:25–40.

56. de Bonis L, Koufos G (1993) The face and the mandible of *Ouranopithecus macedoniensis*: description of new specimens and comparisons. *J Hum Evol* 24:469–491.
57. Güleç ES, Sevim A, Pehlevan C, Kaya F (2007) A new great ape from the late Miocene of Turkey. *Anthropol Sci* 115:153–158.
58. Garcés M, Agustí J, Cabrera L, Parés JM (1996) Magnetostratigraphy of the Vallesian (late Miocene) in the Vallès-Penedès basin (northeast Spain). *Earth Planet Sci Lett* 142:381–396.
59. Agustí J, Cabrera L, Garcés M, Parés JM (1997) The Vallesian mammal succession in the Vallès-Penedès basin (northeast Spain): paleomagnetic calibration and correlation with global events. *Palaeogeogr Palaeoclimatol Palaeoecol* 133:149–180.
60. Daams R, et al (1999) Stratigraphy and sedimentology of the Aragonian in its type area. *Newsl Stratigr* 37:103–139.
61. Van Dam JA, et al (2001) The upper Miocene mammal record from the Teruel-Alfambra region (Spain). The MN system and continental stage/age concepts discussed. *J Vert Pal* 21:367–385.
62. Kälin D, Kempf O (2009) High-resolution stratigraphy from the continental record of the Middle Miocene Northern Alpine Foreland basin of Switzerland. *N Jb Geol Paläont Abh* 254:177–235.
63. Lunkka J-P, Fortelius M, Kappelman J, Sen S (1999) in *Hominoid evolution and Enviromental Change in the Neogene of Europe Volume 1: The Evolution of Terrestrial Ecosystems in Europe*, eds Agustí J, Rook L, Andrews P (Cambridge University Press, Cambridge), pp 238–264.
64. Kappelman J, et al. (2003) in *Geology and Paleontology of the Miocene Sinap Formation, Turkey*, eds Fortelius M, Kappelman, J, Sen S, Bernor RL (Columbia University Press, New York), pp 41–66.
65. Kappelman J et al. (2003) in *Geology and Paleontology of the Miocene Sinap Formation, Turkey*, eds Fortelius M, Kappelman, J, Sen S, Bernor RL (Columbia University Press, New York), pp 90–124.
66. Abdul Aziz H, et al. (2008) Integrated stratigraphy and ^{39}Ar/^{40}Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in eastern Bavaria (Germany). *Int J Earth Sci* 97:115–134.
67. Abdul Aziz H, et al. (2010) Integrated stratigraphy and ^{39}Ar/^{40}Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in western Bavaria (Germany). *Int J Earth Sci* 99:1859–1886.
68. Sen S, Koufos GD, Kondopoulou D, de Bonis L (2000) Magnetostratigraphy of the Late Miocene continental deposits of the Lower Axios valley, Macedonia, Greece. *Bull Geol Soc Greece* sp pbl 9:197–206.
69. Casanovas-Vilar I, et al. (2008) Biochronological, taphonomical and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae). *J Hum Evol* 55:589–603.
70. Ünay E, De Bruijn H, Saraç G (2003) A preliminary zonation of the continental Neogene of Anatolia based on rodents. *Deinsea* 10:539–547.
71. Lorenz HG (1968) Stratigraphical studies and micropaleontology of the brown coal area of Baccinello (Grosseto, Italy). *Riv It Paleont Strat* 74:147–270. [in German]
72. Engesser B (1989) The Late Tertiary small mammals of the Maremma region (Tuscany, Italy). 2nd part: Muridae and Cricetidae (Rodentia, Mammalia). *Bol Soc Paleontol I* 28:227–252.
73. Rook L, Harrison T, Engesser B (1996) The taxonomic status and biochronological implications of new finds of *Oreopithecus* from Baccinello (Tuscany, Italy). *J Hum Evol* 30:3–27.
74. Popov SV, et al. (2004) Lithological-Paleogeographic maps of Paratethys. 10 Maps Late Eocene to Pliocene. *Cour Forsch-Inst Senckenberg* 250:1–46.
75. Harzhauser M, Piller WE (2007) Benchmark data of a changing sea – palaeogography, palaeobiogeography and events in the Central Paratethys during the Miocene. *Palaeogeogr Palaeoclimatol Palaeoecol* 253:8–31.
76. Cabrera L, Roca E, Garcés M, de Porta J (2004) in *Geology of Spain*, ed Vera JA, (SGE-IGME, Madrid), pp 569–573. [in Spanish]
77. Cabrera L, Calvet F (1990) Sequential arrangement of the Neogene sedimentary record in the Vallés-Penedés and Valls-Reus half grabens, Iberian margins, NE Spain. *Terra Abstr* 2:1–110.
78. Cabrera L, Calvet F (1996) in *Tertiary Basins of Spain*, eds Friend PF, Dabrio C (Cambridge University Press, Cambridge), pp. 97–105.
79. Agustí J (1982) Biozonation of the continental Neogene of Catalonia by the means of rodents (Mamm.). *Acta Geol Hisp* 17:21-26. [in Spanish]

80. Agustí J, Cabrera L, Moyà-Solà S (1985) Stratigraphic synopsis of the Neogene of the Vallès-Penedès Basin. *Paleont Evol* 18:57-81. [in Spanish]
81. Alba DM, et al. (2009) Middle Miocene vertebrate localities from Abocador de Can Mata (Els Hostalets de Pierola, Vallès-Penedès Basin, Catalonia, Spain): An update after the 2006-2008 field campaigns. *Paleolusitana* 1:59–73.
82. Alba DM, et al. (2006) The fossil vertebrates from Abocador de Can Mata (Els Hostalets de Pierola, l'Anoia, Catalonia), a succession of localities from the late Aragonian (MN6 and MN7+8) of the Vallès-Penedès Basin. Campaigns 2002–2003, 2004 and 2005. *Est Geol* 62:295–312. [in Spanish]
83. Casanovas-Vilar I (2007) *The rodent assemblages from the Aragonian and the Vallesian (Middle to Late Miocene) of the Vallès-Penedès Basin (Catalonia, Spain)*, phD thesis Universitat Autònoma de Barcelona. http://www.cbm.uam.es/sev/Rodents.pdf
84. Crusafont Pairó M (1950) La cuestión del llamado Meótico español. *Arrahona* 1950:3–10.
85. Garcés M, Cabrera L, Agustí J, Parés JM (1997) Old World first appearence datum of "*Hipparion*" horses: late Miocene large mammal dispersal and global events. *Geology* 25:19–22.
86. Bernor RL, et al. (1988) Systematic, stratigraphic and paleoenvironmental contexts of first appearing *Hipparion* in the Vienna Basin, Austria. *J Vert Pal* 8:427–452.
87. Garcés M, Krijgsman W, Peláez-Campomanes P, Álvarez Sierra MA, Daams R (2003) *Hipparion* dispersal in Europe: magnetostratigraphic constraints from the Daroca area (Spain). *Col-Pa* vol ext 1:17–178.
88. Barry JC, Lindsay EH, Jacobs LL (1982) A biostratigraphic zonation of the middle and upper Siwaliks of the Potwar Plateau of northern Pakistan. *Palaeogeogr Palaeoclimatol Palaeoecol* 37:95–130.
89. Barry JC, Johnson NM, Mahmood-Raza S, Jacobs LL (1985) Neogene mammalian change in southern Asia: correlations with climatic, tectonic, and eustatic events. *Geology* 13:637–640.
90. Jacobs LL, Flynn LJ, Downs WR, Barry JC (1990) in *European Neogene Mammal Chronology*, eds Lindsay EH, Fahlbusch V, Mein P (Plenum Press, New York), pp 573–586.
91. Aguilar J-P, et al. (2004) Mid-Neogene Mediterranean marine-continental correlations: an alternative interpretation. *Palaeogeogr Palaeoclimatol Palaeoecol* 204:165–186.
92. Agustí J, Moyà-Solà (1990) Mammal extinctions in the Vallesian (Upper Miocene). *Lect Notes Earth Sci* 30:425–432.
93. Van Dam JA, et al. (2001) The upper Miocene mammal record from the Teruel-Alfambra region (Spain). The MN system and continental stage/age concepts discussed. *J Vert Pal* 21:367–385.
94. Moyà-Solà S, Köhler M, Alba DM (2001) *Egarapithecus narcisoi*, a new genus of Pliopithecidae (Primates, Catarrhini) from the Late Miocene of Spain. *Am J Phys Anthropol* 114:312–324.

SI Dataset for

An updated chronology for the Miocene hominoid radiation in Western Eurasia

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Contents

How to use this database

Here we provide a list of the localities included in this study in alphabetical order. Most of these localities are mentioned and discussed in the main text and appear in Figs. 1-2. In this appendix we provide further details regarding their location, age and correlation to regional and global time scales. For each record the information is arranged in eleven fields as follows:

Locality: Name of the locality. In case of synonymy the most widely used name is given in this field.

Locality synonyms: Other names given to the locality, usually referring to older names used by some authors.

Area and country: The formation, basin, area or region and the country the locality currently belongs to are given in this field and in this order.

Taxon: The hominoid taxon recovered in the locality. For details on the taxonomy and systematics used in this work see SI Appendix Text 1.

Maximum age: The oldest possible age of the locality. When magnetostratigraphic data are available, this refers to the lower boundary of the geomagnetic chron of the Geomagnetic Polarity Timescale (GPTS) to which the locality is correlated. When the locality is correlated to a regional/local zonation for which the boundaries for the different zones have not been unambiguously correlated to the GPTS, the term ‘circa (ca.)’ precedes the estimated age. In these cases, the estimated age will be the lower boundary of the regional/local zone to which the locality is correlated. And finally, when the correlation relies entirely on the MN zonation, the age of the lower boundary is given. For the Middle Miocene of Western Europe (France, Spain) the age of the MN boundaries is after Agustí et al. (2001), for the same time interval of Central Europe and Turkey the age of the MN boundaries follows Kälin & Kempf (2009). For the Late Miocene, the age of the MN boundaries is after Agustí et al. (2001). In case that two different maximum ages are possible (because of different possible correlations of the MN zones or the regional/local zones to the GPTS, for example) the two possible ages are given. When a question mark is added after the age means that the correlation is highly uncertain.

Minimum age: The youngest possible age of the locality. This age always refers to the top boundary of the geomagnetic chron, regional/local zonation or MN zone to which the locality is correlated (see above for more details).

Preferred correlation to the GPTS: The geomagnetic chron of the GPTS (Ogg & Smith, 2004) to which the locality is correlated.

Local/regional correlations: The regional/local zone to which the locality is correlated. These zones can be based either on marine, freshwater or continental faunas. For details on the different regional scales used see SI Appendix Text 2.

Correlation to the MN zonation: The MN zone to which the locality is correlated. For these MN zones which are known to have diachronic boundaries in Central Europe and Western Europe we indicate if we are considering the age boundaries of one area or the other one.

Remarks: Additional remarks usually give more details on the correlation of the locality to the different time scales. In a few situations, when the stratigraphic provenance of the material is uncertain, this issue is discussed in this field.

References: The references cited refer to the most recent references that add some information on the age of this locality. References to older works dealing with the same question can be found in those works.

Locality Database

The following database includes 61 hominoid-bearing sites from the Miocene of Western Eurasia. Three doubtful citations are excluded from this synthesis: Montrejeau, Kalfa and Eldar. The 1911 geological map of Saint Gaudens reports the presence of Dryopithecinae indet. at Montrejeau (Haute-Garonne, France). Even though the material was never figured nor described, this citation is repeated by some authors (Szalay & Delson, 1979). However, no one knows what the material is or where it is stored (Mein, 1986). *Oreopithecus* sp. has been cited from Kalfa (Moldova) (Lungu, 1974), but the material has never been published and even its existence is uncertain (Delson, 1987). On the other hand, the presence of *Oreopithecus* in Moldova is highly unlikely, since this genus is known to be endemic to the Tusco-Sardinian palaeobioprovince. Szalay & Delson (1979) also mention the presence of *Dryopithecus fontani* at Eldar (Georgia), a locality close to Udabno 1. Nevertheless, this material has not been figured or described and it has not been mentioned in recent publications, so it is questionable if it ever existed.

Locality: Abocador de Can Mata, Barranc de Can Vila 1 (ACM/BCV1).
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: *Pierolapithecus catalaunicus.* Type locality.
Maximum age: 12.014 Ma.
Minimum age: 11.614 Ma.
Preferred correlation to the GPTS: C5r.3r.
Local/regional correlations: *Democricetodon larteti* + *Megacricetodon ibericus* Concurrent range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN 7+8 (Western Europe boundaries).
Remarks: Estimated age 11.93 Ma. This age is estimated from linear interpolation between bounding magnetic reversals of the local magnetostratigraphy of the ACM section.
References: Casanovas-Vilar et al., 2008; Moyà-Solà et al., 2009a; this work [Text S3].

Locality: Abocador de Can Mata, Barranc de Can Vila 4 (ACM/BCV4).
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: Hominidae indet.
Maximum age: 12.014 Ma.
Minimum age: 11.614 Ma.
Preferred correlation to the GPTS: C5r.3r.
Local/regional correlations: The correlation to the Vallès-Penedès zones is ambiguous.
Correlation to the MN zonation: MN 7+8 (Western Europe boundaries).
Remarks: Estimated age 11.91 Ma. This age is estimated from linear interpolation between bounding magnetic reversals of the local magnetostratigraphy of the ACM section.
References: This work [SI Appendix Text 3].

Locality: Abocador de Can Mata, locality C1-E* (ACM/C1-E*).
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: Hominidae indet.
Maximum age: 12.415 Ma.
Minimum age: 12.207 Ma.
Preferred correlation to the GPTS: C5An.2n.
Local/regional correlations: *Democricetodon larteti* + *Megacricetodon ibericus* Concurrent range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN 7+8 (Western Europe boundaries).
Remarks: Estimated age 12.2-12.3 Ma. This age is estimated from linear interpolation between bounding magnetic reversals of the local magnetostratigraphy of the ACM section.
References: This work [SI Appendix Text 3].

Locality: Abocador de Can Mata, locality C3-Ae (ACM/C3-Ae).
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: *Dryopithecus fontani*.
Maximum age: 12.014 Ma.
Minimum age: 11.614 Ma.
Preferred correlation to the GPTS: C5r.3r.
Local/regional correlations: The correlation to the Vallès-Penedès zones is ambiguous.
Correlation to the MN zonation: MN 7+8 (Western Europe boundaries).
Remarks: Estimated age 11.85 Ma. This age is estimated from linear interpolation between bounding magnetic reversals of the local magnetostratigraphy of the ACM section.
References: Moyà-Solà et al., 2009a; this work [SI Appendix Text 3].

Locality: Abocador de Can Mata, locality C3-Aj (ACM/C3-Aj).
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: *Anoiapithecus brevirostris*. Type locality.
Maximum age: 12.014 Ma.
Minimum age: 11.614 Ma.
Preferred correlation to the GPTS: C5r.3r.
Local/regional correlations: *Democricetodon larteti* + *Megacricetodon ibericus* Concurrent range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN 7+8 (Western Europe boundaries).
Remarks: Estimated age 11.94 Ma. This age is estimated from linear interpolation between bounding magnetic reversals of the local magnetostratigraphy of the ACM section.
References: Moyà-Solà et al., 2009b; this work [SI Appendix Text 3].

Locality: Abocador de Can Mata, locality C3-Az (ACM/C3-Az).
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: cf. *Dryopithecus fontani*.
Maximum age: 12.014 Ma.
Minimum age: 11.614 Ma.
Preferred correlation to the GPTS: C5r.3r.
Local/regional correlations: The correlation to the Vallès-Penedès zones is ambiguous.
Correlation to the MN zonation: MN 7+8 (Western Europe boundaries).
Remarks: Estimated age 11.91 Ma. This age is estimated from linear interpolation between bounding magnetic reversals of the local magnetostratigraphy of the ACM section.
References: Moyà-Solà et al., 2009a; this work [SI Appendix Text 3].

Locality: Abocador de Can Mata, locality C4-Ap (ACM/C4-Ap).
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: Hominoidea indet.
Maximum age: 12.014 Ma.
Minimum age: 11.614 Ma.
Preferred correlation to the GPTS: C5r.3r.
Local/regional correlations: The correlation to the Vallès-Penedès zones is ambiguous.
Correlation to the MN zonation: MN 7+8 (Western Europe boundaries).
Remarks: Estimated age 11.85 Ma. This age is estimated from linear interpolation between bounding magnetic reversals of the local magnetostratigraphy of the ACM section.
References: This work [SI Appendix Text 3].

Locality: Abocador de Can Mata, locality C4-Cp (ACM/C4-Cp).
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: Hominoidea indet.
Maximum age: 12.014 Ma.
Minimum age: 11.614 Ma.
Preferred correlation to the GPTS: C5r.3r.
Local/regional correlations: *Democricetodon larteti* + *Megacricetodon ibericus* Concurrent range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN 7+8 (Western Europe boundaries).
Remarks: Estimated age 11.92 Ma. This age is estimated from linear interpolation between bounding magnetic reversals of the local magnetostratigraphy of the ACM section.
References: This work [SI Appendix Text 3].

Locality: Ahmatovska Formation.
Locality synonyms: -

Area and country: Chirpan district, Bulgaria.
Taxon: cf. *Ouranopithecus* sp.
Maximum age: 8.769? Ma.
Minimum age: 4.997? Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN11-MN13?
Remarks: The very preliminary data suggest a Turolian age for this locality.
References: Spassov & Geraads, 2008.

Locality: Baccinello *Cardium* horizon.
Locality synonyms: Baccinello F1 horizon.
Area and country: Baccinello-Cinigiano Basin, Tuscany, Italy.
Taxon: *Oreopithecus bambolii*.
Maximum age: 8.300/7.528 Ma.
Minimum age: 7.58/7.52 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: Upper portion of the Baccinello-Cinigiano basin lithostratigraphical unit B, equivalent to the V-1 mammal assemblage zone of the same basin.
Correlation to the MN zonation: MN12, the Tusco-Sardinian mammal zones have been correlated to the MN zonation (Engesser, 1989; Rook et al., 1996) and considered to be equivalent to the MN12 (V-1 zone) and to the MN12 and part of the MN13 (V-2 zone). The non-endemic assemblages V-0 and V-3 would correlate to the MN11 and to the MN13, respectively. However, it is unclear if V-1 faunas cover part of the MN11 as well or if V-2 faunas extend into the MN13. In this list the lower boundary for the MN12 is given as the maximum age for the V-1 localities, but somewhat older ages, closer to 8.5 Ma are equally likely.
Remarks: The locality is placed below a radiometrically-dated tuff layer that has given an age of 7.5±0.3 Ma (Rook et al., 2000).
References: Benvenuti et al., 1995; Rook et al., 2000.

Locality: Baccinello V-1.
Locality synonyms: -
Area and country: Baccinello-Cinigiano Basin, Tuscany, Italy.
Taxon: *Oreopithecus bambolii*.
Maximum age: 8.300/7.528 Ma.
Minimum age: 7.58/7.52 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: V-1 mammal assemblage zone of the Baccinello-Cinigiano Basin.
Correlation to the MN zonation: MN12, the Tusco-Sardinian mammal zones have been correlated to the MN zonation (Engesser, 1989; Rook et al., 1996) and considered to be equivalent to the MN12 (V-1 zone) and to the MN12 and part of the MN13 (V-2 zone). The non-endemic assemblages V-0 and V-3 would correlate to the MN11 and to the MN13, respectively. However, it is unclear if V-1 faunas cover part of the MN11 as well

or if V-2 faunas extend into the MN13. In this list the lower boundary for the MN12 is given as the maximum age for the V-1 localities, but somewhat older ages, closer to 8.5 Ma are equally likely.
Remarks: The locality occurs in coal seems underlying the lacustrine clays and marlsotnes that include the Baccinello *Cardium* horizon. Therefore, its age can be further constrained thanks to radiometric dating of a suprajacent tuff layer (see comments on locality Baccinello *Cardium* horizon).
References: Benvenuti et al., 1995; Rook et al., 1996; Rook et al., 2000.

Locality: Can Llobateres 1.
Locality synonyms: Can Llobateres.
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: *Hispanopithecus (Hispanopithecus) laietanus*.
Maximum age: 9.779 Ma.
Minimum age: 9.717 Ma.
Preferred correlation to the GPTS: C4Ar.3r.
Local/regional correlations: *Cricetulodon sabadellensis* Local range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN9.
Remarks: Estimated age 9.72 Ma. This age is estimated from linear interpolation between bounding magnetic reversals of the local magnetostratigraphy of Can Llobateres (Vallès Occidental) given in Garcés et al. (1996).
References: Agustí et al., 1996; Agustí et al., 1997; Garcés et al., 1996; this work [SI Appendix Text 3].

Locality: Can Llobateres 2.
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: *Hispanopithecus (Hispanopithecus) laietanus*.
Maximum age: 9.656 Ma.
Minimum age: 9.409 Ma.
Preferred correlation to the GPTS: C4Ar.2r.
Local/regional correlations: *Cricetulodon* + *Progonomys* Interval zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN9.
Remarks: Estimated age 9.65 Ma. This age is estimated from linear interpolation between bounding magnetic reversals of the local magnetostratigraphy of Can Llobateres (Vallès Occidental) given in Garcés et al. (1996).
References: Agustí et al., 1996; Agustí et al., 1997; Garcés et al., 1996; this work [SI Appendix Text 3].

Locality: Can Mata 1.
Locality synonyms: Bretxa de Can Mata, Hostalets Superior, Hostalets de Pierola superior.
Area and country: Vallès-Penedès Basin, Catalonia, Spain.

Taxon: Hominidae indet.
Maximum age: 11.554 Ma.
Minimum age: 11.154 Ma.
Preferred correlation to the GPTS: C5r.2r.
Local/regional correlations: *Hipparion* s.l. + *Megacricetodon ibericus* Concurrent range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN9.
Remarks: Estimated age 11.20 Ma. This age is estimated by considering sedimentation rates computed from the local stratigraphic section of ACM.
References: Moyà-Solà et al., 2009a; this work [SI Appendix Text 3].

Locality: Can Poncic (this is the official current toponym, although it is rarely employed in the paleontological literature).
Locality synonyms: Can Ponsic, Can Ponsich.
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: *Hispanopithecus (Hispanopithecus) crusafonti*. Type locality.
Maximum age: ca. 10.4 Ma.
Minimum age: 9.987 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: *Cricetulodon hartenbergeri* Local range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN9.
Remarks: -
References: Agustí et al., 1997; this work [SI Appendix Text 3].

Locality: Can Vila.
Locality synonyms: Hostalets Inferior, Hostalets de Pierola inferior.
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: ‘*Sivapithecus*’ *occidentalis* nomen dubium. Type locality.
Maximum age: ca. 12.5 Ma.
Minimum age: ca. 11.5 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN7+8 (Western Europe boundaries).
Remarks: The stratigraphic provenance of the material is uncertain given the sketchy description of the site provided in Villalta Comella & Crusafont Pairó (1941). The material was found in whitish clays (Villalta Comella & Crusafont Pairó, 1941) which presumably correspond to the lower part of the Hostalets de Pierola composite section (Moyà-Solà et al., 2009a) since the upper part is predominantly composed of red clays. The, lower part of the Hostalets de Pierola composite section correlates to the *Democricetodon crusafonti* + *Megacricetodon ibericus* Concurrent range zone of the Vallès-Penedès Basin, which would yield an age range of 13/12.8 to 11.9 Ma for the Can Vila site. However, given the uncertainty in the location of the site, younger age cannot be discarded.
References: Moyà-Solà et al., 2004; this work [SI Appendix Text 3].

Locality: Çandir locality 3.
Locality synonyms: -.
Area and country: Çankiri Basin, Central Anatolia, Turkey.
Taxon: *Griphopithecus alpani*.
Maximum age: 14.095 Ma.
Minimum age: 13.369 Ma.
Preferred correlation to the GPTS: C5ACn/C5ABn
Local/regional correlations: The close locality Çandir 2 is correlated to rodent assemblage zone F of Anatolia.
Correlation to the MN zonation: MN6 (Central Europe boundaries).
Remarks: The alternative correlation to chron C5Cn, favored by Begun et al. (2003), requires the assumption of important stratigraphical hiatuses in the Çandir magnetostratigraphical section.
References: Begun et al., 2003; De Bruijn et al., 2003; Krijgsman, 2003.

Locality: Casteani.
Locality synonyms: -
Area and country: Baccinello-Cinigiano Basin, Tuscany, Italy.
Taxon: *Oreopithecus bambolii*.
Maximum age: 8.300/7.528 Ma.
Minimum age: 7.58/7.52 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: V-1 mammal assemblage zone of the Baccinello-Cinigiano Basin.
Correlation to the MN zonation: MN12, the Tusco-Sardinian mammal zones have been correlated to the MN zonation (Engesser, 1989; Rook et al., 1996) and considered to be equivalent to the MN12 (V-1 zone) and to the MN12 and part of the MN13 (V-2 zone). The non-endemic assemblages V-0 and V-3 would correlate to the MN11 and to the MN13, respectively. However, it is unclear if V-1 faunas cover part of the MN11 as well or if V-2 faunas extend into the MN13. In this list the lower boundary for the MN12 is given as the maximum age for the V-1 localities, but somewhat older ages, closer to 8.5 Ma are equally likely. The top boundary for the V-1 zone is determined on the basis of the radiometric dating of a tuff layer interbedded within the Baccinello-Cinigiano succession (Rook et al., 2000).
Remarks: This locality corresponds to a lignite mine which is considered to be equivalent to the coal seams of Baccinello V-1.
References: Azzaroli et al., 1986; Rook et al., 1996.

Locality: Castell de Barberà.
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: cf. *Dryopithecus fontani*.
Maximum age: 11.850 Ma.
Minimum age: 11.614/11.154 Ma.
Preferred correlation to the GPTS: -

Local/regional correlations: *Democricetodon crusafonti* + *Megacricetodon ibericus* Concurrent range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN 7+8 (Western Europe boundaries).
Remarks: -
References: Agustí et al., 1997; this work [SI Appendix Text 3].

Locality: Çorakyerler.
Locality synonyms: -
Area and country: Çankiri Basin, Central Anatolia, Turkey.
Taxon: *Ouranopithecus turkae*. Type locality.
Maximum age: 8.769 Ma.
Minimum age: 7.285/7.140 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: Rodent assemblage zone J of Anatolia.
Correlation to the MN zonation: MN 11-MN12.
Remarks: The rodent fauna suggests a correlation to either zones J or K, although a correlation to zone J (and therefore to MN11) is preferred by Ünay et al. (2006). The macromammal fauna points to an MN11 age as well, but includes certain ruminants that would indicate an MN12 age (*Pliocervus* sp., *Miotragocerus valenciennesi*, *Oioceros rothi*). Accordingly, a somewhat younger age (MN12) for *O. turkae* cannot be discarded.
References: Güleç et al., 2007; Ünay et al., 2006.

Locality: Ebingen.
Locality synonyms: -
Area and country: Swabian Alps, Baden-Württemberg, Germany.
Taxon: Hominidae indet.
Maximum age: ?
Minimum age: ?
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: ?
Remarks: This locality was discovered in the earliest 20th century and primate fossils are the only material recovered, so their age cannot be determined. Nevertheless, an 'indeterminate Vallesian age' has been assigned to this site without providing any argument (Mein, 1986).
References: Mein, 1986; this work.

Locality: Engelswies.
Locality synonyms: -
Area and country: Bavarian Molasse Basin, Baden-Württemberg, Germany.
Taxon: Hominoidea indet.
Maximum age: 16.543 Ma.
Minimum age: 15.974 Ma.
Preferred correlation to the GPTS: C5Cn.1r/C5Cn.2r.

Local/regional correlations: *Keramidomys – Megacricetodon bavaricus* Concurrent range zone of the Swiss Molasse Basin.
Correlation to the MN zonation: MN5 (Central Europe boundaries).
Remarks: -
References: Böhme et al., 2008; Heizmann & Begun, 2001; this work [see main text].

Locality: Eppelsheim.
Locality synonyms: -
Area and country: Dinotheriensande Formation, Rhenish Hesse, Germany.
Taxon: Hominoidea indet.
Maximum age: 11.614/11.154 Ma.
Minimum age: 9.717 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN9.
Remarks: The primate material has not been described or figured.
References: Franzen & Storch, 1999; Franzen et al., 2003.

Locality: Estació Depuradora d'Aigües Residuals del Riu Ripoll, locality 6 (EDAR6).
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: *Hispanopithecus (Hispanopithecus) laietanus*.
Maximum age: ca. 10.4 Ma.
Minimum age: 9.987 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: *Cricetulodon hartenbergeri* Local range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN9.
Remarks: -
References: Checa Soler & Rius Font, 2003; this work [SI Appendix Text 3].

Locality: Estació Depuradora d'Aigües Residuals del Riu Ripoll, locality 8 (EDAR8).
Locality synonyms: Estació Depuradora d'Aigües Residuals del Riu Ripoll, locality 13 (EDAR13).
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: *Hispanopithecus (Hispanopithecus) laietanus*.
Maximum age: ca. 10.4 Ma.
Minimum age: 9.987 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: *Cricetulodon hartenbergeri* Local range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN9.
Remarks: -
References: Checa Soler & Rius Font, 2003; this work [SI Appendix Text 3].

Locality: Fiume Santo.
Locality synonyms: -
Area and country: Sassari, Sardinia, Italy.
Taxon: *Oreopithecus bambolii*.
Maximum age: 7.58/7.52 Ma.
Minimum age: 7.285/7.140 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: V-2 mammal assemblage zone of the Baccinello-Cinigiano Basin.
Correlation to the MN zonation: MN12, the Tusco-Sardinian mammal zones have been correlated to the MN zonation (Engesser, 1989; Rook et al., 1996) and considered to be equivalent to the MN12 (V-1 zone) and to the MN12 and part of the MN13 (V-2 zone). The non-endemic assemblages V-0 and V-3 would correlate to the MN11 and to the MN13, respectively. However, it is unclear if V-1 faunas cover part of the MN11 as well or if V-2 faunas extend into the MN13. In this list the top boundary for the MN12 is given as the minimum age for the V-2 localities, but somewhat younger ages, closer to 6.5 Ma are equally likely. The lower boundary for the V-2 zone is determined on the basis of the radiometric dating of a tuff layer interbedded within the Baccinello-Cinigiano succession (Rook et al., 2000).
Remarks: -
References: Abbazzi et al., 2008; Casanovas-Vilar et al., in press.

Locality: Götzendorf.
Locality synonyms: -
Area and country: Vienna Basin, Lower Austria, Austria.
Taxon: cf. Hominoidea indet.
Maximum age: ca. 9.9 Ma.
Minimum age: ca. 9.7 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: Mollusc zone F2 (Pannonian) of the Vienna Basin.
Correlation to the MN zonation: MN9.
Remarks: -
References: Harzhauser et al., 2004; Nargolwalla et al., 2006.

Locality: Great Trasubbie outcrop.
Locality synonyms: Trasubbie.
Area and country: Baccinello-Cinigiano Basin, Tuscany, Italy.
Taxon: *Oreopithecus bambolii*.
Maximum age: 7.58/7.52 Ma.
Minimum age: 7.285/7.140 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: V-2 mammal assemblage zone of the Baccinello-Cinigiano Basin.
Correlation to the MN zonation: MN12, the Tusco-Sardinian mammal zones have been correlated to the MN zonation (Engesser, 1989; Rook et al., 1996) and considered to be equivalent to the MN12 (V-1 zone) and to the MN12 and part of the MN13 (V-2 zone).

The non-endemic assemblages V-0 and V-3 would correlate to the MN11 and to the MN13, respectively. However, it is unclear if V-1 faunas cover part of the MN11 as well or if V-2 faunas extend into the MN13. In this list the top boundary for the MN12 is given as the minimum age for the V-2 localities, but somewhat younger ages, closer to 6.5 Ma are equally likely. The lower boundary for the V-2 zone is determined on the basis of the radiometric dating of a tuff layer interbedded within the Baccinello-Cinigiano succession (Rook et al., 2000).
Remarks: -
References: Engesser, 1989; Rook et al., 1996.

Locality: Hostalets de Pierola.
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: Hominoidea indet.
Maximum age: ca. 12.5 Ma.
Minimum age: ca. 9.7 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN7+8-MN9 (Western Europe boundaries).
Remarks: The stratigraphic provenance of the material is unknown. Age ranges refer to the whole range of the Hostalets de Pierola composite section.
References: Van der Made & Ribot, 1999; this work [SI Appendix Text 3].

Locality: Klein Hadersdorf.
Locality synonyms: -
Area and country: Vienna Basin, Lower Austria, Austria.
Taxon: *Griphopithecus suessi*.
Maximum age: 11.614 Ma.
Minimum age: 11.118 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: MMi9/MMi13 planktonik foraminifera zones, MNN6/MNN7 calcareous nannoplankton zones.
Correlation to the MN zonation: MN7+8 (Central Europe boundaries).
Remarks: The locality is placed in the same transitional facies that Neudorf-Sandberg (Slovakia).
References: Rabeder & Steininger, 1975; Steininger, 1986.

Locality: La Grive Saint-Alban M.
Locality synonyms: La Grive M, La Grive.
Area and country: Isère, France.
Taxon: *Dryopithecus fontani*.
Maximum age: 13.015/12.765 Ma.
Minimum age: 11.850 Ma.
Preferred correlation to the GPTS: -

Local/regional correlations: *Democricetodon larteti* + *Megacricetodon ibericus* Concurrent range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN7+8 (Western Europe boundaries).
Remarks: The exact provenance of the hominoid specimen (an isolated upper incisor) is not surely known, and the attribution of the fossil to a particular fissure considers the presence of particular features (such as patinas or the color of the sediment) that allow a tentative assignment. This incisor was discovered in the old collections of the Museum of Basel (Andrews et al., 1996) and on the basis of the presence of a grey patina it was assigned to La Grive Saint Alban L3 as well (Mein, 1986). However, P. Mein (pers. com.) had not seen the specimen by that time, and nowadays, on the basis of the occurrence of a red (not grey) patina in the incisor considers that it cannot belong to fissure L3, since red patinas only occur in fissures M and Peyre et Beau. Recently, without providing any additional argument the material has been assigned to fissure M (Begun, 2002), which is somewhat older than L3. Further details on the provenance of the material can be known on the basis of the collecting year. L. Costeur (Museum of Basel, pers. com.) kindly provided the information written in the label of the specimen: ‘La Grive Saint Alban -1905 – Ogiez’. This does not give further details on its provenance but tells us that the specimen was collected or donated to the Museum of Basel by Ogiez in 1905. The excavations at fissure Peyre et Beau concluded in 1894, when the fissure was emptied, so according to the excavation year and considering the occurrence of a red patina we tentatively assign this material to La Grive Saint-Alban M.
References: Mein & Ginsburg, 2002; this work.

Locality: La Grive Saint-Alban L3/La Grive Saint-Alban L5?
Locality synonyms: La Grive L3/La Grive L5.
Area and country: Isère, France.
Taxon: *Dryopithecus fontani*.
Maximum age: 11.850 Ma.
Minimum age: 11.614/11.154 Ma
Preferred correlation to the GPTS: -
Local/regional correlations: *Democricetodon crusafonti* + *Megacricetodon ibericus* Concurrent range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN7+8 (Western Europe boundaries).
Remarks: The exact provenance of the hominoid specimen (an isolated upper third molar) is not surely known, and the attribution of the fossil to a particular fissure considers the presence of particular features (such as patinas or the color of the sediment) that allow a tentative assignment. The upper third molar shows a grey patina that according to Mein (1986) would indicate that it belongs to La Grive Saint-Alban L3. However, Mein (pers. com.) considered that it could well belong to fissure L5. Both fissures are correlated to the *Democricetodon crusafonti* + *Megacricetodon ibericus* Concurrent range zone of the Vallès-Penedès Basin.
References: Mein & Ginsburg, 2002; this work.

Locality: La Tarumba 1.
Locality synonyms: -

Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: *Hispanopithecus (Hispanopithecus) laietanus*. Type locality.
Maximum age: 9.656 Ma.
Minimum age: 9.409 Ma.
Preferred correlation to the GPTS: C4Ar.2r.
Local/regional correlations: *Cricetulodon* + *Progonomys* Interval zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN9.
Remarks: Estimated age 9.50 Ma. This age is estimated from linear interpolation between bounding magnetic reversals of the local magnetostratigraphy of La Tarumba (Vallès Occidental) given in Garcés et al. (1996).
References: Garcés et al., 1996; Agustí et al., 1997; this work [SI Appendix Text 3].

Locality: Lower Sinap Member (unknown locality).
Locality synonyms: -
Area and country: Sinap Formation, Central Anatolia, Turkey.
Taxon: Hominoidea indet.
Maximum age: ca. 14.8 Ma.
Minimum age: ca. 11.1 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN6-MN7+8 (Central Europe boundaries).
Remarks: The exact provenance of the material is unknown. This site has been correlated to Inönü, another Sinap locality with an estimated age of 15 Ma (Kappelman et al., 2003a). Such correlation is based on the presence of the suid *Listriodon splendens* associated to the primate find. *L. splendens* is only recorded at Inönü in the whole Sinap series, but this taxon has a very long range, from MN6 to MN9, so it does not provide any additional information. The age range provided here takes into account the whole temporal range of the Lower Sinap Member.
References: Kappelman et al., 2003a.

Locality: Mariathal.
Locality synonyms: -
Area and country: Molasse Basin, Lower Austria, Austria.
Taxon: Hominidae indet.
Maximum age: ca. 11.2 Ma.
Minimum age: ca. 10.4 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: Mollusc zone C/D (Pannonian) of the Vienna Basin.
Correlation to the MN zonation: MN9.
Remarks: -
References: Nargolwalla et al., 2006; Steininger, 1986.

Locality: Melchingen.
Locality synonyms: -

Area and country: Swabian Alps, Baden-Württemberg, Germany.
Taxon: Hominidae indet.
Maximum age: 11.614/11.154 Ma.
Minimum age: 8.300/7.528 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN9-MN11.
Remarks: The locality is a carstic filling which includes a fauna mixing Vallesian and early Turolian elements. This site has been to the MN9 without providing further arguments (Mein, 1986).
References: Mein, 1986.

Locality: Monte Bamboli.
Locality synonyms: -
Area and country: Monte Bamboli Basin, Tuscany, Italy.
Taxon: *Oreopithecus bambolii*. Type locality.
Maximum age: 7.58/7.52 Ma.
Minimum age: 7.285/7.140 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: V-2 mammal assemblage zone of the Baccinello-Cinigiano Basin.
Correlation to the MN zonation: MN12, the Tusco-Sardinian mammal zones have been correlated to the MN zonation (Engesser, 1989; Rook et al., 1996) and considered to be equivalent to the MN12 (V-1 zone) and to the MN12 and part of the MN13 (V-2 zone). The non-endemic assemblages V-0 and V-3 would correlate to the MN11 and to the MN13, respectively. However, it is unclear if V-1 faunas cover part of the MN11 as well or if V-2 faunas extend into the MN13. In this list the top boundary for the MN12 is given as the minimum age for the V-2 localities, but somewhat younger ages, closer to 6.5 Ma are equally likely. The lower boundary for the V-2 zone is determined on the basis of the radiometric dating of a tuff layer interbedded within the Baccinello-Cinigiano succession (Rook et al., 2000).
Remarks: The exact stratigraphic provenance of the fossils is unknown and because many lignite layers occur in the sequence of Monte Bamboli it is not unlikely that the fossils come from different layers. However, the fauna recovered fully agrees with a correlation to V-2 zone.
References: Engesser, 1989; Rook et al., 1996.

Locality: Montemassi.
Locality synonyms: -
Area and country: Baccinello-Cinigiano Basin, Tuscany, Italy.
Taxon: *Oreopithecus bambolii*.
Maximum age: 8.300/7.528 Ma.
Minimum age: 7.58/7.52 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: V-1 mammal assemblage zone of the Baccinello-Cinigiano Basin.

Correlation to the MN zonation: MN12, the Tusco-Sardinian mammal zones have been correlated to the MN zonation (Engesser, 1989; Rook et al., 1996) and considered to be equivalent to the MN12 (V-1 zone) and to the MN12 and part of the MN13 (V-2 zone). The non-endemic assemblages V-0 and V-3 would correlate to the MN11 and to the MN13, respectively. However, it is unclear if V-1 faunas cover part of the MN11 as well or if V-2 faunas extend into the MN13. In this list the lower boundary for the MN12 is given as the maximum age for the V-1 localities, but somewhat older ages, closer to 8.5 Ma are equally likely.
Remarks: This locality corresponds to a lignite mine which is considered to be equivalent to the coal seams of Baccinello V-1.
References: Azzaroli et al., 1986; Rook et al., 1996.

Locality: Nikiti 1.
Locality synonyms: -
Area and country: Chalkidiki Peninsula, Macedonia, Greece.
Taxon: *Ouranopithecus macedoniensis*.
Maximum age: ca. 9.717 Ma.
Minimum age: ca. 8.769 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN10.
Remarks: The occurrence of some Turolian faunal elements may indicate an age closer to MN11.
References: Koufos, 2006.

Locality: Paşalar.
Locality synonyms: -
Area and country: Gönen Basin, Anatolia, Turkey.
Taxon: *Griphopithecus alpani*.
Maximum age: 14.877 Ma.
Minimum age: 13.734 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: Rodent assemblage zone F of Anatolia.
Correlation to the MN zonation: MN6 (Central Europe boundaries).
Remarks: The macromammal fauna suggests that Paşalar is close in age to Çandir but slightly older (Bernor & Tobien, 1990).
References: Bernor & Tobien, 1990; Pélaez-Campomanes & Daams, 2002; Ünay et al., 2003.

Locality: Paşalar gray sand unit.
Locality synonyms: -
Area and country: Gönen Basin, Anatolia, Turkey.
Taxon: *Kenyapithecus kizili*. Type locality.
Maximum age: 14.877 Ma.
Minimum age: 13.734 Ma.

Preferred correlation to the GPTS: -
Local/regional correlations: Rodent assemblage zone F of Anatolia.
Correlation to the MN zonation: MN6 (Central Europe boundaries).
Remarks: The macromammal fauna suggests that Paşalar is close in age to Çandir but slightly older (Bernor & Tobien, 1990).
References: Bernor & Tobien, 1990; Pélaez-Campomanes & Daams, 2002; Ünay et al., 2003.

Locality: Podere la Crocina.
Locality synonyms: La Crocina, Podere Santa Croce, Baccinello V-2.
Area and country: Baccinello-Cinigiano Basin, Tuscany, Italy.
Taxon: *Oreopithecus bambolii*.
Maximum age: 7.58/7.52 Ma.
Minimum age: 7.285/7.140 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: V-2 mammal assemblage zone of the Baccinello-Cinigiano Basin.
Correlation to the MN zonation: MN12, the Tusco-Sardinian mammal zones have been correlated to the MN zonation (Engesser, 1989; Rook et al., 1996) and considered to be equivalent to the MN12 (V-1 zone) and to the MN12 and part of the MN13 (V-2 zone). The non-endemic assemblages V-0 and V-3 would correlate to the MN11 and to the MN13, respectively. However, it is unclear if V-1 faunas cover part of the MN11 as well or if V-2 faunas extend into the MN13. In this list the top boundary for the MN12 is given as the minimum age for the V-2 localities, but somewhat younger ages, closer to 6.5 Ma are equally likely. The lower boundary for the V-2 zone is determined on the basis of the radiometric dating of a tuff layer interbedded within the Baccinello-Cinigiano succession (Rook et al., 2000).
Remarks: The locality is placed above a radiometrically-dated tuff layer that has given an age of 7.5±0.3 Ma (Rook et al., 2000).
References: Benvenuti et al., 1995; Rook et al., 1996; Rook et al., 2000.

Locality: Polinyà 2.
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: *Hispanopithecus (Hispanopithecus) laietanus*.
Maximum age: 11.614/11.154 Ma.
Minimum age: 9.717 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN9.
Remarks: -
References: Crusafont & Golpe-Posse, 1972.

Locality: Pyrgos Vassilissis.
Locality synonyms: Pyrgos Tour la Reine.

Area and country: Attica, Greece.
Taxon: *Graecopithecus freybergi* nomen vanum. Type locality.
Maximum age: 8.769? Ma.
Minimum age: 7.285/7.140? Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN11-MN12.
Remarks: The mammal fauna is quite fragmentary, however the presence of some Turolian macromammal taxa (*Tragoportax amalthea*, *Gazella deperdita*) may indicate an MN11-MN12 age.
References: Koufos, 2006.

Locality: Ravin de la Pluie.
Locality synonyms: -
Area and country: Axios Valley, Macedonia, Greece.
Taxon: *Ouranopithecus macedoniensis*. Type locality.
Maximum age: 9.409 Ma.
Minimum age: 9.312 Ma.
Preferred correlation to the GPTS: C4Ar.1n.
Local/regional correlations: -
Correlation to the MN zonation: MN10.
Remarks: The magnetostratigraphic sections of the Axios Valley are very short, so the correlation to the GPTS has to be taken with some caution.
References: Koufos, 2006; Sen et al., 2000.

Locality: Ribolla.
Locality synonyms: -
Area and country: Baccinello-Cinigiano Basin, Tuscany, Italy.
Taxon: *Oreopithecus bambolii*.
Maximum age: 8.300/7.528 Ma.
Minimum age: 7.58/7.52 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: V-1 mammal assemblage zone of the Baccinello-Cinigiano Basin.
Correlation to the MN zonation: MN12, the Tusco-Sardinian mammal zones have been correlated to the MN zonation (Engesser, 1989; Rook et al., 1996) and considered to be equivalent to the MN12 (V-1 zone) and to the MN12 and part of the MN13 (V-2 zone). The non-endemic assemblages V-0 and V-3 would correlate to the MN11 and to the MN13, respectively. However, it is unclear if V-1 faunas cover part of the MN11 as well or if V-2 faunas extend into the MN13. In this list the lower boundary for the MN12 is given as the maximum age for the V-1 localities, but somewhat older ages, closer to 8.5 Ma are equally likely.
Remarks: This locality corresponds to a lignite mine which is considered to be equivalent to the coal seams of Baccinello V-1.
References: Azzaroli et al., 1986; Rook et al., 1996.

Locality: Rudabánya 2.
Locality synonyms: -
Area and country: Pannonian Basin, NE Hungary.
Taxon: *Hispanopithecus* (*Rudapithecus*) *hungaricus*. Type locality.
Maximum age: ca. 11.5 Ma.
Minimum age: 9.717 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN9.
Remarks: Constraints on the maximum age of the site are provided by a distantly underlying tuff layer that has been radiometrically dated at ca. 11.5 Ma (Balogh, 1984). This tuff layer does not occur in the same section but can be easily correlated to the Rudabánya 2 section by the means of lithostratigraphy. The occurrence of *Hippotherium intrans*, may indicate that this locality is closer to 10-9.7 Ma (Bernor et al., 2003, 2004).
References: Bernor et al., 2003, 2004.

Locality: Saint Gaudens.
Locality synonyms: -
Area and country: Haute-Garonne, France.
Taxon: *Dryopithecus fontani*. Type locality.
Maximum age: 13.015/12.765 Ma.
Minimum age: 11.614/11.154 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN7+8 (Western Europe boundaries).
Remarks: -
References: Mein, 1986.

Locality: Salmendingen.
Locality synonyms: -
Area and country: Swabian Alps, Baden-Württemberg, Germany.
Taxon: *Neopithecus brancoi* nomen dubium. Type locality.
Maximum age: 11.614/11.154? Ma.
Minimum age: 8.300/7.528? Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN9-MN11.
Remarks: Mein (1986) remarks that the site includes mostly Vallesian taxa, but on basis of the presence of the beaver *Dipoides*, which is not recorded in Europe until the Turolian, assigns and MN11 age to this site. In our opinion Salmendingen may represent a mixed fauna as observed in other carstic sites of the Swabian Alps (Melchingen, Ebingen, Trochtelfingen).
References: Mein, 1986; this work.

Locality: Sant Quirze.
Locality synonyms: Sant Quirze del Vallès, Sant Quirze de Galliners, Trinxera Ferrocarril Sant Quirze
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: Hominidae indet.
Maximum age: 11.850 Ma.
Minimum age: 11.614/11.154 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: *Democricetodon crusafonti* + *Megacricetodon ibericus* Concurrent range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN 7+8 (Western Europe boundaries).
Remarks: -
References: Agustí et al., 1997; this work [SI Appendix Text 3].

Locality: Santiga.
Locality synonyms: -
Area and country: Vallès-Penedès Basin, Catalonia, Spain.
Taxon: *Hispanopithecus (Hispanopithecus) laietanus*.
Maximum age: ca. 10.4 Ma.
Minimum age: 9.987 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: *Cricetulodon hartenbergeri* Local range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN9.
Remarks: -
References: this work [SI Appendix Text 3].

Locality: Serrazzano.
Locality synonyms: -
Area and country: Val di Cecina Basin, Tuscany, Italy.
Taxon: *Oreopithecus bambolii*.
Maximum age: 8.300/7.528 Ma.
Minimum age: 7.58/7.52 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: V-1 mammal assemblage zone of the Baccinello-Cinigiano Basin.
Correlation to the MN zonation: MN12, the Tusco-Sardinian mammal zones have been correlated to the MN zonation (Engesser, 1989; Rook et al., 1996) and considered to be equivalent to the MN12 (V-1 zone) and to the MN12 and part of the MN13 (V-2 zone). The non-endemic assemblages V-0 and V-3 would correlate to the MN11 and to the MN13, respectively. However, it is unclear if V-1 faunas cover part of the MN11 as well or if V-2 faunas extend into the MN13. In this list the lower boundary for the MN12 is given as the maximum age for the V-1 localities, but somewhat older ages, closer to 8.5 Ma are equally likely.
Remarks: This locality corresponds to a lignite mine which is considered to be equivalent to the coal seams of Baccinello V-1.

References: Azzaroli et al., 1986; Rook et al., 1996.

Locality: Sinap locality 8A.
Locality synonyms: -
Area and country: Sinap Formation, Central Anatolia, Turkey.
Taxon: *Ankarapithecus meteai*. Type locality.
Maximum age: 9.987 Ma.
Minimum age: 9.934 Ma.
Preferred correlation to the GPTS: C5n.1r
Local/regional correlations: Rodent assemblage zone I of Anatolia.
Correlation to the MN zonation: MN9.
Remarks: -
References: Kappelman et al., 2003a, 2003b; Ünay et al., 2003.

Locality: Sinap locality 12.
Locality synonyms: -
Area and country: Sinap Formation, Central Anatolia, Turkey.
Taxon: *Ankarapithecus meteai*.
Maximum age: 9.934 Ma.
Minimum age: 9.9717 Ma.
Preferred correlation to the GPTS: C5n.1n/C4Ar.2n.
Local/regional correlations: -
Correlation to the MN zonation: MN9/MN10.
Remarks: -
References: Kappelman et al., 2003a, 2003b.

Locality: St. Stefan im Lavanttal.
Locality synonyms: -
Area and country: Gratkorn Basin, Carinthia, Austria.
Taxon: *Dryopithecus fontani*.
Maximum age: ca. 12.2 Ma.
Minimum age: ca. 12 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: Upper *Ervilia* Zone (Late Sarmatian) of the terrestrial mollusks zones of the Styrian Basin.
Correlation to the MN zonation: MN7+8 (Central Europe boundaries).
Remarks: This is the type locality of *Dryopithecus fontani carinthiacus*, which is here synonymized with *Dryopithecus fontani* (see SI Appendix Text 1).
References: Daxner-Höck, 2010; Harzhauser et al., 2008.

Locality: Teuleria del Firal.
Locality synonyms: El Firal, Seu d'Urgell.
Area and country: Seu d'Urgell Basin, Catalonia, Spain.
Taxon: *Hispanopithecus (Hispanopithecus) crusafonti*.
Maximum age: ca. 10.4 Ma.

Minimum age: 9.987 Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: *Cricetulodon hartenbergeri* Local range zone of the Vallès-Penedès Basin.
Correlation to the MN zonation: MN9.
Remarks: This locality is included within the Ballestar lithostratigraphical unit. Even though Teuleria del Firal has not delivered micrommals two localities (Ballestar, Can Petit) of the Ballestar unit have provided a somewhat scarce micromammal fauna that allow a correlation to the *Cricetulodon hartenbergeri* Local range zone of the Vallès-Penedès Basin.
References: Agustí et al., 1979, 1984; this work [SI Appendix Text 3].

Locality: Trochtelfingen.
Locality synonyms: -
Area and country: Swabian Alps, Baden-Württemberg, Germany.
Taxon: Hominidae indet.
Maximum age: ?
Minimum age: ?
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: ?
Remarks: This locality was discovered in the 19th century and primate fossils are the only material recovered, so their age cannot be determined. Nevertheless, an 'indeterminate Vallesian age' has been assigned to this site without providing any argument (Mein, 1986).
References: Mein, 1986; this work.

Locality: Udabno 1.
Locality synonyms: -
Area and country: Shiraki Formation, Gare-Kaxheti, Georgia.
Taxon: ?*Udabnopithecus garedziensis*.
Maximum age: 9.098 Ma.
Minimum age: 8.769 Ma.
Preferred correlation to the GPTS: C4.An.
Local/regional correlations: Rodent assemblage zone I of Anatolia.
Correlation to the MN zonation: MN10.
Remarks: The primate find is reported from about 40 m above Udabno 1, which has a normal polarity and is clearly below Udabno 2 which has a reverse polarity and has been correlated to chron C4r.2r (Vangenheim et al., 1989; Sen, 1997). Accordingly, Udabno 1 would be correlated to chron C4.An, corresponding to the late Vallesian. The mammal fauna suggests a late Vallesian age (MN10) for the site (Gabunia et al., 2001) and agrees with this correlation.
References: Gabunia et al., 2001; Lordkipanitze et al., 2008; Sen, 1997;Vangenheim et al., 1989.

Locality: Wissberg.
Locality synonyms: -
Area and country: Dinotheriensande Formation, Rhenish Hesse, Germany.
Taxon: Hominidae indet.
Maximum age: 13.734? Ma.
Minimum age: 8.300/7.528? Ma.
Preferred correlation to the GPTS: -
Local/regional correlations: -
Correlation to the MN zonation: MN7+8-MN11? (Central Europe boundaries).
Remarks: The fauna represents a mixture of predominantly Vallesian taxa with Astaracian (*Prodeinotherium bavaricum*, *Anchitherium aurelianense*) and Turolian elements (cf. *Mesopithecus pentelicus*).
References: Franzen & Storch, 1999.

Locality: Xirochori 1.
Locality synonyms: -
Area and country: Axios Valley, Macedonia, Greece.
Taxon: *Ouranopithecus macedoniensis*.
Maximum age: 9.717 Ma.
Minimum age: 9.656 Ma.
Preferred correlation to the GPTS: C4Ar.2n.
Local/regional correlations: -
Correlation to the MN zonation: MN10.
Remarks: The magnetostratigraphical sections of the Axios Valley are very short, so the correlation to the GPTS has to be taken with some caution.
References: Koufos, 2006; Sen et al., 2000.

References

Abbazzi L, Delfino M, Gallai G, Trebini L, Rook L (2008) New data on the vertebrate assemblage of Fiume Santo (North-West Sardinia, Italy), and overview on the Late Miocene Tusco-Sardinian palaeobioprovince. *Palaeontology* 51:425–451.

Agustí J, Gibert J, Moyà-Solà S, Cabrera L (1979) Rodents and insectivores (Mammalia) from the Late Miocene of la Seu d'Urgell (Catalonia, Spain). *Acta Geol Hisp* 14:362–369. [in Spanish]

Agustí J, Moyà-Solà S., Gibert J (1984) Mammal distribution dynamics in the eastern margin of the Iberian Peninsula during the Miocene. *Paléobiol Cont* 14:33–46.

Agustí J, et al. (1996) Can Llobateres: the pattern and timing of the Vallesian hominoid radiation reconsidered. *J Hum Evol* 31:143–155.

Agustí J, Cabrera L, Garcés M, Parés JM (1997) The Vallesian mammal succession in the Vallès-Penedès basin (northeast Spain): paleomagnetic calibration and correlation with global events. *Palaeogeogr Palaeoclimatol Palaeoecol* 133:149–180.

Agustí J, et al. (2001) A calibrated mammal scale for the Neogene of Western Europe. State of the art. *Earth Sci Rev* 52, 247–260.

Andrews P, et al. (1996) in *The Evolution of Western Eurasian Neogene Mammal Faunas*, eds Bernor RL, Fahlbusch V, Mittmann H-W (Columbia University Press, New York), pp 168–207.

Azzaroli A, Boccateli M, Delson E, Moratti G, Torre D (1986) Chronological and paleogeographical background to the study of *Oreopithecus bambolii*. *J Hum Evol* 15:533–540.

Balogh K (1984) *Methods and results of K/Ar method in Hungary*. Unpublished PhD thesis Kossuth University Debrecen (Hungary).

Begun DR (2002) in *The Primate Fossil Record*, ed Hartwig WC (Cambridge University Press, Cambridge), pp 339–368.

Begun DR, Güleç E, Geraads D (2003) The Çandir hominoid locality: implications for the timing and pattern of hominoid dispersal events. *Cour Forsch-Inst Senckenberg* 240:240–265.

Benvenuti M, Bertini A, Rook L, (1995). Facies analysis, vertebrate paleontology and palynology in the Late Miocene Baccinello-Cinigiano basin (southern Tuscany). *Mem Soc Geol Ital* 48:415–423.

Bernor RL, Tobien H (1990) The mammalian geochronology and biogeography of Paşalar, Turkey. *J Hum Evol* 19:551–568.

Bernor RL, Armour-Chelu M, Kaiser TM, Scott RS (2003) An evaluation of the late MN9 (Late Miocene, Vallesian age), Hipparion assemblage from Rudabánya (Hungary): systematic background, functional anatomy and paleoecology. *Col-Pa* vol ext 1:35–45.

Bernor RL, et al. (2004) Recent advances on multidisciplinary research at Rudabánya, Late Miocene (MN9), Hungary: a compendium. *Palaeontogr Ital* 89: 3–36.

Böhme M, Abdul Aziz H, Prieto J, Bachtadse V (2008) in *Giornate de Paleontologia VIII edizione – Simposio della Società Paleotnologica Italiana*, eds Mazzei R, Fondi R, Foresi L, Riforgiato F, Verducci M, pp 120–121.

Casanovas-Vilar I, et al. (2008) Biochronological, taphonomical and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae). *J Hum Evol* 55:589–603.

Casanovas-Vilar I, Van Dam JA, Trebini L, Rook L (in press) The rodents from the Late Miocene *Oreopithecus*-bearing site of Fiume Santo (Sardinia, Italy). *Geobios*.

Checa Soler L, Rius Font L (2003) Paleontological intervention at EDAR Sabadell-Riu Ripoll (Can Llobateres, Sabadell, Vallès Occidental). *Tribuna d'Arqueologia* 1999-2000:7–22 [in Catalan]

Crusafont M, Golpe-Posse JM (1972) Some new early Vallesian vertebrate sites from Sabadell surroundings. *Acta Geol Hisp* 7:69-70. [in Spanish]

Daxner-Höck, G (2010) Sciuridae, Gliridae and Eomyidae (Rodentia, Mammalia) from the Middle Miocene of St. Stefan in the Gratkorn Basin (Styria, Austria). *Ann Naturhist Mus Wien A* 112: 507–536.

De Bruijn H, et al. (2003) Rodents, lagomorphs and insectivores from the middle Miocene hominoid locality of Çandir (Turkey). *Cour Forsch-Inst Senckenberg* 240:51–87.

Delson E (1987) An anthropoid enigma: historical introduction to the study of *Oreopithecus bambolii*. *J Hum Evol* 15:523–531.

Engesser B (1989) The Late Tertiary small mammals of the Maremma region (Tuscany, Italy). 2nd part: Muridae and Cricetidae (Rodentia, Mammalia). *Bol Soc Paleontol I* 28:227–252.

Franzen JL, Storch G (1999) in *Hominoid Evolution and Environmental Change in the Neogene of Europe. Volume 1: The Evolution of Terrestrial Ecosystems in Europe*, eds Agustí J, Rook L, Andrews P (Cambridge University Press, Cambridge, UK), pp 165–190.

Franzen JL, Fejfar O, Storch G, Wilde V (2003) Eppelsheim 2000 – new discoveries at a classic locality. *Deinsea* 10:217–234.

Gabunia L, Gabashvili E, Vekua A, Lordkipanidze D (2001) in *Hominoid Evolution and Environmental Change in the Neogene of Europe. Volume 2: Phylogeny of the Neogene Hominoid Primates of Eurasia*, eds De Bonis L, Koufos G, Andrews P (Cambridge University Press, Cambridge, UK), pp 316–325.

Garcés M, Agustí J, Cabrera L, Parés JM (1996) Magnetostratigraphy of the Vallesian (late Miocene) in the Vallès-Penedès basin (northeast Spain). *Earth Planet Sci Lett* 142:381–396.

Güleç ES, Sevim A, Pehlevan C, Kaya F (2007) A new great ape from the late Miocene of Turkey. *Anthropol Sci* 115:153–158.

Harzhauser M, Daxner-Höck G, Piller WE (2004) An integrated stratigraphy of the Pannonian (Late Miocene) in the Vienna Basin. *Austrian Journal of Earth Sciences* 95/96:6–19.

Harzhauser M, Gross M, Binder H (2008) Biostratigraphy of Middle Miocene (Sarmatian) wetland systems in an Eastern Alpine intramontane basin (Gratkorn Basin, Austria): the terrestrial gastropod approach. *Geol Carpath* 59:45–58.

Heizmann EPJ, Begun DR (2001). The oldest Eurasian hominoid. *J Hum Evol* 41:463–481.

Kälin D, Kempf O (2009) High-resolution stratigraphy from the continental record of the Middle Miocene Northern Alpine Foreland basin of Switzerland. *N Jb Geol Paläont Abh* 254:177–235.

Kappelman J et al. (2003a) in *Geology and Paleontology of the Miocene Sinap Formation, Turkey*, eds Fortelius M, Kappelman, J, Sen S, Bernor RL (Columbia University Press, New York), pp 90–124.

Kappelman J, et al. (2003b) in *Geology and Paleontology of the Miocene Sinap Formation, Turkey*, eds Fortelius M, Kappelman, J, Sen S, Bernor RL (Columbia University Press, New York), pp 41–66.

Koufos GD (2006) The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. *Hell J Geosc* 41:183–214.

Krijgsman W (2003) Magnetostratigraphic dating of the Çandir fossil locality (middle Miocene, Turkey). *Cour Forsch-Inst Senckenberg* 240:41–49.

Lordkipanitze D, Vekua A, Agustí J, Oms O (2008) in *Giornate de Paleontologia VIII edizione – Simposio della Società Paleotnologica Italiana*, eds Mazzei R, Fondi R, Foresi L, Riforgiato F, Verducci M, pp 132.

Lungu AN (1974) The fauna with *Hipparion* of the middle Sarmatian from Moldova and its stratigraphic value. *Mem Bur Rech Géol Min (France)* 78:203–206. [in French]

Mein P (1986) in *Primate Evolution*, eds Else JG, Lee PC (Cambridge University Press, Cambridge, UK), pp 58–70.

Mein P, Ginsburg L (2002) On the relative age of the different Miocene carstic deposits from La Grive-Saint Alban (Isère). *Cah Sci Mus Hist Nat Lyon* 2/2002: 7–47. [in French]

Moyà-Solà S, et al. (2004) *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. *Science* 306:1339–1344.

Moyà-Solà S, et al. (2009a) First partial face and upper dentition of the Middle Miocene hominoid *Dryopithecus fontani* from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, NE Spain): taxonomic and phylogenetic implications. *Am J Phys Anthropol* 139: 26–145.

Moyà-Solà S, et al. (2009b) A unique Middle Miocene European hominoid and the origins of the great ape and human clade. *Proc Natl Acad Sci USA* 106:9601-9606.

Nargolwalla N, Hutxhison MP, Begun DR (2006) Middle and Late Miocene terrestrial vertebrate localities in the Pannonian Basin. *Beitr Paläont* 30:347–360.

Ogg JG, Smith AG (2004) in *A Geologic Time Scale 2004*, eds Gradstein FM, Ogg JG, Smith AG (Cambridge University Press, Cambridge, UK), pp 63–87.

Peláez-Campomanes P, Daams R (2002) Middle Miocene rodents from Paşalar, Anatolia, Turkey. *Acta Palaeontol Pol* 47:125–132.

Rabeder G, Steininger F (1975) in *VI Congress of the Regional Committee of Mediterranean Neogene Stratigraphy Proceedings 1*, ed Sénes J, pp 177–183.

Rook L, Harrison T, Engesser B (1996) The taxonomic status and biochronological implications of new finds of *Oreopithecus* from Baccinello (Tuscany, Italy). *J Hum Evol* 30:3–27.

Rook L, Renne P, Benvenuti M, Papini M (2000) Geochronology of *Oreopithecus*-bearing succession at Baccinello (Italy) and the extinction pattern of European Miocene hominoids. *J Hum Evol* 39:577–582.

Sen S (1997) Magnetostratigraphic calibration of the European Neogene mammal chronology. *Palaeogeogr Palaeoclimatol Palaeoecol* 133:181–204.

Sen S, Koufos GD, Kondopoulou D, de Bonis L (2000) Magnetostratigraphy of the Late Miocene continental deposits of the Lower Axios valley, Macedonia, Greece. *Bull Geol Soc Greece* sp pbl 9:197–206.

Spassov N, Geraads D (2008) The latest prehumans of Europe: discovery of a late Miocene hominoid in Bulgaria of about 7 Ma. *Bulgarian Academy of Sciences News* 54:2–4.

Steininger F (1986) in *Primate Evolution*, eds Else JG, Lee PC (Cambridge University Press, Cambridge, UK), pp 71–84.

Szalay FS, Delson E (1979) *Evolutionary History of the Primates* (Academic Press, San Diego).

Ünay E, De Bruijn H, Saraç G (2003) A preliminary zonation of the continental Neogene of Anatolia based on rodents. *Deinsea* 10:539–547.

Ünay E, De Bruijn H, Suata-Alpaslan F (2006) Rodents from the Upper Miocene hominoid locality Çorakyerler (Anatolia). *Beitr Paläont* 30:453–467.

Van der Made J, Ribot F (1999) Additional hominoid material from the Miocene of Spain and remarks on hominoid dispersals into Europe. *Contr Tert Quatern Geol* 36:25–39.

Vangenheim EA, Gabunia LK, Pevzner Ma, Tsiskarishvili GV (1989) The stratigraphic position of the *Hipparion* fauna sites of Transcaucasia in the light of magnetostratigraphy. *Int Geol Rev* 31: 914–921.

Villalta Comella JF de, Crusafont Pairó M (1941) Find of *Dryopithecus fontani*, Lartet, in the Vindobonian of the Vallès-Penedès Basin. *Bol Inst Geol Min Esp* 20:1–15. [in Spanish]

Chapter 5. New craniodental remains of *Trocharion albanense* Major, 1903 (Carnivora, Mustelidae), from the Vallès-Penedès Basin (Middle to Late Miocene, Barcelona, Spain)

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ARTICLE

NEW CRANIODENTAL REMAINS OF *TROCHARION ALBANENSE* MAJOR, 1903 (CARNIVORA, MUSTELIDAE), FROM THE VALLÈS-PENEDÈS BASIN (MIDDLE TO LATE MIOCENE, BARCELONA, SPAIN)

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ABSTRACT—Cranial and dentognathic remains of *Trocharion albanense* (Carnivora, Mustelidae, Leptarctinae) from the Vallès-Penedès Basin (Barcelona, Spain), ranging from the middle to the late Miocene, are described. Most of the newly described material comes from several sites of the Abocador de Can Mata (ACM) section (in the municipal term of els Hostalets de Pierola), but remains from other Catalan localities (Sant Quirze, Castell de Barberà, and Can Llobateres) are also described. The material from ACM includes two partial crania and several mandibles. This enables description of several aspects of craniodental morphology previously unknown for this taxon, such as the presence of first upper premolars, as well as the presence of a conspicuous and rhomboid double temporal crest. Accordingly, an emended diagnosis of the genus *Trocharion* is provided, together with a differential diagnosis with respect to other leptarctine genera. A cladistic analysis based on craniodental features is consistent with *Trocharion* being the basalmost member of the Leptarctinae, and suggests that the carnassial notch (still present in this taxon) was independently lost in leptarctines and in other mustelids.

INTRODUCTION

The Genus *Trocharion* in the Iberian Peninsula

The mustelid subfamily Leptarctinae is characterized by several craniodental features, which include among others the presence of a double temporal crest (Qiu and Schmidt-Kittler, 1982; Wang et al., 2004). Leptarctines are widely distributed in Europe, Asia, and North America during the Miocene, although occurrences of fossils are relatively rare. The type genus of the subfamily, *Leptarctus* Leidy, 1856, is distributed both across North America (Leidy, 1856; Wortman, 1894; Matthew, 1924; Olsen, 1957a, 1957b, 1958, 1959; Qiu and Schmidt-Kittler, 1982; Lim et al., 2001; Lim and Martin, 2001) and Asia (Zhai, 1964; Qiu and Schmidt-Kittler, 1982); the genus *Mephititaxus* White, 1941, is currently considered a junior subjective synonym of the former, and the genus *Hypsoparia* Dorr, 1954 (see White, 1941; Olsen, 1958; McKenna and Bell, 1997), is also synonymized with the former by some authors (Baskin, 2005), whereas others maintain it as a separate genus (Lim and Martin, 2002). Other genera have been reported from the above-mentioned continents, including *Kinometaxia* Wang, Qiu and Wang, 2004, in Asia (Wang et al., 2004), and *Craterogale* Gazin, 1936, and *Schultzogale* Lim and Martin, 2000, in North America (Gazin, 1936; Lim and Martin, 2000, 2002). In Europe, however, leptarctines are represented by the single genus *Trocharion* Major, 1903 (see also Helbing, 1936; Mein, 1958; Ginsburg, 1999); other putative leptarctines, *Trochotherium* Fraas, 1870, and *Gaillardina* Ginsburg, 1999 (e.g., Ginsburg, 1999; Bonis, 2005), are currently excluded from this subfamily (Wolsan, 1999; Wang et al., 2004; see Discussion for further details).

The single and type species of the genus *Trocharion* is *T. albanense*. It was erected by Major (1903) on the basis of French material from the late Astaracian of La Grive, and it has been later reported from several other localities from Central Europe and the Iberian Peninsula (see review in Ginsburg, 1999). The occurrence of *T. albanense* in the Iberian Peninsula is restricted to the Vallès-Penedès Basin. It was first reported by Villalta Comella and Crusafont Pairó (1944) on the basis of an m1 from the late Aragonian site of Sant Quirze. Later on, further remains of this taxon were reported from the early Vallesian of Can Llobateres (Petter, 1967a) and the late Aragonian of Castell de Barberà (Petter, 1976). Until recently, the available specimens of *T. albanense* from this basin were relatively scarce and mainly consisted on isolated teeth. More abundant and complete material, however, has been recovered during the last 5 years during paleontological field work at Abocador de Can Mata (ACM; Alba et al., 2006a, 2006b, 2007). In this paper, all the available material of this taxon from the Vallès-Penedès Basin is described, including not only the material previously published by other researchers (Villalta Comella and Crusafont Pairó, 1944; Petter, 1967a, 1976), but also the more complete and unpublished material from ACM.

Historical Background

The Vallès-Penedès Basin (Fig. 1), located at the province of Barcelona (Spain), can be divided geographically into two different sectors: the Penedès sector, including the localities from the municipal term of els Hostalets de Pierola; and the Vallès sector, including localities situated near the towns of Sabadell,

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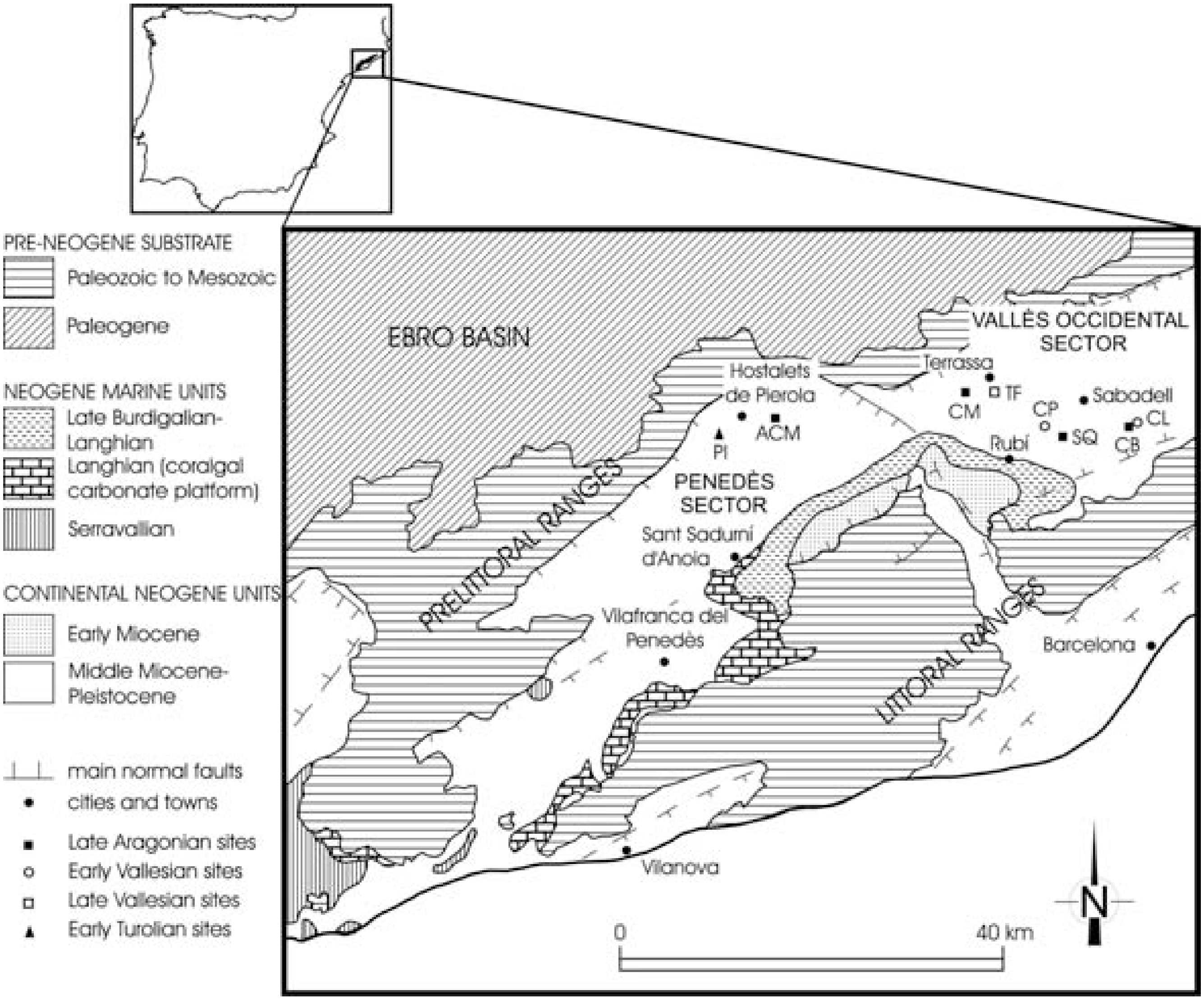

FIGURE 1. Geographical map showing the location of the Vallès-Penedès Basin within the Iberian Peninsula (top left), and schematic geological map of this basin, showing the main geological units as well as some of the main middle and late Miocene sites (modified after Agustí et al., 1985, and Garcés, 1995, reprinted from Casanovas-Vilar et al. 2008a). **Abbreviations**: **ACM**, Abocador de Can Mata; **CB**, Castell de Barberà; **CM**, Can Missert; **CL**, Can Llobateres; **CP**, Can Ponsic; **PI**, Piera; **SQ**, Sant Quirze; **TF**, Torrent de Febulines.

Rubí, and Terrassa, such as Can Llobateres, Castell de Barberà, and Sant Quirze. Mario Guerín discovered the fossiliferous potential of the former area and reported it to paleontologist Josep Ramon Bataller, who surveyed the area and reported several paleontological sites (Bataller, 1938). Subsequently, paleontologists Miquel Crusafont and Josep F. de Villalta further collected abundant fossil material from that area, which led to several publications during the following decades, including the discovery of hominoid remains at Can Vila (Villalta Comella and Crusafont Pairó, 1941).

Among the *Trocharion*-bearing localities from the Vallès sector, the first to be discovered was Sant Quirze, also known as Trinxera del Ferrocarril (Bataller, 1924, 1938). Around 1930, Crusafont discovered, together with Ramón Arquer, the Early Vallesian site of Can Llobateres, about 3 km from Sabadell (Villalta Comella and Crusafont Pairó, 1943a; Crusafont Pairó, 1964). From 1956 to 1960, additional fossils were recovered from this site (Crusafont Pairó, 1964), because the discovery of fossil hominoids (Crusafont Pairó, 1958) led to a large sampling effort. With more than 60 recorded vertebrate species, Can Llobateres 1 represents one of the most diversified mammal assemblages from the Eurasian Miocene (Agustí et al., 1996).

The site of Castell de Barberà was not discovered until the 1970s (Crusafont-Pairó and Golpe, 1972), leading to interesting discoveries of small suoids (Golpe-Posse, 1977) and pliopithecid primates (Crusafont-Pairó and Golpe-Posse, 1981). During the 1970s and 1980s, paleontological surveys and excavations were also carried out at the area of Hostalets (mainly at Can Mata I). However, from the beginning of the 1990s, excavations were resumed at Can Llobateres 2 (Moyà-Solà and Köhler, 1993, 1996), and most of the attention was devoted to the Vallès sector. During the 1980s, a rubbish dump known as Abocador de Can Mata had developed near Can Mata de la Garriga. Over the years, an extension of the dump was planned, and a paleontological intervention was devised in order to control the removal of Miocene sediments by the excavators. From its beginning in November

2002, this paleontological field work has continued almost without interruption (Alba et al., 2006a, 2006b, 2007; Moyà-Solà et al., 2004, 2009; Casanovas-Vilar et al., 2008b). The material of *T. albanense* thus far recovered in the Abocador de Can Mata (ACM) is not only more abundant than that previously recovered from the same basin, but is also more completely preserved than elsewhere, thus showing some previously unknown craniodental features of this taxon.

STRATIGRAPHY AND AGE

The material of *Trocharion albanense* included in this study comes from several localities situated in the Vallès-Penedès Basin, on the NE margin of the Iberian Peninsula (Barcelona, Spain; Fig. 1). This basin is a NNE-SSW-oriented Neogene half-graben, limited by the Littoral and Pre-littoral Catalan Coastal Ranges, which originated due to the rifting of the NW Mediterranean region during the Neogene. Some marine and transitional sequences were deposited in this basin during the early and middle Miocene, although most of the basin infilling is attributable to proximal to distal-marginal alluvial fan sediments (Cabrera and Calvet, 1990, 1996; Bartrina et al., 1992; Roca and Desegaulx, 1992; Roca and Guimerà, 1992; Cabrera et al., 2004).

There are no magnetostratigraphic data available for either Castell de Barberà or Sant Quirze. Their respective rodent assemblages, however, are essentially comparable, corresponding to the *Megacricetodon ibericus* + *Democricetodon crusafonti* local biozone (Alba et al., 2006b; Casanovas-Vilar, 2007:appendix 2.1), which is correlated to MN8 sensu Mein and Ginsburg (2002). This contrasts with the situation of Can Llobateres, for which both sedimentary (Begun et al., 1990) and magnetostratigraphic (Agustí et al., 1996) data are available. The locality of Can Llobateres 1 corresponds to the C4Ar.3r subchron and is attributable to the *Cricetulodon* local biozone, whereas the locality of Can Llobateres 2 corresponds to the C4Ar.2r subchron and is attributable to the *Progonomys* + *Cricetulodon* local biozone (Agustí et al., 1996, 2001; Casanovas-Vilar, 2007:appendix 2.1). In other words, Can Llobateres 1 and 2 record the early/late Vallesian transition (i.e., that between MN 9 and MN10), with an estimated age of 9.7 and 9.6 Ma, respectively, for Can Llobateres 1 and 2 (Agustí et al., 1996). Unlike Can Llobateres, both Sant Quirze and Castell de Barberà correspond to the late Aragonian. Castell de Barberà is considered to be younger than Sant Quirze (Crusafont-Pairó and Golpe, 1972; Aguilar et al., 1979; Agustí Ballester, 1981; Agustí et al., 1985; Casanovas-Vilar, 2007). There has been, however, some confusion regarding the precise dating of this site, which has been attributed to the early Vallesian by De Bruijn et al. (1992). On the basis of the absence of hipparionine horses in Castell de Barberà (see discussion in Casanovas-Vilar, 2007:74, footnote 16), this site is correlated to the latest Aragonian, as proposed by Agustí Ballester (1981) and Agustí et al. (1985, 1997, 2001).

With regard to the Penedès sector, more than twenty classical 'localities' are known from the area of els Hostalets (Crusafont and Truyols, 1954; Golpe-Posse, 1974). Except for Can Mata I, however, they do not correspond to a single stratigraphic level but to fossil findings of uncertain stratigraphic provenance (Agustí et al., 1985; Alba et al., 2006b). Accordingly, an accurate dating of the remains from most classic Hostalets 'localities' is not possible. Be that as it may, *Trocharion albanense* has not been identified among the paleontological collections from classical Hostalets localities. The dating uncertainties surrounding these localities contrasts with the situation of the ACM local stratigraphic series (Alba et al., 2006b; Moyà-Solà et al., 2009), which currently comprises more than 125 mammal sites distributed along a continuous late Aragonian section of nearly 300 m. Thanks to the extensive outcrops generated by the digging activity, and to the continuous paleontological control, the ACM stratigraphic series is based on firm lithostratigraphic, magnetostratigraphic, and biostratigraphic grounds, which allow a precise dating of the several localities thus far discovered.

The faunistic and biostratigraphic background of ACM have been recently updated (Alba et al., 2006b; Casanovas-Vilar et al., 2008a), and the geological background and magnetostratigraphic correlation has been also published recently (Moyà-Solà et al., 2009). On the basis of certain cricetid taxa, Alba et al. (2006b) divided the ACM stratigraphic series into three local biozones. The upper part of the sequence (the *Megacricetodon ibericus* + *Democricetodon crusafonti* local biozone) can be correlated to the MN8 (sensu Mein and Ginsburg, 2002), whereas the intermediate part (the *M. ibericus* + *D. larteti* biozone) can be correlated to the MN7 (sensu Mein and Ginsburg, 2002). BDL1, the oldest locality of the ACM series, corresponds to subchron C5Ar.1 (12.7–12.4 Ma). On the basis of the limited small mammal sample from this locality, Alba et al. (2006b) initially proposed a tentative correlation to the MN6 for the lowest portion of the ACM series. The most extensive rodent assemblage from C9-A1 (unpubl. data), which is only slightly above BDL1, indicates that this locality corresponds to MN7, so that most of the series must be correlated to MN7 and MN8.

Most of the material of *Trocharion* reported in this paper comes from the excavation of four different ACM localities: C4-A1 (= C4-Ae), excavated in 2005, as well as C5-D1 (= C5-Da), C6-A2, and C6-Cb, excavated in 2008. Additional isolated material was recovered from two ACM sectors: BDA, during the 2002–2003 campaign, and C5-D, in 2008. The oldest record corresponds to the remains from BDA; although the exact stratigraphic provenance of this finding was not recorded, localities from this sector correspond to the *M. ibericus* + *D. larteti* local biozone (Alba et al., 2006b) and can be therefore correlated to MN7, with an estimated age of ca. 12.4–11.7 Ma on the basis of magnetostratigraphic data (Moyà-Solà et al., 2009; authors' unpubl. data). The remaining *Trocharion*-bearing sites from ACM correspond to the *M. ibericus* + *D. crusafonti* local biozone (Alba et al., 2006b) and are therefore correlated to MN8, with an estimated age of ca. 11.7–11.5 Ma (subchrons C5r.3r and C5.r.2n) on the basis of magnetostratigraphic correlation (Moyà-Solà et al., 2009; authors' unpublished data).

MATERIALS AND METHODS

Nomenclature

The dental nomenclature employed in this paper is based on Smith and Dodson (2003).

Abbreviations

Metric Abbreviations—BL, labiolingual breadth; **ML**, mesiodistal length.

Institutional Abbreviations—BMNH, Natural History Museum, London, United Kingdom; **IPS**, Institut Català de Paleontologia Barcelona, Spain; **SMN**, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Fossil Locality Abbreviations—ACM, Abocador de Can Mata; **BDA**, Decanting Pond of Rainwater; **C4**, Cell 4; **C5**, Cell 5; **C6**, Cell 6; **CB**, Castell de Barberà; **CL1**, Can Llobares 1; **SQ**, Sant Quirze.

Cladistic Analysis Abbreviations—CI, consistency index; **RI**, retention index; **RC**, rescaled consistency index.

Studied Material

All the fossil remains included in this study are housed at the collections of the Institut Català de Paleontologia (Barcelona, Spain). The remains of *Trocharion* from Can Llobateres were previously described by Petter (1967a), those from Sant Quirze by Villalta Comella and Crusafont Pairó (1944), and those from Castell de Barberà by Petter (1976). The latter author further attributed to (?) *T. albanense* several deciduous teeth from Castell de Barberà; these specimens, however, have not been included in the present study, because on the basis of the morphological features of the dP4, they are most likely attributable to the Mephitidae (Petter, 1976). The remains from ACM, on the contrary, have been collected from 2002 onwards (Alba et al., 2006a, 2007).

Comparative Sample

The material of *T. albanense* described in this paper has been compared to material of this taxon from other European Miocene sites on the basis of published descriptions, figures, and measurements. These localities include Vieux-Collonges (= Mont Ceindre; Mein, 1958), La Grive-Saint-Alban (Major, 1903; Pilgrim, 1933; Helbing, 1936; Viret, 1951), and Baigneaux-en-Beauce (Ginsburg, 2002) in France; Steinheim (Fraas, 1870; Helbing, 1936), Edelbeuren-Maurerkopf (Von Volker, 1999), and perhaps also Melchingen (Pilgrim, 1933; Viret, 1951; see Discussion) in Germany; and Spalte von Neudorf an der March (Zapfe, 1950) in Slovakia.

Cladistic Analysis

In order to decipher the phylogenetic relationships of *Trocharion* as compared to other leptarctine genera, we performed a cladistic analysis based on Wang et al.'s (2004:table 2) matrix, which includes a generic outgroup, several procyonids, and putative stem mustelids (see Wolsan, 1993, for further details on these taxa) and four leptarctine genera. To this database, we added *Trocharion* and further introduced several minor modifications (see Results for additional details). *Gaillardina* and *Trochotherium* were not included in the analysis because they are no longer considered leptarctines (see Discussion), and the aim of the analysis was only to determine the phylogenetic affinities of *Trocharion*. It is necessary to note that Wang et al.'s (2004) matrix was based on the characters and taxa discussed by Wolsan (1993: table 1), with the addition of some additional characters, the removal of certain taxa and the addition of leptarctine genera (other than *Trocharion*). Accordingly, the reader is referred to the two papers mentioned above for details on character definition and coding (see also Results). The analysis was performed with PAUP* (Swofford, 2003), by using maximum parsimony and the 'branch-and-bound' option; characters were treated as ordered, and multiple state characters were treated with the default PAUP* option 'uncertain,' which picks the character state that minimizes tree length. Clade stability was asssessed by means of bootstrap analysis (1000 replicates), and also by means of Bremer decay analysis (Bremer, 1994); the latter measures branch support as the extra steps required in order to 'collapse' a clade in the consensus of near-most-parsimonious trees.

TABLE 1. Fossil material of *Trocharion albanense* Major, 1903, from several localities of the Vallès-Penedès Basin (Barcelona, Spain).

Record no.	Locality	Description
IPS28084	CL1	Partial right M1 germ
IPS28088	CL1	Left m1 with partial roots; very worn
IPS28096	CL1	Right M1 crown; unworn
IPS30991	SQ	Left m1 crown with partial roots; advanced wear
IPS31232	CB	Left M1 crown with partial roots; moderate wear
IPS33217a	CB	Left p2 crown with partial root; moderate wear
IPS33217b	CB	Right p3 crown with partial root; moderate wear
IPS33217c	CB	Left p4 crown with almost complete roots; moderate wear
IPS33217d	CB	Left P3 crown with partial roots; moderate wear
IPS33217e	CB	Left m1 (complete); advanced wear
IPS33217f	CB	Right p4 crown with partial roots; moderate wear
IPS33217g	CB	Left M1 crown with partial roots; moderate wear
IPS33217h	CB	Left P4 with partial roots; moderate wear
IPS33220	CB	Right M1 crown; unworn
IPS33221	CB	Left P4 crown with roots embedded in sediment; unworn
IPS33222	CB	Right M1 crown; unworn
IPS43203	CB	Right p4 (complete); moderate wear
IPS43204	CB	Right m1 crown; slight wear
IPS43205	CB	Left m1 crown; unworn
IPS43206	CB	Right m1 crown with partial roots; slight wear
IPS29705	ACM/C4-A1	Right M1 crown with partial roots; slight degree of wear
IPS29892	ACM/C4-A1	Right mandibular corpus with c1 and partial postcanine series; moderate wear
IPS29979	ACM/BDA	Partial skull with partial tooth series (with moderate degree of wear), skull roof and partial zygomatics, but lacking a large portion of the palate, the neurocranium, and the basicranium
IPS35022	ACM/C4-A1	Right m2 crown with partial roots; slight wear
IPS41716	ACM/C4-A1	Right m1 crown; slight wear
IPS41723	ACM/C4-A1	Right M1 crown; slight wear
IPS41738	ACM/C4-A1	Right M1 partial crown with partial roots; slight wear
IPS43128	ACM/C6-A	Right partial mandibular corpus with p2–3; moderate wear
IPS43358	ACM/C6-A2	Right m1 crown with partial roots; unworn
IPS43434	ACM/C6-A	Left M1 crown; unworn
IPS43490	ACM/C5-D1	Right m2 crown with partial roots; slight wear
IPS43761	ACM/C6-Cb	Left m1 crown with partial roots; very advanced wear
IPS43811	ACM/C5-D1	Left mandibular fragment with m1; slight wear
IPS44028	ACM/C6-Cb	Partial skull with partial tooth series (with advanced degree of wear) and skull roof, but lacking most of the neurocranium, the basicranium, and the zygomatic arches
IPS44029	ACM/C5-D1	Left M1 crown
IPS44170	ACM/C5-D	Complete right hemimandible and partial left hemimandible

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Infraorder ARCTOIDEA Flower, 1869
Parvorder MUSTELIDA Tedford, 1976
Superfamily MUSTELOIDEA Fischer von Waldheim, 1817
Family MUSTELIDAE Fischer von Waldheim, 1817
Subfamily LEPTARCTINAE Gazin, 1936, sensu Qiu and Schmidt-Kittler, 1982

Type Genus—*Leptarctus* Leidy, 1856.

Included Genera—See the Introduction.

Emended Diagnosis—After Qiu and Schmidt-Kittler, 1982; Wang et al., 2004. Skull with double temporal crests. Strong, broad, and deep zygomatic arches. Strong postorbital processes of the frontal. Small orbits. Partially roughened area on the temporal. Bulla extending downwards, with longitudinal crest and cleft. Postglenoid process and bulla in close contact. Postglenoid foramen on the back of postglenoid process. Foramen ovale on the lateral side of eustachian tube. Stylomastoid foramen deep in a depression. Mandible with a strong subangular lobe and deep

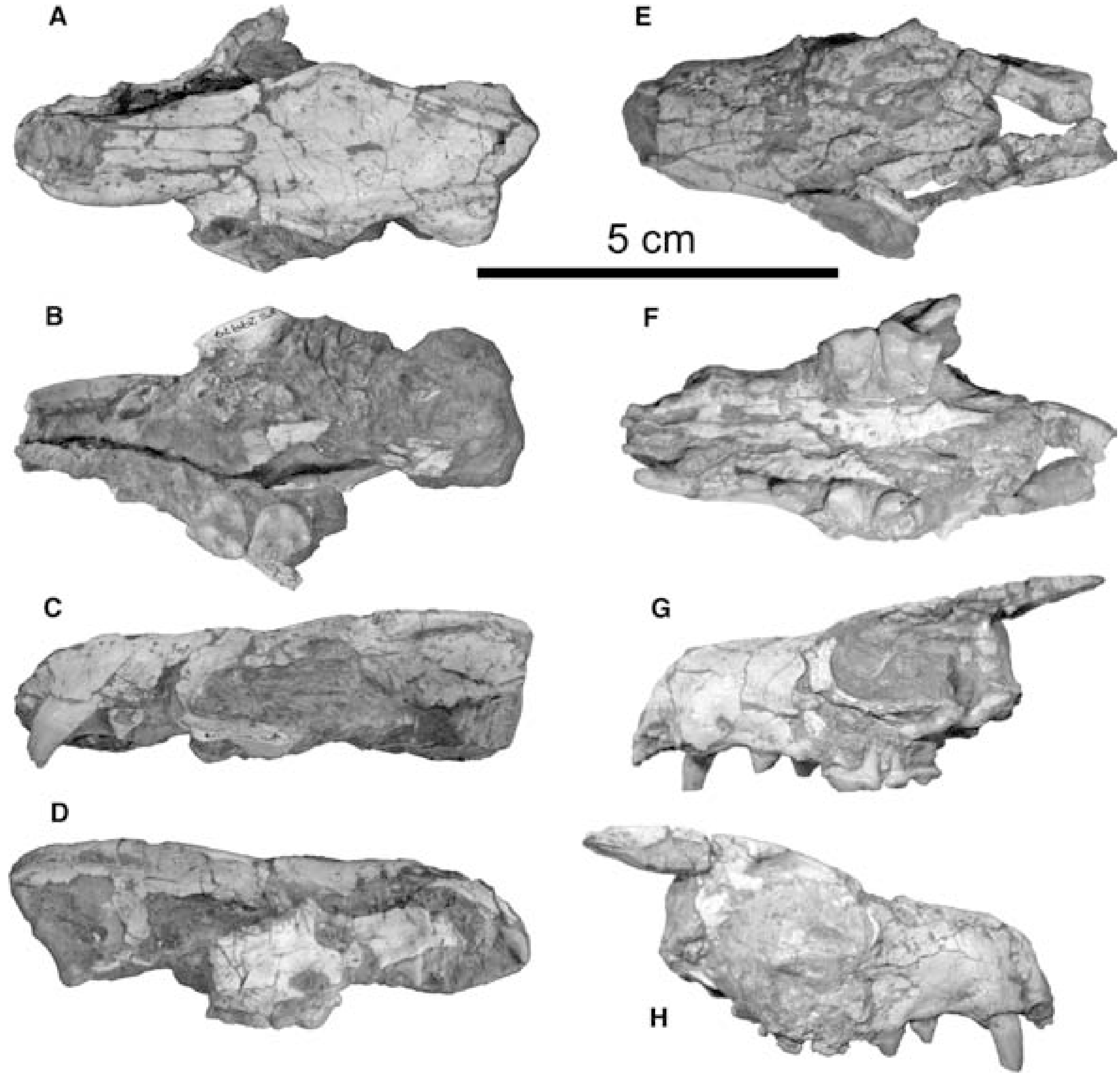

FIGURE 2. Cranial remains of *Trocharion albanense* Major, 1903 from two localities of the Vallès-Penedès Basin (Barcelona, Spain). **A**–**D**, partial cranium IPS29979, **A**, dorsal; **B**, basal; **C**, left; **D**, right; **E**–**H**, partial cranium IPS44028, **E**, dorsal; **F**, basal; **G**, left; **H**, right.

masseteric fossa. m2 biradiculate, consisting of a large and deep-basined trigonid and a reduced talonid.

Genus *TROCHARION* Major, 1903

Type Species—*Trocharion albanense* Major, 1903.

Emended Diagnosis—As for the type and only species.

TROCHARION ALBANENSE Major, 1903
(Figs. 2–5)

Lutra (Potamotherium) valetoni Geoffroy Saint-Hilaire, 1833: Fraas, 1870:165, plate IV:fig. 18.

Trocharion fraasi Helbing, 1936:51 (conditional proposal).

Holotype—Right mandible with p4–m2 (BMNH 5307). This specimen was first described by Major (1903), but was not figured until Pilgrim (1933).

Type Locality—La Grive-Saint-Alban (Isère, France).

Studied Material—Isolated teeth from Sant Quirze, Can Llobateres 1, and Castell de Barberà, as well as craniodental material from several localities from Abocador de Can Mata (see list in Table 1).

Measurements—See Table 2 for raw measurements, and Figure 6 for dental proportions.

Age and Distribution—In the Iberian Peninsula, this taxon is exclusively known from the Vallès-Penedès localities discussed in this paper (see also Villalta Comella and Crusafont Pairó, 1944;

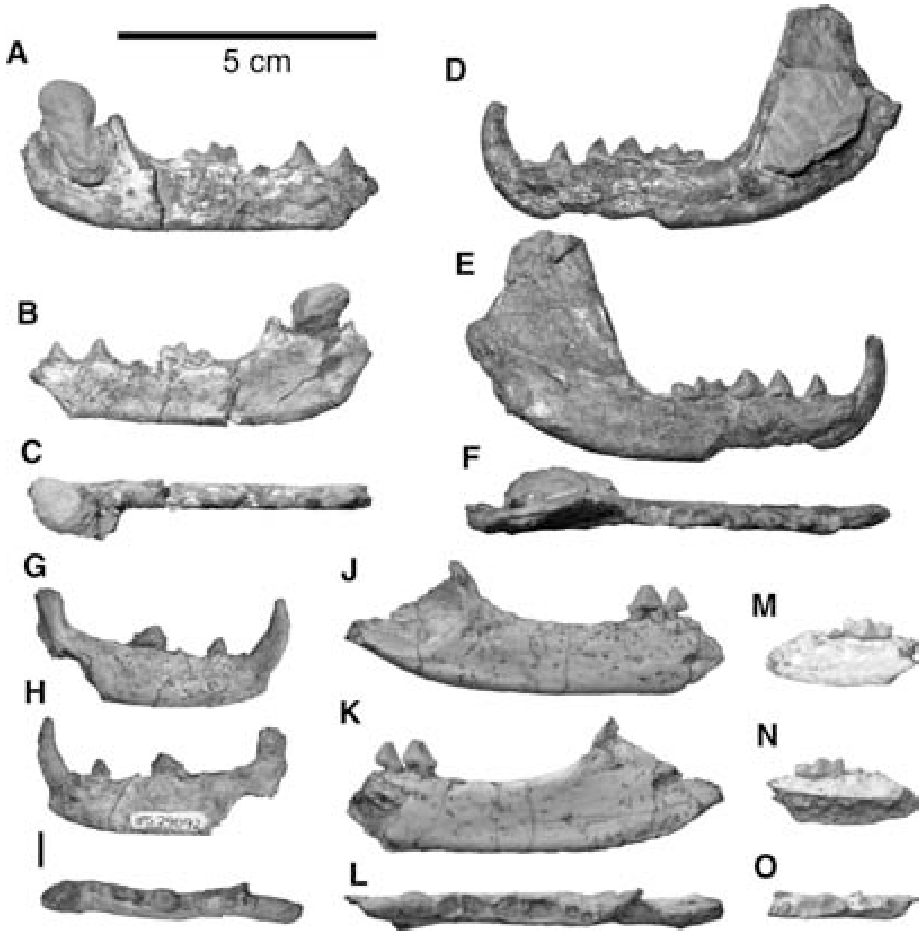

FIGURE 3. Mandibular remains of *Trocharion albanense* Major, 1903, from several localities of the Vallès-Penedès Basin (Barcelona). **A–C**, right hemandible IPS44170, **A**, labial; **B**, lingual; **C**, occlusal; **D–F**, left hemimandible IPS44170, **D**, labial; **E**, lingual; **F**, occlusal; **G–I**, right mandibular corpus IPS29892, **G**, labial; **H**, lingual; **I**, occlusal; **J–L**, right partial mandibular corpus IPS43128, **J**, labial; **K**, lingual; **L**, occlusal; **M–O,** left mandibular fragment IPS43811, **M**, labial; **N**, lingual; **O**, occlusal.

Petter, 1967a, 1976; Alba et al., 2006b), ranging from the middle to the late Miocene; in chronological order: ACM/BDA (MN7, ca. 12.4–11.7 Ma); ACM/C5-D1, ACM/C5-D and ACM/C4-A1 (MN8, ca. 11.7–11.5 Ma), ACM/C6-Cb and ACM/C6-A2 (MN8, ca. 11.5 Ma), Sant Quirze (MN8), and Castell de Barberà (MN8); and Can Llobateres 1 (MN9, ca. 9.7 Ma). In the rest of Europe, the earliest record corresponds to the MN5 French localities of Vieux-Collonges (= Mont Ceindre; Mein, 1958; Ginsburg, 1990a, 2001), Baigneaux-en-Beauce, Lasse, Noyant-sous-le-Lude, Savigné-sur-Lathan, Hommes, and Pont Boutard à Saint-Michel-sur-Loire (Ginsburg, 1980, 1990a, 1990b, 2001, 2002), and Edelbeuren-Maurerkopf (MN5) in Germany (Von Volker, 1999). Later on, this taxon is also present in several MN6 localities, including Hambach 6C in Germany (Mörs, 2002) and Neudorf-Spalte in Slovakia (Zapfe, 1950). Finally, this taxon is also present in late Astaracian localities roughly contemporaneous with those studied in this paper: La Grive M and L7 (MN7) and La Grive L3 (MN8) in France (Pilgrim, 1933; Viret, 1951; see Mein and Ginsburg, 2002, for further details on the fauna and dating of the several fissure fillings from La Grive) and Steinheim (MN7 and MN8) in Germany (Helbing, 1936). The youngest record is attributable to Can Llobateres 1 (MN9); the attribution to this taxon of remains from the MN9 site of Melchingen (Viret, 1951; Zapfe, 1950) is currently uncertain (see Discussion).

Emended Diagnosis—Small-sized mustelid with an elongated cranium, long muzzle, and narrow palate, with the posterior border of the latter situated at the level of M1. Superiorly flattened neurocranium with a well-developed, double temporal crest that displays a rhomboidal shape, beginning at the level of the moderate postorbital process of the frontal and posteriorly diverging until about the frontoparietal suture. Deep zygomatic arches. Mandible with a low corpus, with two small and rounded mental foramina under the p2 and p3. Shallow ramus originating just behind the m2, with a narrow molar sulcus. Posterior mandibular foramen situated behind the m2, and partial condyloid process situated at level of the same molar. Deep masseteric fossa and broad but thin coronoid process. Dental formula: 3.1.4.1/3?.1.4.2. Spatulate upper incisors, the I3 being larger and more asymmetrical than the I1 and I2. Upper canine smooth without wrinkles. P1 very small, unicuspid, and uniradiculate; P2 biradiculate with an asymmetrical triangular profile in lateral view. From mesial to distal, the premolars become increasingly larger and display a greater development the occlusal relief, with the P2 and P3 being unicuspid and displaying a complete cingulum, whereas the P4 is multicuspid. P4 with carnassial notch, and an elongated but distinct protocone much larger than the hypocone. M1 very similar in size to the P4, with a subtrapezoidal occlusal outline longer on the labial moiety of the crown. Paracone, metacone, and metastyle of M1 aligned on the labial side, and protocone, hypocone, and metaconule linked to one another by a sharp crest; continuous lingual cingulum around the base of the protocone. M2 absent. Smooth lower canine. Lower premolars unicuspid, the first one uniradiculate, the remaining ones biradiculate, increasing in size from mesial to distal. The two lower molars are biradiculate, low-crowned, and inflated, the first one being much larger than the second one. m1 with a triangular trigonid displaying

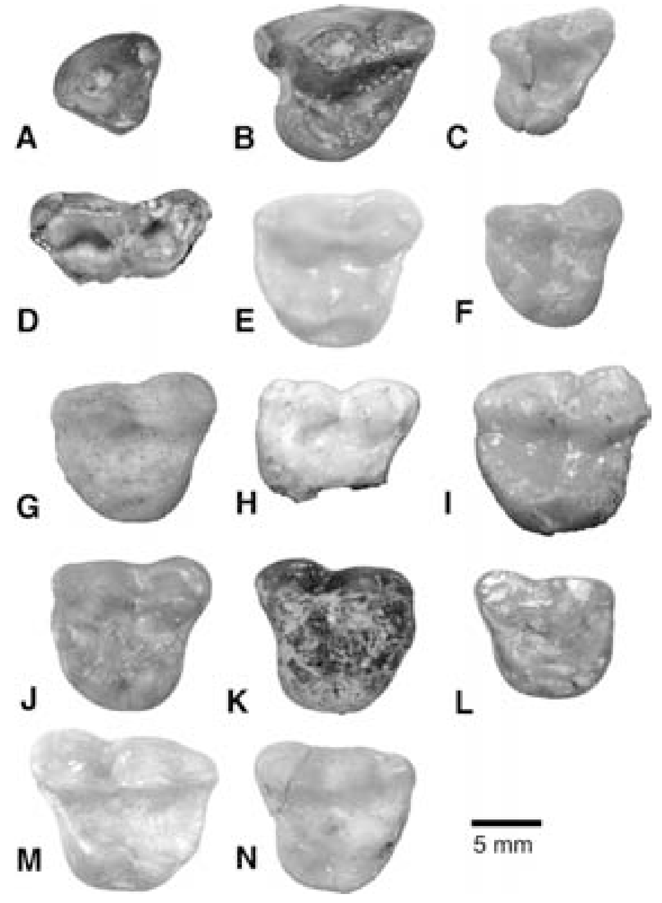

FIGURE 4. Isolated upper cheek teeth of *Trocharion albanense* Major, 1903, from several localities of the Vallès-Penedès Basin (Barcelona, Spain), all in occlusal view. **A**, left P3 IPS33217d; **B**, left P4 IPS33217h; **C**, left P4 IPS33221; **D**, right M1 IPS28084; **E**, right M1 IPS28096; **F**, right M1 IPS33222; **G,** right M1 IPS33220; **H,** right M1 IPS41738; **I,** right M1 IPS41723; **J**, right M1 IPS29705; **K**, left M1 IPS33217g; **L**, left M1 IPS31232; **M**, left M1 IPS44029; **N**, left M1 IPS43434.

three equally low main cuspids and being as long as the talonid, which displays three subequal cuspids enclosed within the distal marginal ridge. Tricuspid m2, with protoconid and metaconid linked by a transverse cristid, and hypoconid situated on the distolabial corner of the talonid, which is subequal in size to the trigonid.

Diferential Diagnosis—Cranially, *Trocharion* differs from other Leptarctinae by the rhomboidal shape of the double temporal crests, contrasting with the more parallel or even opposite condition of other leptarctines. *Trocharion* further differs from other leptarctines by the long and narrow muzzle, the more anterior situation of the posterior border of the palate, and by the more marked postorbital process of the frontal in the former. With regard to mandibular features, *Trocharion* differs from *Leptactus* by the lack of a second mental foramen under the p2 (condition unknown in other leptarctines). Dentally, *Trocharion* differs from other leptarctines (but apparently not *Gaillardina*) by the retention of a vestigial P1 and p1 (although the latter can be only ascertained in *Leptarctus* and *Hypsoparia*). *Trocharion* also differs from other leptarctines except *Hypsoparia* by the presence of a carnassial notch and, except from *Leptarctus* and *Hypsoparia*, by the more elongated and less distinct protocone on the P4; *Trocharion* further differs from *Leptarctus* and *Craterogale* by the lack of a distinct hypocone on the P4. *Trocharion* differs from

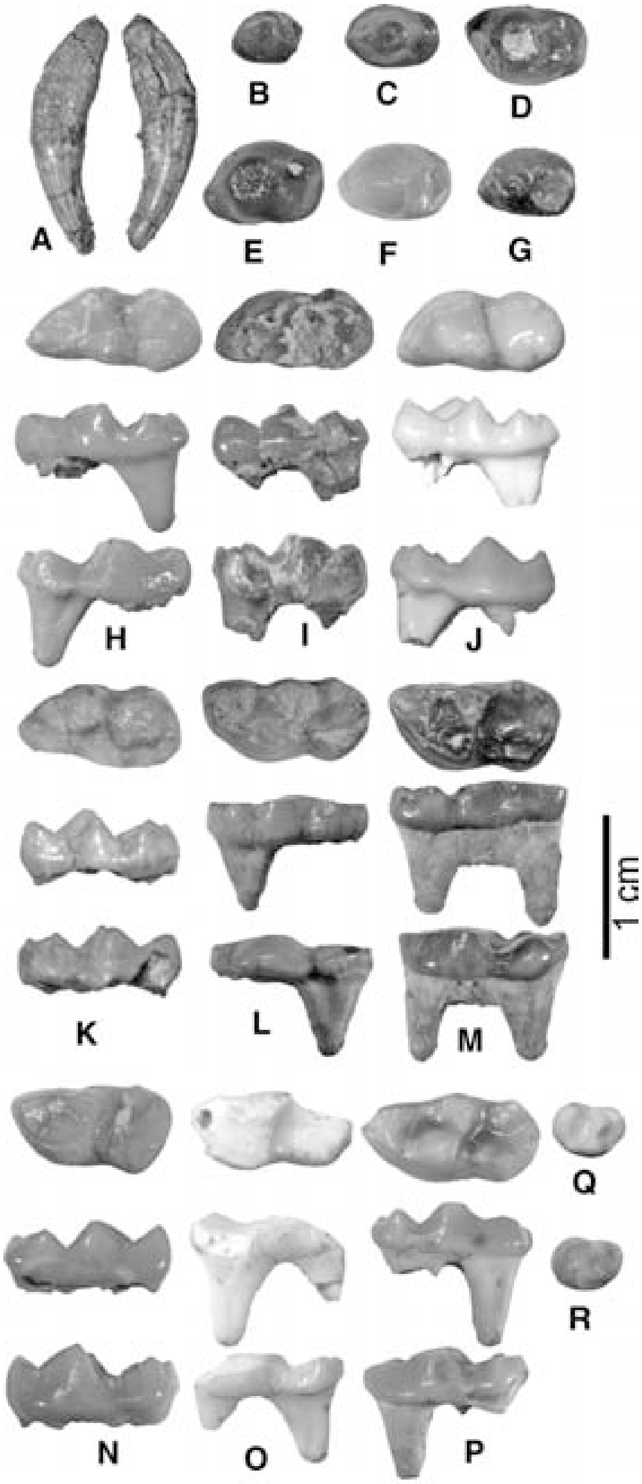

FIGURE 5. Isolated lower cheek teeth of *Trocharion albanense* Major, 1903, from several localities of the Vallès-Penedès Basin (Barcelona, Spain), all in occlusal view except for the c1 (labial and lingual) and m1 (occlusal, lingual and labial). **A**, right c1 IPS44170; **B**, left p2 IPS33217a; **C**, right p3 IPS33217b; **D**, left p4 IPS33217c; **E,** right p4 IPS33217f; **F**, right p4 IPS44170; **G**, right p4 IPS43203; **H**, right m1 (IPS43206); **I**, right m1 IPS43204; **J**, right m1 IPS43358; **K**, right m1 IPS41716; **L**, left m1 IPS28088; **M**, left m1 IPS33217e; **N,** left m1 IPS43205; **O**, left m1 IPS43761; **P**, left m1 IPS30991; **Q,** right m2 IPS43490; **R,** right m2 IPS35022.

TABLE 2. Dental measurements of *Trocharion albanense* Major, 1903, from several localities of the Vallès-Penedès Basin (Barcelona, Spain).

Record no.	Tooth	BL	MD	Site
IPS28084	M1	—	8.1	CL1
IPS28088	m1	4.5	8.9	CL1
IPS28096	M1	6.2	6.8	CL1
IPS29705	M1	6.5	7.0	ACM/C4-A1
IPS29892	p4	4.0	6.2	ACM/C4-A1
IPS29892	m2	2.8	3.6	ACM/C4-A1
IPS29979	P4	8.0	8.7	ACM/BDA
IPS29979	M1	6.9	7.3	ACM/BDA
IPS30991	m1	4.7	9.1	SQ
IPS31232	M1	5.8	6.1	CB
IPS33217a	p2	2.3	3.7	CB
IPS33217b	p3	4.6	5.2	CB
IPS33217c	p4	4.7	7.1	CB
IPS33217d	P3	4.6	6.1	CB
IPS33217e	m1	4.6	9.4	CB
IPS33217f	p4	4.6	7.3	CB
IPS33217g	M1	7.4	7.4	CB
IPS33217h	P4	8.0	8.6	CB
IPS33220	M1	6.0	6.7	CB
IPS33221	P4	6.3	—	CB
IPS33222	M1	6.0	6.3	CB
IPS41716	m1	4.3	8.9	ACM/C4-A1
IPS41723	M1	6.6	7.0	ACM/C4-A1
IPS41738	M1	—	7.9	ACM/C4-A1
IPS43128	p2	2.5	3.5	ACM/C6-A
IPS43128	p3	3.1	4.0	ACM/C6-A
IPS43203	p4	3.7	5.9	CB
IPS43204	m1	3.8	7.9	CB
IPS43205	m1	4.4	9.1	CB
IPS43206	m1	3.8	8.7	CB
IPS43358	m1	4.6	9.2	ACM/C6-A2
IPS43434	M1	6.2	6.9	ACM/C6-A
IPS43490	m2	3.2	4.3	ACM/C5-D1
IPS43761	m1	4.2	8.2	ACM/C6-Cb
IPS43811	m1	4.8	9.6	ACM/C5-D1
IPS44028	right C1	2.9	3.8	ACM/C6-Cb
IPS44028	right P2	1.9	3.6	ACM/C6-Cb
IPS44028	left P2	1.9	3.6	ACM/C6-Cb
IPS44028	right P3	3.8	5.2	ACM/C6-Cb
IPS44028	left P4	7.0	7.1	ACM/C6-Cb
IPS44028	left M1	6.7	7.4	ACM/C6-Cb
IPS44029	left M1	6.8	8.2	ACM/C5-D1
IPS44170	right c1	4.2	5.3	ACM/C5-D
IPS44170	left c1	4.5	5.9	ACM/C5-D
IPS44170	right p2	2.3	4.0	ACM/C5-D
IPS44170	left p2	2.3	4.2	ACM/C5-D
IPS44170	right p3	3.1	5.5	ACM/C5-D
IPS44170	left p3	3.3	5.5	ACM/C5-D
IPS44170	right p4	4.3	7.1	ACM/C5-D
IPS44170	left p4	4.4	6.9	ACM/C5-D
IPS44170	right m1	—	9.7	ACM/C5-D
IPS44170	left m1	4.7	9.6	ACM/C5-D
IPS44170	right m2	3.3	4.8	ACM/C5-D

other leptarctines except *Leptarctus* by having a M1 not mesiodistally shorter than the P4 and with a more subquadrangular occlusal outline (instead of being wider than long). Regarding the lower dentition (unknown for *Kinometaxia*, *Craterogale*, *Schultzogale*, and *Gaillardina*), *Trocharion* differs from *Leptarctus* by the shorter talonid of m2, and from both *Leptarctus* and *Hypsoparia* by the lack of a postcanine diastema.

Description

Preservation—The material of *T. albanense* from Sant Quirze and Can Llobateres is very scarce: the former includes a single m1 (Fig. 5P), whereas the latter includes two M1 (Fig. 4D, E) and one m1 (Fig. 5L). The material from Castell de Barberà is much more abundant, but similarly it only includes isolated teeth: one P3 (Fig. 4A), two P4 (Fig. 4B, C), two M1 (Fig. 4G, K), one p2 (Fig. 5B), one p3 (Fig. 5C), three p4 (Fig. 5D, E, G), and four m1 (Fig. 5H, I, M, N). Some of the specimens from Castell de Barberà, catalogued under the record IPS33217, probably belong to a single individual, which might include the right p2–4 series and the left P3–M1 series; the left m1 IPS33217e (Fig. 5M), however, most likely belongs to a second individual, at least as judged from its more advanced degree of wear. The material from ACM is much more completely preserved, and includes two partial crania (Fig. 2) and several mandibular fragments (Fig. 3), besides several isolated teeth: three M1 (Fig. 4J, M, N), one c1 (Fig. 5A), one p4 (Fig. 5F), two m1 (Fig. 5J, O), and one m2 (Fig. 5Q). All the mandibular specimens lack the symphysis but partially preserve the sub-angular and the coronoid processes. The two cranial specimens provide information from several anatomical regions (the muzzle, the skull roof, and the orbits) that were previously unknown for this genus. The basicranium is not well preserved.

When all the available specimens together are taken into account, all the upper teeth are preserved, except for the crown of the first upper premolar; the presence of this tooth, however, can be unambiguously ascertained due to the preservation of its alveolus in IPS44028 (Fig. 2F). The crown of the upper canine is only partially preserved, because the apex is broken away in both IPS29979 (Fig. 2C, D) and IPS44028 (Fig. 2F, H). Neither the crowns nor the alveoli of the lower incisors are preserved in any of the specimens. The crown of the p1 is neither preserved, although its alveolus is present in both IPS44170 (Fig. 3F) and IPS29892 (Fig. 3I). The crown of the lower canine lacks the apex in IPS44170 (Fig. 3D–F) but is completely preserved in IPS29892 (Fig. 3G–I), although the latter specimen is partially corroded. Besides the p1, the remaining lower cheek teeth are all preserved when the several specimens are taken into account simultaneously. IPS44170 includes the two hemimandibles from a single specimen (Fig. 3A–F), with a left partial series (c1, p2–3, and m1), as well as the complete right c1–m2 series (although the c1, p4, and m2 are detached from the mandible).

Cranium and Mandible—The skull (Fig. 2) is elongated, flattened, and slightly inflated at the basicranial region. The muzzle is long (about half skull length) and displays a large nasal aperture and a narrow palate; the posterior border of the latter reaches the level of the posterior teeth (M1). The nasals are straight, with the frontonasal sutures ending behind the anterior orbital rim and being aligned with the frontomaxillary suture. The face is separated from the neurocranium by a moderate postorbital constriction under the temporal ridge. There are two well-developed, symmetrical temporal crests (i.e., a double temporal crest) along all the preserved upper-lateral margins of the neurocranium. These crests originate at the frontolacrimal sutures, just over the moderate postorbital process of the frontal. Initially they diverge from one another while progressively ascending, until reaching their maximum height behind the orbit, at the level of the temporal fossa. Posteriorly from the frontoparietal suture, however, these crests progressively converge, thus defining a rhomboid or diamond-shaped morphology; they might have even merged together at the posterior portion of the neurocranium, but this cannot be ascertained because this anatomical region is not preserved in the available material. Between the two crests there is a slightly roughened area without appreciable sutures. Rugosities can be observed laterally below the crests, albeit they are discontinuous and not very marked. In lateral view, the orbits are small but display stout margins. The zygomatic arches, albeit incompletely preserved (being broken from the level of M1 distalwards), appear robust and quite deep. There is a single infraorbital foramen, which is large and rounded, being situated at the level of P3/P4. The frontolacrimal sutures end well into mid length of the orbital rim. In basal view, the palate is relatively narrow, defining a U-shaped dental arcade.

TABLE 3. Data matrix for PAUP* analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphictis	0	0	1	0	0	0	0	0/1	0	1	?	0/1	0	0	0	0	0	1	0	0/2	1	0	0	0	0	0	0	0	0	0	0
Bavarictis	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	0	0/2	1	0	0	1	0	0	1	0	0	0	0
Pseudobassaris	0	0	0	0	1	0	1	0	2	1	0	1	0	1	0	0	0	0	0	0/2	1	0	0	1	0	0	0/1	0	0	0	0
Broiliana	0	0	0	1	1	0	1	0	2	1	0	0	0	0/1	0	0	0	1	0	0	0/1	0	0	2	0	0	0	0	0	0	0
Mustelictis	0	0	0	0	0	0	0	0	3	1	0	1	0	1	0	0	0	0/1	0	0/2	1	0	0	0/1	0	0	1	0	0	0	0
Franconictis	?	0		1	1	0	1	1	3	1	1	?	0	1	0	0	0	1	0	2	1	0	0	0	0	0	1	0	0		
Stromeriella	0	0	0	1	1	0	2	1	3	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Bathygale	1	1	1	1	1	0	1/2	1	3	1	0	1	0	1	0	0	0	1	0	4	1	0/1	1	1	0/1	0	1	0	0		
Plesictis	0	1	1	1	0/1	0	1	1	3	1	0	1	0	1	0	0	1	1	0	3/4	1	0/1	1	1	0/1	0	1	0	0	0	0
Paragale	1	0	1	1	1	0	2	2	4	1	?	1	2	1	0	1	2	1	?	4	2/3	1	2	1	1	0	1	0	0	0	0
Plesiogale	0	0	1	1	1	?	?	?	4	1	1	1/2	2	1	0	1	2	1	?	4	3	1	3	1	1	1	1	0	0	0	0
Schultzogale	0	1	?	1	?	0	2	2	5	1	?	2	?	1	0	1	0	1	?	4	?	?	?	?	?	?	?	?	?	1	1
Kinometaxia	0	1	1	1	1	0	2	2	5	?	?	2	2	1	0	1	2	1	?	4	?	?	?	?	?	?	?	?	0	1	1
Craterogale	0	1	1	1	1	0	2	2	4	1	?	2	2	1	0	1	0	1	?	4	?	?	?	?	?	?	?	?	1	2	1
Leptarctus	0	1	1	1	1	0	2	2	4	1	?	2	1	1	1	0	0	1	?	4	?	?	1	3	0	0	1	0	1	2	1
Trocharion	0	1	0	?	?	?	?	?	?	?	?	1	0	1	0	0	0	1	?	4	1	0	1	3	0	0	1	0	?	1	?
Neomustelids	0	0	1	1	1	0	2	2	6	1	1	1/2	2	?	0	1	2	1	?	4	1	?	0	0	1	0	1	0	0	0	0

All taxa except *Trocharion* and all characters are taken from Wang et al. (2004:table 2; char. 1–28 after Wolsan, 1993). A new state has been added for character 13 'occurrence of P4 carnassial notch': 0 = present, 1 = vestigial, 2 = absent. Character 2 in *Bathygale* has been coded as '1' instead of '2' because only two character states were defined by Wolsan (1999:351). Character 13 has been coded as '?' in *Schultzogale* because the P4 is too damaged to be certain on this feature (Wang et al., 2004:414). Characters 16 and 25 in *Leptarctus* have been coded as '0' instead of '1,' because in this taxon the M1 is not smaller than the P4 (Qiu and Schmidt-Kittler, 1982:fig. 5) and the m2 is double-rooted (Olsen, 1957b:453; Qiu and Schmidt-Kittler, 1982:136). Character 23 in *Leptarctus* has been coded as '1' instead of '4,' because the m1 metaconid is subequal in height to the paraconid, as in *Trocharion*.

The mandible (Fig. 3) is low, moderately high, and slenderly built. The shape of the symphysis cannot be ascertained. In lateral view, the corpus is low, maintaining the same height from the canine until the level of the m2. There is no molar sulcus, because the ramus does not overlap with the m2. On the labial side, there are two small and rounded mental foramina under the p2 and p3. The ramus begins just behind the m2; it is relatively broad and much higher than the corpus. The angular process is not preserved; the mandibular condyle is also incompletely preserved and deformed. The masseteric fossa is shallow but marked. On the lingual side there is a posterior mandibular foramen behind the m2. There is a shallow but marked insertion area for the temporal, inferiorly limited by a marked ridge that begins distally from the m2 and ends on the condyle. The coronoid process is broad and thin.

Upper Dentition—The three upper incisors (Fig. 3F–H) are small, uniradiculate, and spatulate, very similar to one another except by the fact that the I3 is larger than the remaining ones, from which it further differs by being asymmetrical. The canine crown (Fig. 3B, C, F–H), as far as it can be ascertained, displays an elliptical basal profile, and in lateral view it is slightly curved distally. On the base of the crown, there is no trace of cingulum, whereas on the distal aspect of the crown, there is a shallow crest that starts in the base of the crown and finishes in the apex.

There are four premolars (Figs. 2B–D, F–H, 4A–C). No crown of the P1 has been preserved, but this tooth was undoubtedly present at least in some specimens, as shown by the alveoli preserved in IPS44028, which further indicates that this premolar was small, uniradiculate, and presumably unicuspid. The P2 is also unicuspid, displays a triangular occlusal outline, and possesses a subtle cingulum on the distal margin of the crown. The P2 is presumably higher than the P1 and lower than the P3. The P3 (Fig. 4A) is globular and low-crowned, and like the P2 shows a triangular occlusal outline. It displays a well-developed, single main cusp (the paracone) on the labial moiety of the crown, although somewhat mesially from it there is also a small parastyle. In the lingual side in IPS33217d and IPS44028, it can be appreciated that the crown base is surrounded by a continuous cingulum. On the latter side of the crown, there is a vestigial talonid that bears no cusp. The P4 (Fig. 4B, C), like the preceding premolar, also displays a triangular occlusal outline, although being labiolingually broader. Moreover, this premolar is clearly larger than the preceding ones, and displays a more developed occlusal relief. As shown by IPS29979, IPS44028, and IPS33217h, on the labial moiety of the crown there is a large and conical paracone as well as an elongated metacone, separated from one another by a moderately developed depression (carnassial notch) on the labial moiety of the crown. Next to these cusps, there is also a small parastyle, mesially separated from the paracone and metacone by a deep groove. On the lingual side, which is lower than the labial one, there is a crest containing the elongated but distinct protocone and the much smaller hypocone. There are also two secondary cusps: a small and conical paraconule, situated mesially from the protocone; and a small accessory cuspule, situated on the distolingual corner of the crown, and separated from the hypocone by a deep groove.

With regard to the M1 (Figs. 2B, D, F–H, 3D–N), it is very similar in size to the P4, but displays a subtrapezoidal occlusal contour, with the labial moiety of the crown being longer than the lingual one. This tooth displays five main cusps; the paracone, situated on the mesiolabial corner of the crown, is a conical and well-defined cusp. Occasionally, as shown by IPS41738, IPS29705, and IPS28096, there is a badly developed paraconule on the mesiolabial corner of the crown. Depending on the specimen, the paraconule can join the paracone directly (IPS28096), join it by through a subtle crest (IPS41738), or be completely isolated from it (IPS29705). The similarly conical and equally protruding metacone is situated somewhat more distally than the paracone. A well-developed and continuous labial cingulum is present from the paraconule (when present) or from the metacone until the metastyle; the latter, situated on the distolabial portion of the crown, is usually individualized, although in some specimens (IPS33220 and IPS41738) it is subdivided into two accessory cuspules. The paracone, metacone, and metastyle are linked by a sharp and mesiodistally aligned crest, except in some cases (IPS31232) where the metastyle is situated more distolabially than the metacone and paracone. On the lingual side, besides the two main cusps (protocone and hypocone), there is a small

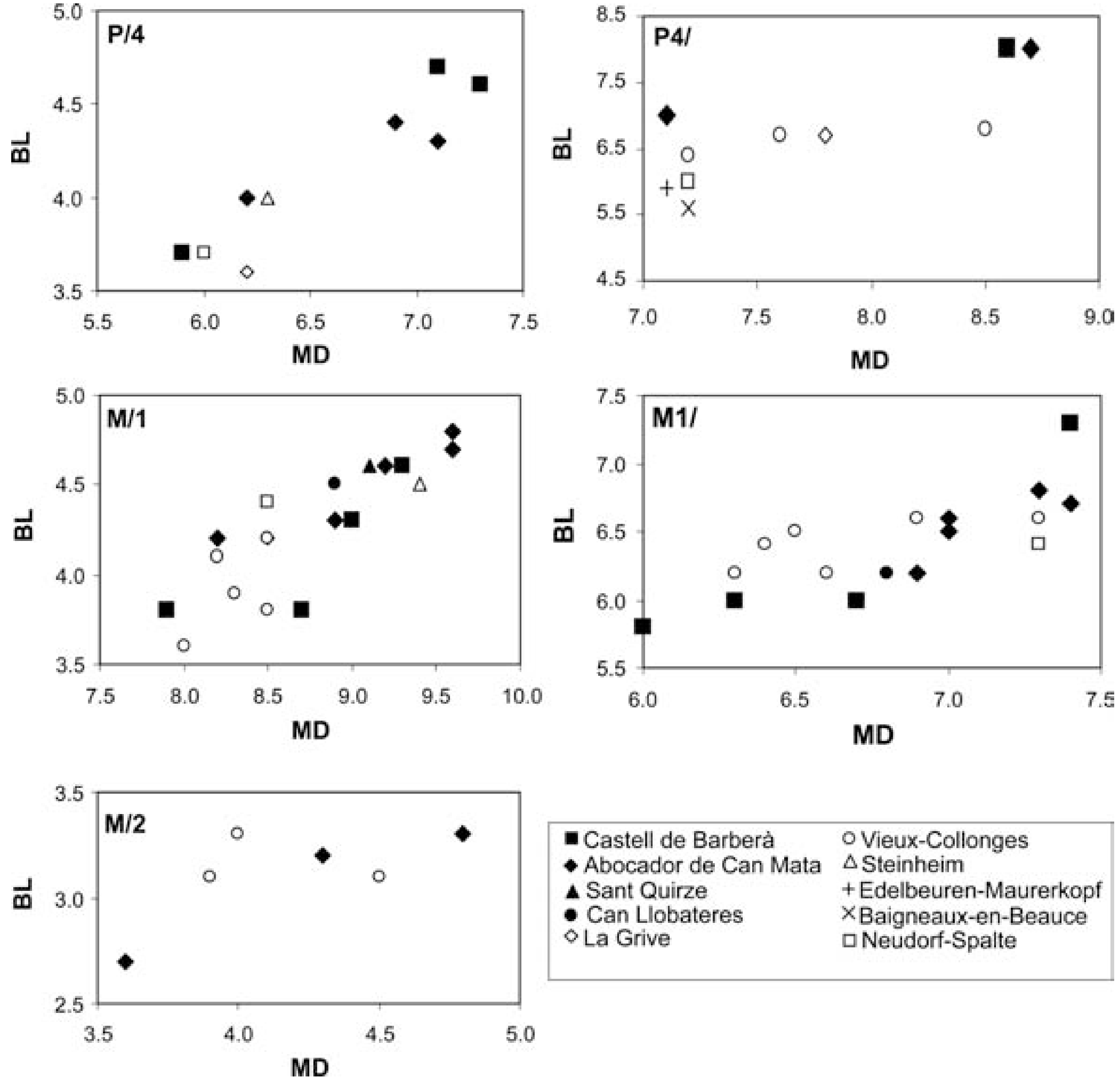

FIGURE 6. Dental proportions of *Trocharion albanense* Major, 1903, from several localities of the Vallès-Penedès Basin (Barcelona, Spain), as compared to other European localities. Data for the latter were taken from the following references: Zapfe (1950) for Spalte von Neudorf a. d. March (Slovakia); Pilgrim (1933) and Viret (1951) for La Grive-Saint-Alban (France); Helbing (1936) for Steinheim (Germany); Mein (1958) for Vieux-Collonges (= Mont Ceindre; France); Ginsburg (2002) for Baigneaux-en-Beauce (France); Von Volker (1999) for Edelbeuren-Maurerkopf (Germany).

secondary cusp (hypoconule) situated on the distolingual portion of the crown, as well as, in some specimens (IPS29705), an additional accessory cuspule situated between the hypoconule and the metastyle. The protocone, transversely aligned on the mesiolingual portion of the crown, is the largest cusp. It displays a continuous lingual cingulum around its base. This cusp is linked to the base of paracone by a crest that sometimes displays several wrinkles or even accessory cuspules. The protocone is also connected to the conical hypocone, which is situated on the distolingual portion of the crown, by a mesiodistal crest, which further incorporates the hypoconule and finishes on the base of the metastyle. Depending on the specimens, this crest can be sharp or rather rugose, even displaying two or three additional accessory cuspules between the hypoconule and the metastyle in some specimens (IPS29705, IPS41738, IPS29979). The M2 is not present.

Lower Dentition—No lower incisors are preserved, so that their number and morphology cannot be ascertained. The lower canine (Figs. 3D–I, 5A) is low-crowned and moderately curved in distal direction, displaying an elliptical basal contour, and smooth lingual and labial sides. In IPS29979, a wear facet can be appreciated, extending from the mesiolingual portion of the apex until the distolabial portion of the crown base, resulting from wear against the upper canine.

There are four lower premolars (Figs. 3A–L, 5B–G), which increase in size from p1 to p4. The morphology of the p1 can be only partially ascertained due to incomplete preservation, although it is unicuspid and uniradiculate. The remaining premolars are similar to one another, by being low-crowned, inflated, biradiculate, and unicuspid. The single main cusp tends to be mesially situated, although the p2 (Fig. 5B) displays a less asymmetrical contour than the p3 (Fig. 5C). The latter displays a subtle lingual cingulid close to the crown base. The p4 (Fig. 5E–G), with a triangular lateral profile, displays a narrow lingual cingulid. This premolar displays a single main mesial cuspid, linked by a weak crest to a small and badly developed cuspulid situated on the mesial portion of the crown. On the distal portion, there are two blunt and wrinkled (in IPS44170) or smooth (in IPS29892 and IPS33217c) crests, which originate from the single main cusp, ending on a valley on the distal portion of the crown.

With regard to the lower molars, the m1 (Figs. 3A–F, M–O, 5H–P) is biradiculate, with an inflated and very low crown (lower than that of the p4) that displays a rectangular occlusal profile, being longer than wide. Generally, the crown is widest at the level of the mesial cuspids (protoconid and metaconid), although in some specimens (IPS43205) both the mesial and distal portions of the crown are equally wide. The trigonid has a triangular shape and bears three main cuspids, connected to one another by a blunt crest: the protoconid, situated on the mesiolabial portion of the crown, and which usually represents the highest area of the trigonid; the paraconid, which is the mesialmost cusp, being positioned on the lingual side; and the more distal metaconid, which is as protruding as the paraconid. The talonid, which is half lower than the trigonid, consists of three different well-developed main cuspids: the entoconid, situated close to the metaconid, on the lingual side; the smaller hypoconid, on the labial side; and the even smaller hypoconulid, situated on the labial side of the crown near hypoconid; there is no entoconulid. These cusps of the talonid are linked by a sharp crest that distally closes the talonid basin, which depending on the specimen can be sharp (IPS43811), wrinkled (IPS41716), or even display some accessory cuspulids (IPS43204 and IPS44170). The trigonid and talonid are partially separated from one another by a labial and a lingual cleft. The m2 (Figs. 3G–I, 5Q–R) is a biradiculate tooth much smaller than the m1 (about half its size). It displays a rectangular occlusal profile, being longer than wide. The trigonid displays two distinct cuspids linked to one another by an oblique cristid: the protoconid, centered on the midline of the mesiodistal crown axis; and the metaconid, situated on the mesiolingual side. The talonid is subequal in size to the trigonid and displays a single cuspid, the hypoconid, situated on the distolabial side of the crown.

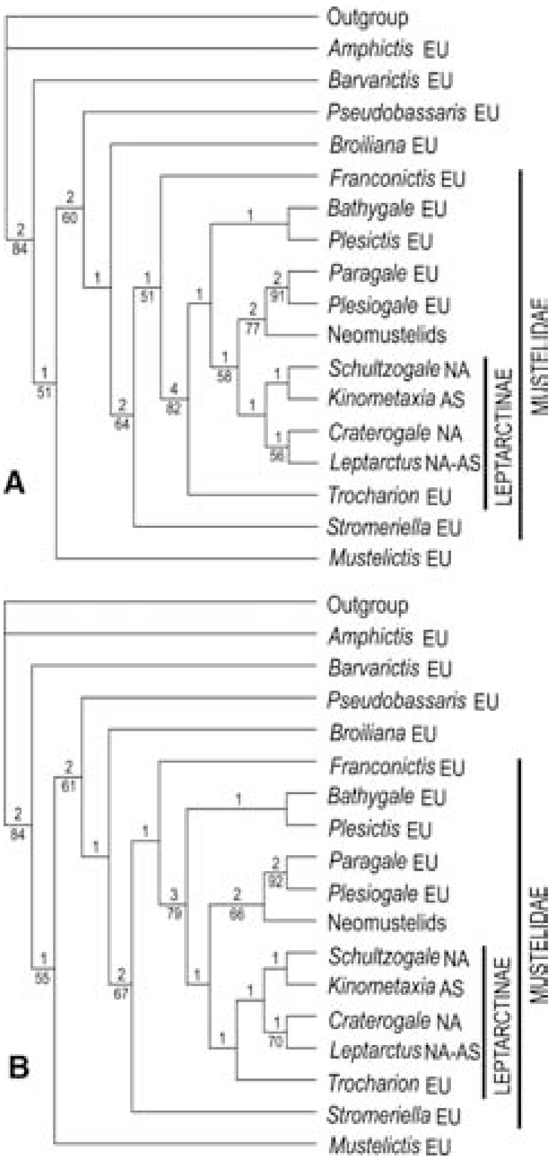

FIGURE 7. Results of the cladistic analysis by means of the Branch and Bound option of PAUP* on a 18 × 31 data matrix (Table 3). **A**, The single shortest tree (length = 75 steps) recovered by using all characters; CI = 0.6400, RI = 0.7955, RC = 0.5091. **B**, The single shortest tree (length = 71 steps) recovered by removing character 13 (i.e., 'presence/absence of carnassial notch'); CI = 0.6479, RI = 0.7967, RC = 0.5162. Bremer decay indices are given above each non-terminal clade, whereas bootstrap proportions for 1000 replicates are given below (only for clades found in more than 50% of the replicates). The geographic provenance of each taxon is signaled by the following abbreviations (following Wolsan, 1993): **EU**, Europe; **AS**, Asia; **NA**, North America; neomustelids display a wider distribution across North and South America, Eurasia, and Africa.

CLADISTIC ANALYSIS

The data matrix employed in the cladistic analysis is reported in Table 3; character states were taken from Wang et al. (2004), except for the addition of *Trocharion*—which the latter authors did not include in their analysis, due to the lack of cranial material—and for some minor changes and corrections. In particular, character 2 in *Bathygale* Wolsan, 1993, and character 23 in *Leptarctus* were coded as '1,' because the character states employed by Wang et al. (2004) were not defined by Wolsan (1993). Also, characters 16 and 25 in *Leptarctus* were coded as '0' (contra Wang et al., 2004), because the M1 of this taxon is not smaller than the P4, and its m2 is two-rooted (Qiu and Schmidt-Kittler, 1982). Furthermore, an intermediate stage has been introduced regarding character 13, 'presence/absence of the carnassial notch.' As previously noted by Qiu and Schmidt-Kittler (1982), *Trocharion* and *Hypsoparia* display a true carnassial notch. Although the latter is lacking in several leptarctines such as *Craterogale*, in *Leptarctus* the paracone and metacone are separated by a long depression that stretches to the crown base (Qiu and Schmidt-Kitter, 1982), which we interpret as a vestigial condition.

The results of the cladistic analysis are reported in Figure 7. The analysis yields a single shortest tree with a length of 75 steps (Figure 7A). This tree closely resemble the strict consensus obtained by Wang et al. (2004:fig. 5A), according to which a leptarctine clade (including *Leptarctus*, *Craterogale*, *Kinometaxia*, and *Schultzogale*) is sister to the clade including neomustelids (or 'mustelids of modern aspect'; Baskin, 1998) and *Paragale* Petter, 1967b + *Plesiogale* Pomel, 1847 (which are here considered stem neomustelids). It must be stressed, however, that if *Trocharion* is included within the Leptarctinae, the most-parsimonious tree fails to recover the monophyly of this group, because *Trocharion* is placed in a very basal position, preceding the divergence between leptarctines and neomustelids. The neomustelid and mustelid clades (if *Mustelictis* is excluded) are relatively well supported by bootstrap results (77% and 64%, respectively) and Bremer indices of 2. On the contrary, neither the leptarctine clade that excludes *Trocharion* nor the leptarctine + neomustelid clade is particularly well supported (bootstrap results only slightly above 50% and Bremer indices of 1). The clade including neomustelids, leptarctines, and the putative stem mustelids *Bathygale* and *Plesictis* Pomel, 1846 ('clade E' of Wolsan, 1993), is the best supported, with bootstrap proportion of 82% and a Bremer index of 4. To sum up, the cladistic analysis reported in Figure 7A is quite inconclusive regarding the phylogenetic position of *Trocharion*, although it clearly shows that this taxon occupies a more basal position than previously hypothesized by Wang et al. (2004).

To a large extent, the exceedingly basal position of *Trocharion* stems from the retention of a carnassial notch in the P4, among other plesiomorphic features. Because the loss of this feature has been previously suggested to be homoplastic with non-leptarctine mustelids (Qiu and Schmidt-Kittler, 1982), we re-ran the analysis by removing character 13, 'presence/absence of carnassial notch.' The resulting analysis yields a single shortest tree (Figure 7B), with a length of 71 steps. This most-parsimonious tree yields very similar results to the preceding analysis, but this time it does recover a monophyletic Leptarctinae, in which *Trocharion* occupies the basal-most position. Nevertheless, the leptarctine clade is not stable, irrespective of whether *Trocharion* is included into it or not, as indicated by bootstrap proportions below 50% and a Bremer index of 1.

DISCUSSION

Comparison with Other Middle Miocene European Musteloids

The craniodental differences between *Trocharion* and other leptarctines are reported in the differential diagnosis. With regard to other middle Miocene musteloids from Europe, besides the diagnostic characters of the Leptarctinae, there are several dental features that enable the distinction between them and *Trocharion*. An exhaustive list cannot be provided here, because this is outside the scope of this paper. Nevertheless, the most obvious differences relate to P4, M1, m1, and m2 proportions and occlusal details. Thus, as compared to the musteline *Martes* Pinel, 1792, and to the gulonines (including *Trochictis* von Meyer, 1842), *Trocharion* differs by the more elongated (less conical) protocone and the presence of a carnassial notch in P4, the relatively much broader M1 crown (which is longer labially than lingually), by the protoconid of the m1 subequal in size relative to paraconid and metaconid, and by the biradiculate m2. The conical protocone of the P4, together with the trigonid much higher than the talonid in m1, further serve to distinguish *Trocharion* from lutrines such as *Paralutra* Roman and Viret, 1834, and the potamotheriine *Potamotherium* Geoffroy Saint-Hilaire, 1833; the latter genus further differs from *Trocharion* by the reduced metaconid relative to paraconid in m1. As compared to melines such as *Taxodon* Lartet, 1851, and *Palaeomeles* Villalta Comella and Crusafont Pairó, 1943b, *Trocharion* differs by the M1 occlusal morphology (which displays more elongated, labiolingually compressed cusps and a more reduced hypocone), the presence of a distinct entoconid in m1, and the biradiculate m2; more specifically, *Palaeomeles* further differs from *Trocharion* by the narrower crown of the P4, the higher size discrepancy between the M1 and the much smaller P4, and the extremely long talonid of the m1. Finally, *Trocharion* differs from mephitids such as *Proputorius* Filhol, 1890, by the occlusal morphology of the M1 (which lacks a distinct hypocone and displays a continuous cingulum) and of the m1 (which displays a protoconid much higher than the remaining cuspids and lacks a distinct entoconid), as well as by the biradiculate m2.

Nomenclatural and Taxonomic Issues

Trocharion albanense was originally described by Major (1903) on the basis of the lower dentition, but the holotype mandible from La Grive was not figured until Pilgrim (1933), who provided an extended diagnosis of this genus and species on the basis of dental features. Just a year before the original description of the species, Schlosser (1902) erected a new species of the genus *Promephitis* Gaudry, 1861 (Musteloidea, Mephitidae), *P. gaudryi*, on the basis of an isolated m1 from Melchingen (Germany). This specimen was later referred to *Trocharion* by Pilgrim (1933), but most recently Ginsburg (1999) listed *P. gaudryi* as a valid species. Given the scarcity of the available material of the latter taxon, its taxonomic status must remain uncertain until more complete material becomes available (Wang and Qiu, 2004). It should be noted, however, that if it finally proved to be synonymous with *T. albanense*, the nomen *Trocharion gaudryi* (Schlosser, 1902) would have priority over *T. albanense* Major, 1903.

Besides *T. albanense*, two other putative leptarctines are known from Europe: *Trochotherium cyamoides* Fraas, 1870, and *Gaillardina transitoria* (Gaillard, 1899). With regard to the former, *Trochotherium* is recorded together with *Trocharion* in the late Aragonian sites of Steinheim (Helbing, 1936) and La Grive (Viret, 1935, 1951). The dentitions of the two genera are very different: whereas *Trocharion* displays an essentially primitive morphology, *Trochotherium* shows several extremely derived features, such as the presence of multiple roots on the P4 and m1, further displaying a peculiar carnassial morphology with almost a single-domed cone without other distinct cusps (Fraas, 1870; Wolsan, 1999; Wang et al., 2005). Moreover, some taxonomic and nomenclatural issues arise regarding some cranial material from Steinheim, as a result of Helbing's (1936) attribution to *T. albanense* of a basicranial specimen that had been previously employed as the holotype of *Palaeomephitis steinheimensis* Jäger, 1839 (SMN 4743). According to Helbing's view, *Palaeomephitis steinheimensis* should be considered a junior subjective synonym of *T. albanense*. Qiu and Schmidt-Kittler (1982), however, disputed the adequacy of this synonymy on the basis of middle ear features, which rather suggest a mephitid status for this taxon (Wolsan, 1999). According to the latter, *Palaeomephitis steinheimensis* would be a senior subjective synonym of *Trochotherium cyamoides*, and *Palaeomephitis* Jäger, 1839, a senior subjective synonym of *Trochotherium* Fraas, 1870. Given the uncertainties surrounding the association of this material, for the time being we will continue employing the nomen *Trochotherium cyamoides*, albeit noting that it should be excluded from the Leptarctinae and that, in any case, *P. steinheimensis* cannot be considered a synonym of *T. albanense*.

Regarding *Gaillardina*, recorded from La Grive (MN7 and MN8; Mein and Ginsburg, 2002), it was classified into the Leptarctinae by Ginsburg (1999), given the possession of a double temporal crest. However, as noted by Wang et al. (2004), the M1 of this taxon does not display the typically bunodont leptarctine morphology, but rather a derived mustelid condition, as shown by the expanded lingual cingulum around the protocone (a morphology more typical of the Guloninae and Melinae). On this basis, Wang et al. (2004) consider it more likely that the double temporal crest of this taxon is an independent acquisition, so that it must be excluded from the Leptarctinae. As such, *Trocharion* remains as the only representative of the Leptarctinae in Europe. Apparently, this genus is represented by a single species. Helbing (1936), when describing the *Trocharion* material from Steinheim (Germany), concluded that the differences with respect to the material from the type locality (La Grive) did not justify a distinction at the species level. Nevertheless, this author conditionally proposed the species *Trocharion fraasi* Helbing, 1936, in case future discoveries might substantiate such distinction. Although according to the International Code of Zoological Nomenclature, new names proposed conditionally before 1961 may be available (ICZN, 1999:Article 15.1), later authors have customarily included the Steinheim material within the hypodigm of *T. albanense* (Villalta Comella and Crusafont Pairó, 1944; Mein, 1958; Petter, 1976; Qiu and Schmidt-Kittler, 1982; Ginsburg, 2002). This view is consistent with the cheek teeth proportions of the material from the Vallès-Penedès Basin reported in this study, which largely overlap from the range displayed by the material from other European sites previously attributed to *T. albanense* (see Fig. 6).

Systematics and Phylogeny

The lack of cranial material of *T. albanense* hindered for many years the understanding of the species in a broad taxonomic context. The upper dentition, for example, was not described and compared with other leptarctine genera until Qiu and Schmidt-Kittler (1982), who first classified *Trocharion* into this family. In their revision of the Leptarctinae, however, these authors did not provide any formal diagnosis of the genus *Trocharion*.

The features shown by the newly recovered, more complete material of *Trocharion* from ACM indicate that this taxon fits with previous diagnoses of the Leptarctinae, based on craniodental characters (Qiu and Schmidt-Kittler, 1982; Wang et al., 2004), except for the retention in this genus of both upper and lower first premolars. On the other hand, the ACM cranial material of *T. albanense* from ACM shows several details of craniodental anatomy that were previously unknown for this genus, and which do not fit previous assumptions based on other members of this group (Wang et al., 2004). This requires the proposal of an emended diagnosis for *T. albanense*, which is the type and only species of the genus *Trocharion*. This emended diagnosis incorporates previously unknown cranial features, such as the rhomboidal shape of the double temporal crests, as well as the presence of the long muzzle compared with the length of the skull, and the shape of the palate. Dentally, the presence of P1 and p1 is confirmed in this taxon. These features, together with several occlusal details of the P4 and M1, are unique among the Leptarctinae, and allow us to distinguish *Trocharion* from the remaining genera of this subfamily, as stated on the differential diagnosis that is proposed in this paper.

Regarding the phylogenetic affinities of *Trocharion*, in the past it was sometimes considered a Melinae (Viret, 1946; Petter, 1967a), although most classical works (Pilgrim, 1933; Helbing, 1936; Villalta, 1944; Petter, 1976) considered it a member of the Mephitidae closely allied to *Mephitis* É. Geoffroy Saint-Hilaire and G. Cuvier, 1795. The leptarctine status of *Trocharion* has been noticed from Qiu and Schmidt-Kittler (1982) onwards, being later accepted by Ginsburg (1999) and further confirmed by the results of the present study. This notwithstanding, several features of *Trocharion* do suggest a remarkably plesiomorphic position for this taxon within the Leptarctinae. The previous cladistic analysis of Wang et al. (2004) concluded that leptarctines are characterized by several synapomorphies, including: (a) a double temporal crest; (b) presence of a partially roughened temporal region; (c) short rostrum; (d) small orbits; and (e) deep zygomatic arches. On the basis of their results, Wang et al. (2004) further suggested that "*Trocharion* should have a cranial morphology at least as advanced as *Kinometaxia* or *Schultzogale*" (Wang et al., 2004:417). Unfortunately the transverse foramen and the ventral projection of the bulla that can be observed in *Kinometaxia*, and which apparently represents an autapomorphy of the latter taxon (Wang et al., 2004), cannot be ascertained due to incomplete preservation in *Trocharion*.

The leptarctine status of *Trocharion* is strengthened by several features reported in this paper, such as the double temporal crest and deep zygomatic arches. At the same time, however, this genus lacks several of the putative leptarctine synapomorphies hypothesized by Wang et al. (2004), as shown by the long muzzle, the less roughened temporal area, the retention of P1, and the possession of a true carnassial notch in the P4. On the basis of the latter feature, Qiu and Schmidt-Kittler (1982) argued that *Trocharion* was a primitive leptarctine, although they suggested that *Craterogale* occupied a more basal position. The results of the cladistic study reported in this paper are not conclusive regarding the phylogenetic position of *Trocharion*, although they indicate that this taxon occupies a more basal position than previously suspected. In particular, our results fail to conclusively support that *Trocharion* is more closely related to leptarctines than to leptarctines + neomustelids, suggesting that this taxon is either a basal leptarctine or a more primitive mustelid. The failure to show conclusively the leptarctine status of *Trocharion* is attributable to the lack of several leptarctine derived features (which would be expected if it is a basal member of the group), as well as to the lack of fossil material showing the condition for several middle-ear features.

The unexpected phylogenetic placement of *Trocharion* in a very basal position, even preceding the leptarctine-neomustelid splitting, depends to a large extent on the possession of a carnassial notch in the former. According to Baskin (1998:155), the primitive retention of a carnassial notch would characterize the paraphyletic group of the 'paleomustelids,' and the cladistic analysis by Wang et al. (2004) further suggests that the loss of the carnassial notch might be a synapomorphy of the clade constituted by leptarctines and neomustelids. Although the presence of this notch in the P4 is primitive for mustelids (Wolsan, 1993; Baskin, 1998), there are good reasons to suspect that it was independently lost in leptarctines and in other mustelids (Qiu and Schmidt-Kittler, 1982). This was recently disputed by Wang et al. (2004), who further considered that *Trocharion* merely displays a remnant carnassial notch. In fact, however, both *Trocharion* and *Hypsoparia* (the latter sometimes synonymized with *Leptarctus*) still retain a true carnassial notch (Qiu and Schmidt-Kittler, 1982; Lim and Martin, 2002:271), whereas only *Leptarctus* s.s. displays a truly vestigial condition. The leptarctines *Craterogale* and *Kinometaxia* do not display a carnassial notch, whereas in *Schultzgale* this condition cannot be ascertained on the basis of currently available material (Wang et al., 2004). Taken together, the dental similarities between *Trocharion*, *Leptarctus*, and *Hypsoparia* strongly suggest that the retention of a carnassial notch is primitive for the Leptarctinae and should not be taken as evidence as to exclude the former genus from this subfamily. We therefore favor the interpretation that *Trocharion* is the basal-most member of the Leptarctinae and that the carnassial notch was independently lost twice, while noting at the same time that further data are required to test the monophyly of leptarctines, some of which might be alternatively interpreted as successive stem mustelids.

Zoogeographic Remarks

If the hypothesis favored here—that *Trocharion* is the basalmost member of the Leptarctinae—is correct, interesting zoogeographic considerations arise. Given the presence of leptarctines across North America, Asia, and Europe, the question arises as to where this group originated. The almost simultaneous appearance in the fossil record during the Early Miocene of *Schultzogale*, *Craterogale*, and *Leptarctus* in North America, and of *Kinometaxia* in Asia, certainly indicates a previous history of diversification of the family that has left no known record (Wang et al., 2004). In spite of its putative more plesiomorphic status, *Trocharion* does not appear until somewhat later, during the earliest middle Miocene of Europe. As noted by Wang et al. (2004), the higher diversity of leptarctines in North America may suggest an origin there. On the contrary, the dental and middle-ear similarities of leptarctines with Early Miocene European basal musteloids such as *Paragale* and *Plesiogale* point out towards an Eurasian origin (Qiu and Schmidt-Kittler, 1982). Given the fact that *Paragale* and *Plesiogale*, preceding by several million years the appearance of the earliest leptarctines, appear to be more closely related to neomustelids (Qiu and Schmidt-Kittler, 1982; Wang et al., 2004; this study), it is likely that both groups diverged during the late Oligocene, so that the earliest leptarctines remain to be discovered or recognized in either Eurasia or North America. The basal position of *Trocharion* within the Leptarctinae proposed here tends to favor the former paleobiogeographic scenario. However, given such a gap in the leptarctine fossil record, it is not possible to reconstruct with any certainty the leptarctine dispersal events that must have taken place during the Early Miocene.

CONCLUSIONS

All the available craniodental remains of the leptarctine carnivoran *Trocharion albanese* from the Vallès-Penedès Basin (Barcelona, Spain) are described. Several of these specimens had been previously described and figured by several authors, but most of the material, recovered from several localities of the Abocador de Can Mata series, remained unpublished. This new material shows several important craniodental features previously unknown for this taxon, such as the retention of p1 and P1, and the presence of double temporal crests with a rhomboidal shape. Accordingly, an emended diagnosis of this species (the type and only species of the genus *Trocharion*), together with a differential diagnosis with respect to other leptarctine genera, and an emended diagnosis of the subfamily Leptarctinae, are provided. The genera *Gaillardina* and *Trochotherium*, traditionally classified into this subfamily, are best classified into other taxa: the Melinae or Guloninae in the case of *Gaillardina*, and the Mephitidae in the case of *Trochotherium*. As such, *Trocharion* is the only Leptarctinae that has been currently recorded in the European continent. A cladistic analysis based on craniodental features is consistent with *Trocharion* being the basalmost member of the Leptarctinae, and suggest that the carnassial notch (still present in this taxon) was independently lost in leptarctines and other mustelids, although the monophyly of the Leptarctinae is not well supported even if *Trocharion* is excluded from it. Although the putative plesiomorphic status of *Trocharion* tends to favor a Eurasian origin of the family, this issue is far from being settled.

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LITERATURE CITED

Aguilar, J.-P., J. Agustí, and J. Gibert. 1979. Rongeurs miocènes dans le Valles-Penedes. 2: Les Rongeurs de Castell de Barbera. Palaeovertebrata 9:17–32.

Agustí Ballester, J. 1981. Roedores Miomorfos del Neógeno de Cataluña. Centre de Publicacions i Intercanvi Científic, Universitat de Barcelona, Barcelona, Spain, 60 pp.

Agustí, J., L. Cabrera, and S. Moyà-Solà. 1985. Sinopsis estratigráfica del Neógeno de la fosa del Vallés-Penedés. Paleontologia i Evolució 18:57–81.

Agustí, J., L. Cabrera, M. Garcés, and J. M. Parés. 1997. The Vallesian mammal succession in the Vallès-Penedès basin (northeast Spain): paleomagnetic calibration and correlation with global events. Palaeogeography, Palaeoclimatology, Palaeoecology 133: 149–180.

Agustí, J., L. Cabrera, M. Garcés, W. Krijgsman, O. Oms, and J. M. Parés. 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. Earth-Science Reviews 52:247–260.

Agustí, J., M. Köhler, S. Moyà-Solà, L. Cabrera, M. Garcés, and J. M. Parés. 1996. Can Llobateres: the pattern and timing of the Vallesian hominoid radiation reconsidered. Journal of Human Evolution 31:143–155.

Alba, D. M., J. Galindo, I. Casanovas Vilar, and S. Moyà-Solà. 2006a. La intervenció paleontològica al dipòsit controlat de residus de Can Mata (els Hostalets de Pierola, Anoia): campanya novembre 2002–agost 2003. Tribuna d'Arqueologia 2003–2004:7–22.

Alba, D. M., J. Galindo, I. Casanovas-Vilar, J. M. Robles, S. Moyà-Solà, M. Köhler, M. Garcés, L. Cabrera, S. Almécija, C. Rotgers, M. Furió, and C. Angelone. 2007. La intervenció paleontològica a la nova fase del dipòsit controlat de Can Mata (Els Hostalets de Pierola, Anoia): campany es 2002–2003, 2004 i 2005. Tribuna d'Arqueologia 2006:7–33.

Alba, D. M., S. Moyà-Solà, I. Casanovas-Vilar, J. Galindo, J. M. Robles, C. Rotgers, M. Furió, C. Angelone, M. Köhler, M. Garcés, L. Cabrera, S. Almécija, and P. Obradó. 2006b. Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l'Anoia, Cataluña), una sucesión de localidades del Aragoniense superior (MN6 y MN7+8) de la cuenca del Vallès-Penedès. Campañas 2002–2003, 2004 y 2005. Estudios Geológicos 62:295–312.

Bartrina, M. T., L. Cabrera, M. J. Jurado, J. Guimerà, and E. Roca. 1992. Evolution of the central Catalan margin of the Valencia trough (western Mediterranean). Tectonophysics 203:219–247.

Baskin, J. A. 2005. Carnivora from the late Miocene Love Bone Bed of Florida. Bulletin of the Florida Museum of Natural History 45:413–434.

Baskin, J. A. 1998. Mustelidae; pp. 152–173 in C. M. Janis, K. M. Scott and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America, Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge, U.K.

Bataller, J. R. 1924. Contribució a l'estudi de nous mamífers fòssils de Catalunya. Arxius de l'Institut de Ciències 12:36–41.

Bataller, J. R. 1938. Els Ratadors Fòssils de Catalunya. Impremta de la Casa d'Assistència President Macià, Barcelona, Spain, 64 pp.

Begun, D. R., S. Moyà-Solà, and M. Köhler. 1990. New Miocene hominoid specimens from Can Llobateres (Vallès Penedès, Spain) and their geological and paleoecological context. Journal of Human Evolution 19:255–268.

Bonis, L. de 2005. Carnivora (Mammalia) from the late Miocene of Akkaşdaği, Turkey. Geodiversitas 27:567–589.

Bowdich, T. E. 1821. An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travellers. J. Smith, Paris, France, 115 pp.

Bremer, K. 1994. Branch support and tree stability. Cladistics 10:295–304.

Cabrera, L., and F. Calvet. 1990. Sequential arrangement of the Neogene sedimentary record in the Vallès-Penedès and Valls-Reus half grabens, Iberian margins, NE Spain. Terra Abstracts 2:1–110.

Cabrera, L., and F. Calvet. 1996. Onshore Neogene record in NE Spain: Vallès-Penedès and El Camp grabens (NW Mediterranean); pp. 97–105 in P. F. Friend and C. Dabrio (eds.), Tertiary Basins of Spain. Cambridge University Press, Cambridge, U.K.

Cabrera, L., E. Roca, M. Garcés, and J. de Porta. 2004. Estratigrafía y evolución tectonosedimentaria oligocena superior-neógena del sector central del margen catalán (Cadena Costero-Catalana); pp. 569–573 in J. A. Vera (ed.), Geología de España. SGE-IGME, Madrid, Spain.

Casanovas-Vilar, I. 2007. The rodent assemblages from the late Aragononian and the Vallesian (middle to late Miocene) of the Vallès-Penedès Basin (Catalonia, Spain). Ph.D. dissertation, Universitat Autònoma de Barcelona, Spain, 286 pp.

Casanovas-Vilar, I., D. M. Alba, S. Almécija, J. M. Robles, J. Galindo, and S. Moyà-Solà. 2008a. Taxonomy and paleobiology of the genus *Chalicomys* Kaup, 1832 (Rodentia, Castoridae), with the description of a new species from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, Spain). Journal of Vertebrate Paleontology 28:851–862.

Casanovas-Vilar, I., D. M. Alba, S. Moyà-Solà, J. Galindo, L. Cabrera, M. Garcés, M. Furió, J. M. Robles, M. Köhler, and C. Angelone. 2008b. Biochronological, taphonomical and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae). Journal of Human Evolution 55:589–603.

Crusafont Pairó, M. 1958. Nuevo hallazgo del póngido vallesiense *Hispanopithecus*. Boletín Informativo del Instituto de Paleontología de Sabadell 13–14:37–41, 6–8.

Crusafont Pairó, M. 1964. La biota de Can Llobateres (Sabadell) y su significación biológica. Cursillos y Conferencias del Instituto "Lucas Mallada" 9:177–179.

Crusafont-Pairó, M., and J. M. Golpe. 1972. Dos nuevos yacimientos del vindoboniense en el Vallés. Acta Geológica Hispánica 7:71–72.

Crusafont-Pairó, M., and J. M. Golpe-Posse. 1981. Estudio de la dentición inferior del primer pliopitécido hallado en España (Vindoboniense terminal de Castell de Barberà, Cataluña, España). Butlletí Informatiu de l'Institut de Paleontologia de Sabadell 13:25–38.

Crusafont, M., and J. Truyols. 1954. Catálogo Paleomastológico del Mioceno del Vallés-Penedés y de Calatayud-Teruel. Segundo Cursillo Internacional de Paleontología. Museo de la Ciudad de Sabadell, Sabadell, Spain, 25 pp.

De Bruijn, H., R. Daams, G. Daxner-Höck, V. Fahlbusch, L. Ginsburg, P. Mein, and J. Morales. 1992. Report of the RCMNS working group on fossil mammals Reisenburg 1990. Newsletters on Stratigraphy 26:65–118.

Dorr, J. A. 1954. *Hypsoparia bozemanensis*: a new genus and species of Leptarctine mustelid from the late Miocene Madison Valley Formation of Montana. Annals of the Carnegie Museum 33: 179–184.

Filhol, H. 1890. Études sur les Mammifères fossiles de Sansan. Bibliothèque de l'École des Hautes Études, section Sciences Naturelles 37:1–319.

Fischer von Waldheim, G. 1817. Adversaria zoologica. Mémoires de la Société Imperiale des Naturalistes de Moscou 5:368–428.

Flower, W. H. 1869. On the value of the characters of the base of the cranium in the classification of the order Carnivora, and on the systematic position of *Bassaris* and other disputed forms. Proceedings of the Zoological Society of London 1869:4–37.

Fraas, O. 1870. Die Fauna von Steinheim, mit Rüecksicht auf die miocänen Säugethier- und Vogelreste des Steinheimer Beckens. Württembergische Naturwissenschaftliche Jahrhfte 26:145–306.

Gaillard, C. 1899. Mammifères miocènes nouveaux ou peu connus de La Grive-Saint-Alban (Isère). Archives du Muséum d'Histoire Naturelle de Lyon 78:1–78.

Gaudry, A. 1861. Résultats des fouilles entreprises en Grèce sous les auspices de l'Académie. Compte Rendus de l'Académie des Sciences Paris 52:722–724.

Gazin, C. L. 1936. A new mustelid carnivore from the Neogene beds of northwestern Nebraska. Journal of Washington Academy of Science 26:199–207.

Geoffroy Saint-Hilaire, É. 1833. Considérations sur les ossements fossiles, la plupart inconnus, trouvés et observés dans les bassins de l'Auvergne. Revue Encyclopedique 59:76–95.

Geoffroy Sain-Hilaire, É., and G. Cuvier. 1795. Mémoire sur une nouvelle division des mammifères, et sur les principes qui doivent servir de base dens cette sorte de travail. Magasin Encyclopédique 2: 164–190.

Ginsburg, L. 1990a. Les quatre faunes de Mammifères miocènes des faluns du synclinal d'Esvres (Val-de-Loire, France). Comptes Rendus de l'Académie des Sciences, Paris 310:89–90.

Ginsburg, L. 1990b. The faunas and stratigraphical subdivisions of the Orleanian in the Loire Basin (France); pp. 157–176 in E. H. Lindsay, V. Fahlbush, and P. Mein (eds.), European Neogene Mammal Chronology. Plenum Press, New York.

Ginsburg, L. 1999. Order Carnivora; pp. 109–148 in G. E. Rössner, and K. Heissig (eds.), The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, München, Germany.

Ginsburg, L. 2001. Les faunes de mammifères terrestres du Miocène moyen des Faluns du bassin de Savigné-sur-Lanthan (France). Geodiversitas 23:381–394.

Ginsburg, L. 2002. Les carnivores fossiles des sables de l'Orléanais. Annales de Paléontologie 88:115–146.

Golpe-Posse, J. M. 1974. Faunas de yacimientos con suiformes en el Terciario español. Paleontología y Evolución 8:1–87.

Golpe-Posse, J. M. 1977. *Barberahyus castellensis* n.g.n.sp., tayasuido del Vindoboniense terminal de Castell de Barberà (Cuenca del Vallès, España). Paleontología y Evolución 12:31–43.

Helbing, H. 1936. Die Carnivoren des Steinheimer Beckens. A. Mustelidae. Palaeontographica Supplement 8:1–56.

International Commission on Zoological Nomenclature (ICZN). 1999. International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature, London.

Jäger, G. F. 1839. Über die fossilen Säugethiere, welche in Würtemberg in verschiedenen Formationen aufgefunden worden sind, nebst geognostischen Bemerkungen über diese Formationen. Abtheilung 2:71–212. Carl Erhard, Stuttgart, Germany.

Kretzoi, M. 1943. *Kochitis centenii* n. g. n. sp., ein altertumlicher Creodonte aus dem Oberoligozan Siebenburgens. Foldtany Kozlony 52:10–195.

Lartet, E. 1851. Notice sur la Colline de Sansan, suvie d'une récapitulation des diverses espèces d'animaux dertébrés fossiles trouvés soit a Sansan, soit dans d'autres gisements du terrain tertiaire Miocène dans le Bassin Sous-Pyrénéen. J.-A. Portes, Imprimeur de la Préfecture et Libraire, 45 pp.

Leidy, J. 1856. Notice of extinct Vertebrata, discovered by Dr. F. V. Hayden, during the expedition to the Sioux County under the command of Lieut. G. K. Warren. Proceedings of the Academy of Natural Science of Philadelphia 8:311–312.

Lim, J.-D., and L. D. Martin. 2000. A new primitive Leptarctinae (Mustelidae) from the North America Miocene. Neues Jahrbuch fur Geologie und Palaontologie-Monatshefte 10:632–640.

Lim, J.-D., and L. D. Martin. 2001. New evidence for plant-eating in a Miocene mustelid. Current Science 81:314–317.

Lim, J.-D., and L. D. Martin. 2002. A new fossil mustelid from the Miocene of South Dakota, USA. Naturwissenschaften 89:270–274.

Lim, J.-D., L. D. Martin, and R. W. Wilson. 2001. A new species of *Leptarctus* (Carnivora: Mustelidae) from the late Miocene of Texas. Journal of Paleontology 75:1043–1046.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Vol. I: Regnum Animale. Editio Decima, Reformata. Laurentii Salvii, Stockholm, Sweden, 823 pp.

Major, F. 1903. New Carnivora from the middle Miocene of La Grive Saint Alban, Isère, France. Geological Magazine 10:534–537.

Matthew, W. D. 1924. Third contribution to the Snake Creek Fauna. Bulletin of the American Museum of Natural History 50:59–210.

McKenna, M. C., and S. K. Bell. 1997. Classification of Mammals above the Species Level. Columbia University Press, New York, 640 pp.

Mein, M. P. 1958. Les mammifères de la faune siderolithique de Vieux-Collonges. Nouvelles Archives du Muséum Naturelle de Lyon 5:1–122.

Mein, M. P., and L. Ginsburg. 2002. Sur l'âge relatif des différents dépôts karstiques miocènes de La Grive-Saint-Alban (Isère). Cahiers scientifiques 2/2002:7–47.

Mörs, T. 2002. Biostratigraphy and paleocology of continental Tertiary vertebrate faunas in the Lower Rhine Embayment (NW-Germany). Netherlands Journal of Geosciences/Geologie en Mijnbouw 81:177–183.

Moyà-Solà, S., and M. Köhler. 1993. Recent discoveries of *Dryopithecus* shed new light on evolution of great apes. Nature 365:543–545.

Moyà-Solà, S., and M. Köhler. 1996. A *Dryopithecus* skeleton and the origins of great-ape locomotion. Nature 379:156–159.

Moyà-Solà, S., M. Köhler, D. M. Alba, I. Casanovas-Vilar, and J. Galindo. 2004. *Pierolapithecus catalaunicus*, a new middle Miocene great ape from Spain. Science 306:1339–1344.

Moyà-Solà, S., M. Köhler, D. M. Alba, I. Casanovas-Vilar, J. Galindo, J. M. Robles, L. Cabrera, M. Garcés, S. Almécija, and E. Beamud. 2009. First partial face and upper dentition of the middle Miocene hominoid *Dryopithecus fontani* from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, NE Spain): taxonomic and phylogenetic implications. American Journal of Physical Anthropology 139:126–145.

Olsen, S. J. 1957a. Leptarctines from the Florida Miocene (Carnivora, Mustelidae). American Museum Notitates 1861:1–7.

Olsen, S. J. 1957b. The lower dentition of *Mephititaxus ancipidens* from the Florida Miocene. Journal of Mammalogy 38:452–454.

Olsen, S. J. 1958. The skull of *Leptarctus ancipidens* from the Florida Miocene. Contribution to Florida Vertebrate Paleontology Special Publication 2:1–11.

Olsen, S. J. 1959. The middle ear of the Miocene mustelid *Leptarctus*. Journal of Paleontology 33:451–452.

Petter, G. 1967a. Mustélidés nouveaux du Vallésien de Catalogne. Annales de Paléontologie 53:93–113.

Petter, G. 1967b. *Paragale hürzeleri* nov. gen., nov. sp., Mustélidé nouveau de l'Aquitanien de l'Allier. Bulletin de la Societé géologique de France 9:19–23.

Petter, G. 1976. Étude d'un nouvel ensemble de petits carnivores du Miocène d'Espagne. Géologie Méditerranéenne 3:135–154.

Pilgrim, G. E. 1933. The genera *Trochictis*, *Enhydrictis*, and *Trocharion*, with remarks on the taxonomy of the Mustelidae. Proceedings of the Zoological Society of London 1932:845–867.

Pinel, P. 1792. Recherches sur une nouvelle méthode de classification des quadrupèdes, fondée sur la structure mécanique des parties osseuses qui servent à l'articulation de la mâchoire inférieure. Actes de la Societé d'Histoire Naturelle de Paris 1:50–60.

Pomel, A. 1846. Mémoire pour servir à la géologie paléontologique des terrains tertiaires du département de l'Allier. Bulletin de la Societé géologique de France 3:353–373.

Pomel, A. 1847. Note sur des animaux fossiles découverts dans le département de l'Allier. Bulletin de la Societé géologique de France 4:378–385.

Qiu, Z.-X., and N. Schmidt-Kittler. 1982. On phylogeny and zoogeography of the leptarctines (Carnivora, Mammalia). Paläontologische Zeitschrift 56:131–145.

Roca, E., and P. Desegaulx. 1992. Geological evolution and vertical movement analysis of the Valencia Trough area (western Mediterranean). Marine Petrology and Geology 9:167–185.

Roca, E., and J. Guimerà. 1992. The Neogene structure of the eastern Iberian margin: structural constraints on the crustal evolution of the Valencia Trough (Western Mediterranean). Tectonophysics 203:203–218.

Roman F., and J. Viret. 1834. La faune de Mammifères du Burdigalien de la Romieu (Gers). Mémoires de la Société géologique de France 9:1–67.

Schlosser, M. 1902. Beiträge zur Kenntniss der Säugerthierreste aus den süddeutschen Bohnerzen. Geologische und Palaeontologische Abhandlungen, Jena 5:117–258.

Smith, J. B., and P. Dodson. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. Journal of Vertebrate Paleontology 23:1–12.

Swofford, D. L. 2003. PAUP* 4.0. Sinauer Associates, Sunderland, Massachusetts.

Tedford, R. H. 1976. Relationship of pinnipeds to other carnivores (Mammalia). Systematic Zoology 25:363–374.

Villalta Comella, J. F. de, and M. Crusafont Pairó. 1941. Hallazgo del "Dryopithecus fontani", Lartet, en el Vindoboniense de la cuenca Vallés-Penedés. Boletín del Instituto Geológico y Minero de España 20:1–15.

Villalta Comella, J. F. de, and M. Crusafont Pairó. 1943a. Tres nuevas localidades de mamíferos del Pontiense del Vallés-Panadés (Provincia de Barcelona). Boletín de la Real Sociedad Española de Historia Natural 41:215–222.

Villalta Comella, J. F. de, and M. Crusafont Pairó. 1943b. Los vertebrados del Mioceno continental de la Cuenca del Vallés-Penedés (Provincia de Barcelona). I. Insectívoros—II. Carnívoros. Boletín Geológico y Minero de Espana 56:145–336.

Villalta Comella, J. F. de, and M. Crusafont Pairó. 1944. Nuevos carnívoros del Vindoboniense de la cuenca del Vallés-Panadés. Notas y Comunicaciones del Instituto Geológico y Minero de España 13:55–88.

Viret, J. 1935. Sur la présence de *Trochotherium cyamoides* Fraas à la Grive Saint-Alban. Comptes rendus sommaires des Séances de la Société géologique de France 1935:85–87.

Viret, J. 1946. Sur la position systématique du Mélidé Miocène *Trocharion albanense* Major. Bulletin de la Société Linnéenne de Lyon 4:25–28.

Viret, J. 1951. Catalogue critique de la faune des Mammifères Miocènes de La Grive-Saint-Alban (Isère). I: Chiroptères, Carnivores, Édentés Pholidotes. Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon 3:1–102.

Von Meyer, H. 1842. Mitheilungen an Professor Brown gerictet. Neues Jahrbuch fur Mineralogie, Geologie, Geognasie und Petrafakten-Kunde 1842:583–589.

Von Volker, J. S. 1999. Litho- and biostratigraphical investigations in the Upper Freshwater Molasse of the district Bilverach a.d. Riss (Upper Swabia). Stuttgarter Beitrage zur Naturkunde Ser. B 276:1–138.

Wang, X., and Z. Qiu. 2004. Late Miocene *Promephitis* (Carnivora, Mephitidae) from China. Journal of Vertebrate Paleontology 24:721–731.

Wang, X., Z. Qiu, and B. Wang. 2004. A new Leptarctinae (Carnivora: Mustelidae) from the Early Miocene of the northern Tibetan Palteau: implications for the phylogeny and zoogeography of basal mustelids. Zoological Journal of the Linnean Society 142: 405–421.

Wang, X., D. P. Whistler, and G. Takeuchi. 2005. A new basal skunk *Martinogale* (Carnivora, Mephitinae) from late Miocene Dove Spring Formation, Caliornia, and origin of New World mephitines. Journal of Vertebrate Paleontology 25:936–949.

White, T. E. 1941. Addition to the Miocene fauna of Florida. Proceedings of the New England Zoological Club 18:91–98.

Wolsan, M. 1993. Phylogeny and classification of early European Mustelida (Mammalia: Carnivora). Acta Theriologica 38:345–384.

Wolsan, M. 1999. Oldest mephitine cranium and its implications for the origin of skunks. Acta Palaeontologica Polonica 44:223–230.

Wortman, J. 1894. On the affinities of *Leptarctus primus* of Leidy. Bulletin of the American Museum of Natural History 6:229–231.

Zapfe, H. 1950. Die Fauna der miozänen Spaltenfüllung von Neudorf a. d. March (ČSR). Carnivora. Sitzungsberichten der Österreichischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse Abteil I 159:109–141.

Zhai, R. J. 1964. *Leptarctus* and other Carnivora from the Tung Gur Formation, Inner Mongolia. Vertebrata PalAsiatica 8:18–30. [Chinese with an English summary]

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Chapter 6. New craniodental remains of the barbourofelid *Albanosmilus jourdani* (Filhol, 1883) from the Miocene of the Vallès-Penedès Basin (NE Iberian Peninsula) and the phylogeny of the Barbourofelini

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New craniodental remains of the barbourofelid *Albanosmilus jourdani* (Filhol, 1883) from the Miocene of the Vallès-Penedès Basin (NE Iberian Peninsula) and the phylogeny of the Barbourofelini

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Available remains of the barbourofelin *Albanosmilus jourdani* from the Middle to Late Miocene of the Vallès-Penedès Basin (NE Iberian Peninsula) are described. In addition to the dentognathic remains described by previous authors, the new material includes a complete cranium, a calvarium and several mandibles from Abocador de Can Mata, Creu Conill 20 and Hostalets Superior. It is concluded that *Albanosmilus*, previously considered a subjective junior synonym of *Sansanosmilus*, must be resurrected as a polytypic genus including *A. jourdani* (= *A. vallesiensis*). The most plesiomorphic North American barbourofelin, previously included in *Barbourofelis*, is also transferred into *Albanosmilus* as *A. whitfordi*. An emended diagnosis of *Albanosmilus* is provided. The results of a cladistic analysis support the monophyly of the family Barbourofelidae and the tribe Barbourofelini, further indicating that amongst the latter, *Sansanosmilus* occupies the basalmost position. The two *Albanosmilus* species are more derived, although the analysis fails to resolve conclusively whether *A. whitfordi* is more closely related to *A. jourdani* or *Barbourofelis* s.s. From a palaeobiogeographical viewpoint, our results suggest that: (1) barbourofelins originated in Eurasia during the early Middle Miocene; (2) *Barbourofelis* originated in North America during the late Middle Miocene, following the dispersal of Eurasian *Albanosmilus* into that continent; and (3) the presence of *Barbourofelis* in Turkey during the Late Miocene may represent a later independent dispersal event from North America back into Eurasia.

Keywords: *Sansanosmilus*; *Barbourofelis*; Nimravidae; Barbourofelidae; Afrosmilini; false sabre-toothed cats

Introduction

Barbourofelids are extinct carnivorans with hyperdeveloped and compressed upper canines that, together with nimravids, may be termed 'false' sabre-toothed cats, as opposed to the 'true' sabre-toothed cats of the felid subfamily Machairodontinae. Initially distinguished at the tribe level within Felidae (Schultz *et al.* 1970), barbourofelids were later recognized as a subfamily of Nimravidae (Neff 1983; Hunt 1987; Bryant 1991; McKenna & Bell 1997; Martin 1998; Peigné 2003).

Subsequently, Morales *et al.* (2001) advocated a closer relationship with felids, which is further supported by the fact that a sister-group relationship between Nimravinae and Barbourofelinae would imply a ghost lineage for the latter of about 35 million years (Peigné 2003). Recently, Morlo *et al.* (2004) elevated this group to family rank, distinguished from both Nimravidae and Felidae on the basis of dental and cranial features, particularly of the tympanic region (see also Peigné & de Bonis 2003).

Barbourofelid fossils are relatively scarce but are nevertheless widely distributed across Africa, Eurasia and North America. The following genera are included: *Barbourofelis* Schultz *et al.*, 1970, from the late Middle and Late Miocene of North America (Schultz *et al.* 1970; Geraads & Güleç 1997; Morlo *et al.* 2004; Tseng *et al.* 2010); *Ginsburgsmilus* Morales, *et al.* 2001, from the Early Miocene of Kenya and Uganda (Morales *et al.* 2001; Morlo *et al.* 2004; Werdelin & Peigné 2010); *Afrosmilus* Kretzoi, 1929, from the Early Miocene of Kenya, Namibia and Spain (Schmidt-Kittler 1987; Morales *et al.* 2001, 2007; Morlo *et al.* 2004; Werdelin & Peigné 2010); *Syrtosmilus* Ginsburg, 1978, from the Early Miocene of Libya (Ginsburg 1978; Morlo *et al.* 2004; Werdelin & Peigné 2010); *Prosansanosmilus* Heizmann *et al.*, 1980, from the Early (MN4) and Middle (MN5) Miocene of Central Europe; *Vampyrictys* Kurtén,

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1976, from the early Late Miocene of Tunisia (Kurtén 1976; Morlo *et al.* 2004; Werdelin & Peigné 2010); and *Sansanosmilus* s.l. Kretzoi, 1929, from the Middle (MN5 to MN7+8) and Late (MN9) Miocene of Eurasia (see below). We follow Morales *et al.* (2001) in grouping the above-listed genera into Afrosmilini, with the exception of *Sansanosmilus* s.l. and *Barbourofelis*, which can be grouped into the tribe Barbourofelini. As will be explained later, we here recognize *Albanosmilus* Kretzoi, 1929 as a distinct valid genus instead of a junior subjective synonym of *Sansanosmilus*.

Sansanosmilus and *Barbourofelis*

Although barbourofelid origins are unclear, this family underwent an early radiation in the Early Miocene of Africa (Morales *et al.* 2001; Morlo *et al.* 2004), later dispersing into Eurasia during the late Early Miocene. Barbourofelids are first recorded there by *Prosansanosmilus peregrinus* Heizmann *et al*., 1980 and *Afrosmilus hispanicus* Morales *et al*., 2001 in MN4 (Morales *et al.* 2001; Morlo *et al.* 2004), although *Prosansanosmilus eggeri* Morlo *et al*., 2004 from MN5 of Europe is apparently more plesiomorphic (Morlo *et al.* 2004).

Barbourofelins might have locally evolved in Eurasia from *P. eggeri* or another species of *Prosansanosmilus* (Nagel 2009). North American members of this group, in turn, could have originated from a Eurasian barbourofelin that dispersed into North America around the MN7+8/MN9 boundary (Geraads & Güleç 1997), being subsequently recorded until the Late Miocene (Bryant 1991; Morlo *et al.* 2004; Tseng *et al.* 2010).

Two Eurasian *Sansanosmilus* species are generally recognized: *S. palmidens* (de Blainville, 1843), from MN5 to MN6 or MN7+8 of France (Ginsburg 1961, 1999, 2001; Fortelius 2011) and MN6 of China (Chen & Wu 1976; Qiu & Qiu 1995); and *S. jourdani* (Filhol, 1883), from MN9 of Turkey (Viranta & Werdelin 2003; Morlo 2006), MN7+8 and MN9 of Germany (Fraas 1885; Heizmann 1973; Morlo 2006; Fortelius 2011), MN6 of Slovakia (Sabol *et al.* 2004), MN9 of Hungary (Bernor *et al*. 2002; Werdelin 2005), MN7 of France (Filhol 1883; Depéret 1892; Viret 1951; Mein & Ginsburg 2002; Fortelius 2011), MN9 or MN10 of Portugal (Roman 1907), and MN6, MN7+8 and MN9 of Spain (Crusafont-Pairó & Ginsburg 1973; Alberdi Alonso 1981; Ginsburg *et al.* 1981; Fraile *et al*. 1997; Álvarez-Sierra *et al*. 2003; Azanza *et al*. 2004; Peigné *et al.* 2006). *Sansanosmilus* is also recorded from several late Aragonian and early Vallesian localities in the Vallès-Penedès Basin. It is currently uncertain whether this material is referable to *S. jourdani* and/or to the purportedly different (sub)species *S. jourdani vallesiensis* de Beaumont & Crusafont-Pairó, 1982, also referred to as either *Sansanosmilus vallesiensis* (Morlo *et al.* 2004; Nagel 2009) or *?Barbourofelis vallesiensis* (Geraads & Güleç 1997). Originally based on remains from the Vallès-Penedès Basin, the barbourofelid from the Austrian locality of Atzelsdorf (MN9) has been also attributed to this taxon (Nagel 2009), which is here considered a junior synonym of *Albanosmilus jourdani*.

In North America (USA), barbourofelids are represented by up to four species customarily classified in the genus *Barbourofelis* (e.g. Tseng *et al.* 2010): *B. morrisi* Schultz *et al*., 1970, from the late Middle and early Late Miocene (12.0–9.5 Ma); *B. loveorum* Baskin, 1981, from the Late Miocene (9.5–8.0 Ma); *B. fricki* Schultz *et al.*, 1970, from the Late Miocene (9.0–7.0 Ma); and *B. whitfordi* (Barbour & Cook, 1914), from the late Middle and Late Miocene (12.0–7.0 Ma), which is here also transferred to *Albanosmilus*. Several authors have considered that *Barbourofelis* is also present in Eurasia. Geraads & Güleç (1997), in particular, not only tentatively transferred *S. vallesiensis* to *Barbourofelis* (see also Schultz *et al.* 1970) but included the Turkish species *Sansanosmilus piveteaui* (Ozansoy 1965) in the latter genus, which is the attribution followed here.

We describe here new dental, mandibular and cranial remains of the Eurasian barbourofelid *Albanosmilus jourdani* from the Vallès-Penedès Basin, together with previously published remains of this taxon from the same basin. The new remains include a complete cranium, a calvarium and several mandibles, which contribute to a better understanding of the taxonomic and phylogenetic status of other Eurasian barbourofelin species, as well as of their phylogenetic relationships with American members of this tribe.

Material and methods

Dental nomenclature

The dental nomenclature employed in this paper is based on Smith & Dodson (2003). Standard dental measurements (labiolingual breadth and mesiodistal length) are employed. Cranial and mandibular measurements are based on Schultz *et al.* (1970).

Anatomical and morphometric abbreviations

BL: labiolingual crown breadth; **d**: deciduous; **C**: upper canine; **c**: lower canine; **I**: upper incisor; **i**: lower incisor; **L**: left; **LC**: maximum cranial length (from the anterior part of the crown of I1 to the posterior end of the condyles); **LM**: maximum mesiodistal mandibular length; **LS**: maximum length of the symphysis; **M**: upper molar; **m**: lower molar; **ML**: mesiodistal crown length; **P**: upper premolar; **p**: lower premolar; **R**: right; **WC**: maximum cranial width (greatest width across the zygomatic arches); **WCO**: maximum width across condyles; **WF**: maximum width of the flange; **WM**: maximum mandibular width (from the upper crown of the c1 to the basalmost border of the flange); **WM1**: maximum width of the mandibular corpus under the m1; **WP**: maximum palate width (at the level of the upper carnassials); **WPC**: maximum palate width (at the level of the upper canines).

Cladistic abbreviations. CI: consistency index; **RI**: retention index; **RC**: rescaled consistency index.

Institutional abbreviations. AMNH: American Museum of Natural History, New York, USA; **ICP**: Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Catalonia, Spain; **IPS**: 'Institut de Paleontologia de Sabadell', acronym of the collections of the ICP.

Locality abbreviations. ACM: local stratigraphical series of Abocador de Can Mata; **B40OV/S5**: Autovia Orbital de Barcelona, stretch Olesa de Montserrat – Viladecavalls, Sector 5 (Viladecavalls); **C3**: Cell 3; **C4**: Cell 4; **C6**: Cell 6; **C7**: Cell 7; **C8**: Cell 8; **CB**: Castell de Barberà; **CCN20**: Creu Conill 20; **CG1**: local stratigraphical section of Can Guitart 1; **CL1**: Can Llobateres 1; **CM1**: Can Mata 1 (= Bretxa de Can Mata); **CMS**: Can Missert (= Cerámicas Terras SA); **CPO**: Can Poal; **CP1**: Can Poncic 1; **HI**: Hostalets Inferior (= Lower Hostalets de Pierola); **HS**: Hostalets Superior (= Upper Hostalets de Pierola); **SA**: Santiga; **SQ**: Sant Quirze (= Trinxera del Ferrocarril).

Material

All specimens of *Albanosmilus jourdani* described in this paper (see Table 1) are housed at the ICP. This material comes from several Middle and Late Miocene localities from the Vallès-Penedès Basin. Part of the material was previously described by de Villalta Comella & Crusafont Pairó (1943a, b) in the case of SQ and CM1, and by de Beaumont & Crusafont-Pairó (1982) for CB, CL1, CP and SA.

The remaining material is unpublished, and comes from the localities of CCN20 (reported but not described by Casanovas-Vilar *et al.* 2006) and CM (reported but not described by Agustí *et al*. 1985, 2005), as well as from several localities of the ACM local stratigraphical series: C3-Ak, C4-C2, C5-C4, C6-Ak, C6-C3, C7-A and C8-B/C.

The latter series includes the most complete material of this species recovered to date, and although the record of this taxon has been previously reported (Alba *et al*. 2006, 2007, 2009; Casanovas-Vilar *et al*. 2008b; Robles *et al*. 2010), no description has been provided and only two specimens have been preliminarily figured (Robles *et al*. 2010).

Morphological and morphometrical comparisons

The barbourofelid material described in this paper has been compared to several species of this family (both afrosmilins and barbourofelins) from Eurasia, Africa and North America on the basis of published descriptions, figures and measurements. In addition to *Albanosmilus jourdani* from Austria, Spain and Germany (Ginsburg *et al*. 1981; de Beaumont & Crusafont-Pairó 1982; Morlo 2006; Nagel 2009), these taxa include: *Ginsburgsmilus napakensis* Morales *et al*., 2001 from Uganda (Morales *et al*. 2001; Morlo *et al*. 2004); *Afrosmilus africanus* (Andrews, 1914) from Kenya (Morales *et al*. 2001; Morlo *et al*. 2004); *A. turkanae* Schmidt-Kittler, 1987 from Kenya (Morales *et al*. 2001; Morlo *et al*. 2004); *A. hispanicus* from Spain (Morales *et al*. 2001; Morlo *et al*. 2004); *Prosansanosmilus eggeri* from Germany (Morlo *et al*. 2004); *P. peregrinus* from Germany and France (Morlo *et al*. 2004); *Sansanosmilus palmidens* from France, Austria and China (Chen & Wu 1976; Morlo *et al*. 2004; Nagel 2009); *A. whitfordi* from the USA (Schultz *et al*. 1970; Tseng *et al*. 2010); *Barbourofelis piveteaui* from Turkey (Geraads & Güleç 1997); *B. loveorum* from the USA (Baskin 1981); and *B. fricki* and *B. morrisi* from North America (Schultz *et al*. 1970). Furthermore, original remains and casts of several North American barbourofelins housed at the AMNH have been studied by one of the authors (DMA) (see Online Supplementary Material Appendix 1). In addition to comparisons of craniodental morphology, dental size and proportions have been compared using bivariate plots of MD vs. BL for P3, P4, p4 and m1.

Computed tomography

Computed tomography (CT) was employed in order to recognize internal anatomical structures. Cranium IPS49575 was scanned with a medical CT (Sensations 16, Siemens) at the Hospital Mútua de Terrassa (Barcelona, Spain). The scan was performed at 140 kV and 350 mA, obtaining 0.521 mm pixels and an output of 512 × 512 pixels per slice, with an inter-slice space of 0.2 mm. The slices figured in this paper were obtained using the CT software MIMICS (Materialise, Belgium).

Cladistic analysis

The cladistic analysis performed to decipher the phylogenetic relationships of Barbourofelini is based on a data matrix (Online Supplementary Material, Table 1) compiled from matrices previously published by Geraads & Güleç (1997, tables 1 and 2) and Morlo *et al.* (2004, table 2 and appendix), with several additions and modifications. This data matrix includes 35 characters for 18 taxa (plus a hypothetical outgroup), including the barbourofelids *Syrtosmilus syrtensis*, *Ginsburgsmilus napakensis*, *Afrosmilus turkanae*, *A. africanus*, *A. hispanicus*, *Prosansanosmilus eggeri*, *P. peregrinus*, *Sansanosmilus palmidens*, *Albanosmilus jourdani* (= *A. vallesiensis*), *A. whitfordi*, *Barbourofelis morrisi*, *B. loveorum*, *B. fricki* and *B. piveteaui*, as well as the nimravids *Eofelis edwarsii* (Filhol, 1872) (MP22, France) and *Nimravus intermedius* (Filhol, 1872) (MP22 to MP25, France), the stem felids *Proailurus lemanensis* Filhol, 1879 (*c*. 29–22 Ma, France) and early representatives of the genus *Pseudaelurus* Gervais, 1850 (MN3–MN5,

Table 1. Specimens of *Albanosmilus jourdani* from the Vallès-Penedès Basin (Catalonia, Spain) described in this paper, indicating the corresponding figures of this and previous works. Abbreviations: **BC**, Beaumont & Crusafont-Pairó (1982); **VCA**, Villalta Comella & Crusafont Pairó (1943a); **VCB**, Villalta Comella & Crusafont Pairó (1943b).

Site	Age	Record No.	Description	Figures
ACM/C3-Ak	11.8 Ma	IPS41943	L partial hemimandible with di1 (root) and di2-dp4	3A-C
ACM/C4-C2	11.9 Ma	IPS43115	L dp3 (root and crown)	—
ACM/C4-C2	11.9 Ma	IPS46478	L mandibular fragment with dp3 (partial) and dp4	3G-I
ACM/C4-C2	11.9 Ma	IPS46491	L i3 (partial root and crown)	—
ACM/C5-C4	11.8 Ma	IPS42178	Distal fragment of L P4 crown	—
ACM/C6-Ak	11.7 Ma	IPS46487a	R partial hemimandible with i2 and i3-m1	2A-C
ACM/C6-Ak	11.7 Ma	IPS46487b	L partial hemimandible with i1-m1	2D-F
ACM/C6-Ak	11.7 Ma	IPS46487c	R maxillary fragment with P3-P4	—
ACM/C6-Ak	11.7 Ma	IPS46487d	L premaxillary fragment with I1-I3	6E-H
ACM/C6-C3	11.6 Ma	IPS50909	R di3 (crown and root)	—
ACM/C6-C3	11.6 Ma	IPS50911	L i3 crown	—
ACM/C7-A	11.6 Ma	IPS54866	L partial hemimandible with c1 (partial) and p4	2G-I
ACM/C8-B/C	11.5 Ma	IPS49575	Cranium with L I3–P4 and R I2–I3 and P3–P4	5A-D, 8, 10A
ACM/C6-C	11.6 Ma	IPS56248	Calvarium	6I-M
CB	11.2–10.3 Ma	IPS31231	L P4	9M-O, BC Pl IV Fig 3
CB	11.2–10.3 Ma	IPS54950	L P4	9J-L
CCN20	11.1 Ma	IPS28723	L mandibular fragment with p4-m1	3M-O
CL1	c. 9.7 Ma	IPS15113	R P4	9S-U
CL1	c. 9.7 Ma	IPS15120	R C1 crown fragment	10D-E
CL1	c. 9.7 Ma	IPS15034	Upper incisors (R I3 crown, R I1–I2 crowns with partial roots, L I1 root and L I2–I3 crowns with partial roots)	6A
CL1	c. 9.7 Ma	IPS15035	R I2	—
CL1	c. 9.7 Ma	IPS15040	R partial palate with I2–I3 and C1 partial crown	6B-D
CMS	c. 11.1–10.5 Ma	IPS31259	R p4 (crown and partial roots)	4I-J
CP	10.4–10.0 Ma	IPS15027	L P4 (crown and almost complete roots)	9A-C, BC Pl IV Figs 1a-c
CM1	c. 11.2 Ma	IPS2035	R partial hemimandible with dc1 and dp3–dp4	3D-F, VCA Figs. 29–30, Pl XII Figs 5–5c, VCB Pl I Figs 5–5b
HS	<11.1 Ma	IPS16579	L mandibular fragment with p4-m1	3J-L
SA	10.4–10.0 Ma	IPS11343	L C1 apical crown fragment	10F-G, BC Pl IV Figs 6a-c
SA	10.4–10.0 Ma	IPS15031	R P4	9V-X, BC Pl IV Fig 2
SA	10.4–10.0 Ma	IPS15037	R p3 (crown and root)	4A-B, BC Pl IV Figs 5a-b
SA	10.4–10.0 Ma	IPS15038	L p4 (crown and partial roots)	4Q-R, BC Pl IV Figs 4a-b
SA	10.4–10.0 Ma	IPS31204	R i3	BC Pl IV Fig 7
SA	10.4–10.0 Ma	IPS54867	R I1	BC Pl IV Fig 7
SA	10.4–10.0 Ma	IPS36393	Partial mandible with R m1	2J-K, BC Pl III Figs 1a-c
SA	10.4–10.0 Ma	IPS54868	L I1	BC Pl IV Fig 7
SQ	11.8–11.1 Ma	IPS2017	R c1	VCA Pl XIII Figs 2–2a, VCB Pl I Figs 3–3a
SQ	11.8–11.1 Ma	IPS2018	L c1	VCA Fig 32, Pl XIII Figs 1–1a, VCB Pl I Figs 2–2a
SQ	11.8–11.1 Ma	IPS2021	L p4	4S-T, VCA Fig 34, Pl XX Figs 5–5a, VCB Pl II Figs 4–4a
SQ	11.8–11.1 Ma	IPS2022	L p3 (crown and root)	4C-D, VCA Fig 33, Pl XX Figs 7–7a, VCB Pl II Figs 3–3a
SQ	11.8–11.1 Ma	IPS2023	L p3 (crown and root)	4E-F
SQ	11.8–11.1 Ma	IPS2024	L P4 (crown with almost complete roots)	9D-F, VCA Fig 31, Pl XII Figs 1–1b, VCB Pl II Figs 1–1b
SQ	11.8–11.1 Ma	IPS2025	L P4 (crown with almost complete roots)	9G-I
SQ	11.8–11.1 Ma	IPS2026	R P4	9P-R, VCA Pl XII Figs 1–1a, VCB Pl II Figs 2–2a

(Continued on next page)

Table 1. Specimens of *Albanosmilus jourdani* from the Vallès-Penedès Basin (Catalonia, Spain) described in this paper, indicating the corresponding figures of this and previous works. Abbreviations: **BC**, Beaumont & Crusafont-Pairó (1982); **VCA**, Villalta Comella & Crusafont Pairó (1943a); **VCB**, Villalta Comella & Crusafont Pairó (1943b). *(Continued).*

Site	Age	Record No.	Description	Figures
SQ	11.8–11.1 Ma	IPS2027	L m1 (partial crown and roots)	4Y-Z, VCA Pl XII Figs 3–3a, VCB Pl II Figs 5–5a
SQ	11.8–11.1 Ma	IPS2028	R m1 (crown and roots)	4W-X, VCA Fig 35, Pl XII Figs 4–4a, VCB Pl II Figs 6–6a
SQ	11.8–11.1 Ma	IPS2029	R p4 (crown and partial roots)	4K-L, VCA Pl XII Figs 6–6a, VCB Pl II Figs 7–7a
SQ	11.8–11.1 Ma	IPS2030	L p4 (crown and roots)	4M-N
SQ	11.8–11.1 Ma	IPS2031	L m1 (crown and partial roots)	4U-V
SQ	11.8–11.1 Ma	IPS2032	R C1 crown fragment	10B-C, VCB Pl III Figs 1–1a
SQ	11.8–11.1 Ma	IPS2034	L P3	9Y-A’
SQ	11.8–11.1 Ma	IPS2036	R i1	—
SQ	11.8–11.1 Ma	IPS2037	R i2	—
SQ	11.8–11.1 Ma	IPS2038	L I1	VCA Pl XIII Fig 4, VCB Pl I Fig 1
SQ	11.8–11.1 Ma	IPS2040	L M1	9B’-D’
SQ	11.8–11.1 Ma	IPS30992.1	R c1	VCA Pl XIII Figs 3–3a, VCB Pl I Fig 4
SQ	11.8–11.1 Ma	IPS30992.2	R p3 (crown and partial root)	4G-H
SQ	11.8–11.1 Ma	IPS30992.3	R p4 (crown and partial roots)	4O-P
SQ	11.8–11.1 Ma	IPS30992.4	R m1 (partial crown and roots)	4A’-B’

Europe, Africa and North America). Character statements are reported in Appendix 2, where we further specify the equivalence between our characters and those employed by Geraads & Güleç (1997) and Morlo *et al.* (2004).

A maximum parsimony analysis was performed in PAUP* 4.0 (Swofford 2003) using the ‘branch-and-bound’ command with the default options, except for activating the auto-increase option for the maximum number of trees. Two taxa (*Syrtosmilus* and *Ginsburgsmilus*) were not included in the final analysis due to excessive missing data. All characters were parsimony-informative. Character polarity was determined using a hypothetical ancestor. Characters were treated as unordered. Inapplicable data were coded as missing data, as recommended by Strong & Lipscomb (2005). Clade stability was assessed using bootstrap analyses (1000 replicates) and Bremer Support (Bremer 1994). The CI and RI (Farris 1989) were employed as metrics of phylogenetic homoplasy.

Age and geological context

Vallès-Penedès Basin

The barbourofelid remains described in this paper come from several localities in the Vallès-Penedès Basin (Catalonia, Spain; Fig. 1). This basin is a NNE–SSW-oriented half graben, limited by the Littoral and Pre-littoral Catalan Coastal Ranges (NE Iberian Peninsula), which was generated by the rifting of the NW Mediterranean region during the Neogene (Cabrera & Calvet 1990, 1996; Bartrina *et al.* 1992; Roca & Desegaulx 1992; Roca & Guimerà 1992; Cabrera *et al.* 2004; de Gibert & Casanovas Vilar 2011). The basin infill consists of more than 2000 metres of sediment that, with some Early and Middle Miocene shallow marine and transitional sequences, mostly corresponds to distal-marginal alluvial fan sediments (Agustí *et al.* 1985; Cabrera & Calvet 1990, 1996; Cabrera *et al.* 1991, 2004; Roca & Desegaulx 1992; Casanovas-Vilar *et al.* 2011b). Five depositional units are distinguished (Agustí *et al.* 1985), the fossil remains described in this paper coming from the upper continental complex, which ranges from MN6 to MN11.

Late Aragonian localities

The oldest remains described in this paper come from the 250 m thick ACM series (Alba *et al.* 2006, 2009, 2011b), in the area of els Hostalets de Pierola, which is characterized by Middle to Late Miocene alluvial sequences that were deposited in the distal to marginal, inter-fan zones of the coalescing alluvial fan systems of els Hostalets de Pierola and Olesa (Moyà-Solà *et al.* 2009). Classical localities from this area (Crusafont & Truyols 1954; Golpe-Posse 1974) have been traditionally grouped into HI (Aragonian levels) and HS (Vallesian levels) (Crusafont & Truyols 1954; Golpe-Posse 1974; Agustí *et al.* 1985, 1997). However, the age of the ACM localities and most isolated finds can be accurately estimated on the basis of firm lithostratigraphical, magnetostratigraphical and biostratigraphical correlation (Moyà-Solà *et al.* 2009; Alba *et al.* 2009, 2011b). The entire ACM series corresponds to the late Aragonian (Middle Miocene), although early Vallesian (Late Miocene) sediments outcrop nearby (Moyà-Solà *et al.* 2009; Carmona *et al.* 2011; Alba *et al.* 2011b).

Table 2. Dental measurements (in mm) of *Albanosmilus jourdani* from the Vallès-Penedès Basin (Catalonia, Spain).

Record No.	Site	Tooth	BL	MD
IPS41943	ACM/C3-Ak	L di1	1.7	1.9
IPS41943	ACM/C3-Ak	L di2	1.8	3.0
IPS41943	ACM/C3-Ak	L di3	2.5	4.5
IPS50909	ACM/C6-C3	R di3	4.4	3.0
IPS41943	ACM/C3-Ak	L dc1	2.7	4.3
IPS43115	ACM/C4-C2	L dp3	3.5	8.9
IPS46478	ACM/C4-C2	L dp3	3.6	—
IPS41943	ACM/C3-Ak	L dp3	3.9	10.8
IPS2035	CM1	R dp3	3.4	9.8
IPS46478	ACM/C4-C2	L dp4	5.2	—
IPS41943	ACM/C3-Ak	L dp4	6.3	16.6
IPS2035	CM1	R dp4	5.1	15.1
IPS46487b	ACM/C6-Ak	L i1	5.1	2.6
IPS2036	SQ	R i1	4.4	3.1
IPS46487a	ACM/C6-Ak	R i2	5.3	4.1
IPS46487b	ACM/C6-Ak	L i2	4.4	4.4
IPS2037	SQ	R i2	5.1	5.9
IPS46487a	ACM/C6-Ak	R i3	6.3	4.5
IPS46487b	ACM/C6-Ak	L i3	6.1	4.4
IPS46491	ACM/C4-C2	L i3	5.3	5.4
IPS50911	ACM/C6-C3	L i3	4.5	3.9
IPS31204	SA	R i3	4.5	11.0
IPS46487a	ACM/C6-Ak	R c1	6.7	4.2
IPS46487b	ACM/C6-Ak	L c1	6.0	4.6
IPS2017	SQ	R c1	8.9	5.8
IPS2018	SQ	L c1	8.0	5.6
IPS30992.1	SQ	R c1	8.4	6.1
IPS46487a	ACM/C6-Ak	R p3	3.8	7.4
IPS46487b	ACM/C6-Ak	L p3	3.9	6.9
IPS2022	SQ	L p3	5.2	8.5
IPS2023	SQ	L p3	4.9	8.4
IPS30992.2	SQ	R p3	4.7	8.9
IPS15037	SA	R p3	4.0	6.0
IPS46487a	ACM/C6-Ak	R p4	6.4	16.2
IPS46487b	ACM/C6-Ak	L p4	7.2	14.6
IPS2021	SQ	L p4	8.9	17.0
IPS54866	ACM/C7-A	L p4	7.5	17.3
IPS2029	SQ	R p4	8.8	—
IPS2030	SQ	L p4	7.3	17.7
IPS16579	HS	L p4	—	17.8
IPS30992.3	SQ	R p4	7.2	18.4
IPS28723	CCN	L p4	7.6	17.0
IPS15038	SA	L p4	6.7	18.0
IPS31259	CM	R p4	7.5	19.0
IPS46487a	ACM/C6-Ak	R m1	8.6	21.5
IPS46487b	ACM/C6-Ak	L m1	9.5	21.9
IPS2027	SQ	L m1	9.4	—
IPS2028	SQ	R m1	10.1	25.0
IPS2031	SQ	L m1	9.7	23.3
IPS16579	HS	L m1	9.2	22.9
IPS30992.4	SQ	R m1	9.0	—
IPS28723	CCN	L m1	11.6	26.0
IPS36393	SA	R m1	9.7	22.4
IPS15034	CL1	L I1	3.6	3.8
IPS46487d	ACM/C6-Ak	L I1	5.7	4.1
IPS2038	SQ	L I1	5.4	5.0
IPS54867	SA	R I1	4.6	5.4
IPS54868	SA	L I1	4.6	5.3
IPS15034	CL1	L I2	3.7	3.0
IPS15034	CL1	R I2	4.7	5.0
IPS46487d	ACM/C6-Ak	L I2	5.6	4.8
IPS49575	ACM/C8-B/C	R I2	4.7	5.4
IPS15040	CL1	R I2	5.4	5.0
IPS15035	CL1	R I2	5.6	5.4
IPS15034	CL1	L I3	7.0	5.0
IPS15034	CL1	R I3	6.7	4.7
IPS46487d	ACM/C6-Ak	L I3	6.9	5.7
IPS49575	ACM/C8-B/C	R I3	4.2	5.8
IPS49575	ACM/C8-B/C	L I3	7.6	5.5
IPS15040	CL1	R I3	7.4	6.4
IPS2032	SQ	R C1	>7.5	—
IPS15120	CL1	R C1	>7.7	—
IPS49575	ACM/C8-B/C	L C1	19	7.1
IPS54866	ACM/C7-A	L C1	9.6	6.2
IPS11343	SA	L C1	>5.0	—
IPS46487c	ACM/C6-Ak	R P3	4.1	8.5
IPS49575	ACM/C8-B/C	R P3	4.4	10.4
IPS49575	ACM/C8-B/C	L P3	4.3	9.6
IPS2034	SQ	L P3	5.2	10.6
IPS46487c	ACM/C6-Ak	R P4	—	32.4
IPS49575	ACM/C8-B/C	R P4	8.4	34.3
IPS49575	ACM/C8-B/C	L P4	9.7	33.2
IPS15113	CL1	R P4	9.2	37.9
IPS15027	CP	L P4	9.2	33.4
IPS2024	SQ	L P4	12.5	—
IPS2025	SQ	L P4	9.6	34.7
IPS2026	SQ	R P4	11.7	—
IPS31231	CB	L P4	10.3	39.0
IPS15031	SA	R P4	8.2	33.0
IPS54950	CB	L P4	9.6	34.0
IPS2040	SQ	L M1	5.8	3.7

For abbreviations of fossil localities see Material and methods.

From a biostratigraphical viewpoint, the ACM series corresponds to MN7 and MN8 *sensu* Mein & Ginsburg (2002), which must be understood as regional biozones that respectively correspond to the *Megacricetodon ibericus* + *Democricetodon larteti* and *M. ibericus* + *Democricetodon crusafonti* concurrent range zones (Alba *et al*. 2006, 2009; Casanovas-Vilar *et al.* 2011a). On the basis of magnetostratigraphical correlation (Moyà-Solà *et al*. 2009), the ACM series ranges from *c*. 12.5 to 11.4 Ma (Casanovas-Vilar *et al.* 2011a; Alba *et al.* 2011b), and estimated interpolated ages for the localities can be provided on the basis of average local sedimentation rates for each subchron. The oldest ACM localities with *Albanosmilus* remains are correlated with C5r.3r: C4-C2 (11.9 Ma, MN7 or MN8), C3-Ak (11.8 Ma, MN7 or MN8), C5-C4 (11.8 Ma, MN8) and C6-Ak (11.7 Ma, MN8). The remaining locality, C6-C3 (11.7 Ma, MN8), is correlated with C5r.2n, as are the two isolated records from C7-A (stratigraphically 2 m above C6-C3, 11.6 Ma, MN8) and C6-C (10 m above C6-C3, 11.6 Ma, MN8). The isolated record from C8-B/C, situated 13 m above C6-C3, is correlated with C5r.2r (11.5 Ma, MN8). Finally, CM1 is a classical locality from the same area that is stratigraphically situated above the uppermost

ACM localities but still corresponds to latest Aragonian, with an estimated age of *c.* 11.2 Ma (Alba *et al.* 2011b), although palaeomagnetic sampling would be required in order to confirm a correlation with C5r.2r (like the youngest ACM localities) rather than C5r.1n.

Three additional Vallès-Penedès sites attributed to the latest Aragonian record the presence of *Albanosmilus jourdani*: CB, SQ and CMS. Unfortunately, no magnetostratigraphical data are available for these localities, so their ages remain uncertain. On the basis of their assemblages, they have been attributed to the *M. ibericus* + *D. crusafonti* biozone (Agustí *et al.* 2005; Alba *et al*. 2006, 2010a, 2011a; Casanovas-Vilar *et al.* 2011a), thus being correlated with the MN8 *sensu* Mein & Ginsburg (2002). Such correlation, however, strongly relies on the lack of *Hippotherium* remains, because latest Aragonian (MN8) and earliest Vallesian (MN9a) rodent assemblages from the Vallès-Penedès Basin are very similar (Agustí *et al.* 1997, 2001; Casanovas-Vilar *et al.* 2006). Thus, whereas the late Aragonian age of SQ remains undisputed, on the basis of a surface-collected hipparionin tooth (Crusafont-Pairó & Golpe-Posse 1974b; Rotgers & Alba 2011) and the relative stratigraphical proximity with CL1, an estimated age range of 11.2–10.5 Ma is favoured here for CB, following Rotgers & Alba (2011) and Alba & Moyà-Solà (2012). Traditionally, CMS has been also attributed to the latest Aragonian (Agustí *et al*. 1985, 1997, 2001, 2005), despite Crusafont-Pairó & Golpe-Posse (1974a) initially reporting the presence of *Hippotherium*. On biostratigraphical grounds, Agustí *et al*. (2005) favoured an MN8 age for CMS, and no *Hippotherium* remains have been found among the classical collections of CMS. However, given the occurrence of this taxon in nearby sites from B40OV/S5 (Alba *et al.* 2010b; Tomàs *et al.* 2010) and CPO (Robles *et al.* 2011), an early MN9 age seems more likely (Robles *et al.* 2011). Given the absence of *Cricetulodon* (Agustí *et al.* 2005), an estimated age range of 11.1–10.5 Ma is tentatively attributed here to CMS.

Early Vallesian localities

The oldest undoubted Vallesian site yielding *Albanosmilus jourdani* in the Vallès-Penedès Basin corresponds to CCN20 and is situated in the lower part of one of the four sections (CG1, Terrassa) of the Montagut composite section (Garcés *et al*. 1996; Agustí *et al*. 1997; Casanovas-Vilar *et al*. 2006). CCN20 contains the First Appearance Datum (FAD) of *Hippotherium* in the Vallès-Penedès Basin (Garcés *et al*. 1996; Agustí *et al*. 1997), thus corresponding to the *M. ibericus* + *Hipparion* s.l. concurrent range zone (Agustí *et al*. 1997; Casanovas-Vilar *et al.* 2011a), and correlates with the base of chron C5r.1n having an estimated age of 11.1 Ma (Garcés *et al*. 1996). An unpublished specimen of *Albanosmilus* is also reported here from the Vallesian (MN9) levels of els Hostalets de Pierola (HS), consequently younger than 11.1 Ma. Additional *Albanosmilus* remains are available from the localities of CP1 in Sant Quirze, and SA in Santa Perpètua de la Mogoda. These sites are somewhat younger than CCN20 but still MN9 in age, being correlated with the *C. hartenbergeri* local range zone, and having an estimated age of 10.4–10.0 Ma (Casanovas-Vilar *et al.* 2011a).

The youngest record of *A. jourdani* from the Vallès-Penedès Basin corresponds to the late MN9 locality of CL1, situated in the lower portion of the 20 m thick Can Llobateres local stratigraphical section (Agustí *et al*. 1996, 1997; Alba *et al.* 2011c, d), and deposited in an distal channelized alluvial plain related to the Castellar alluvial fan (Agustí *et al*. 1996, 1997). Biostratigraphical data indicate that Can Llobateres records the lower/late Vallesian transition (the MN9/MN10 boundary) (Agustí *et al*. 1996, 1997, 2001; Casanovas-Vilar *et al.* 2011a), with CL1 corresponding to the *Cricetulodon sabadellensis* local range zone (Casanovas-Vilar *et al.* 2011a), which spans from 10.0 to 9.7 Ma, whereas magnetostratigraphical data further permit the correlation of this locality with C4Ar.3r, giving an estimated age of 9.72–9.78 Ma (Agustí *et al*. 1996, 1997, 2001; Casanovas-Vilar *et al.* 2011a).

Systematic palaeontology

Class **Mammalia** Linnaeus, 1758
Order **Carnivora** Bowdich, 1821
Suborder **Feliformia** Kretzoi, 1945
Family **Barbourofelidae** Schultz *et al*., 1970
Subfamily **Barbourofelinae** Schultz *et al*., 1970
Tribe **Barbourofelini** Schultz *et al*., 1970
Genus ***Albanosmilus*** Kretzoi, 1929

1929 *Albanosmilus* Kretzoi: 1306.

1945 *Sansanosmilus* Kretzoi: Simpson: 120 (senior subjective synonym on the basis of the Principle of the First Reviser).

1952 *Grivasmilus* de Villalta & Crusafont: 308 (junior objective synonym).

Type species. *Albanosmilus jourdani* (Filhol, 1883).

Other included species. *Albanosmilus whitfordi* (Barbour & Cook, 1915).

Emended diagnosis. Mid-sized barbourofelin with dental formula 3I1C2P1M/3I1C2P1M. Brachycephalic cranium with short and broad muzzle. Palate broadest at the level of P4. Broad and robust zygomatic arches. Orbital closure with complete postorbital bars. Large infraorbital foramen above P3. Large postcanine fossa. High sagittal crest and robust occipital crests. Large frontal sinus. Mastoid process located at the level of the inflated bullae. Comma-shaped condylar foramen under the occipital condyle. Foramen ovale situated next to the foramen rotundum at the base of the bulla, close to the well-developed retroarticular process.

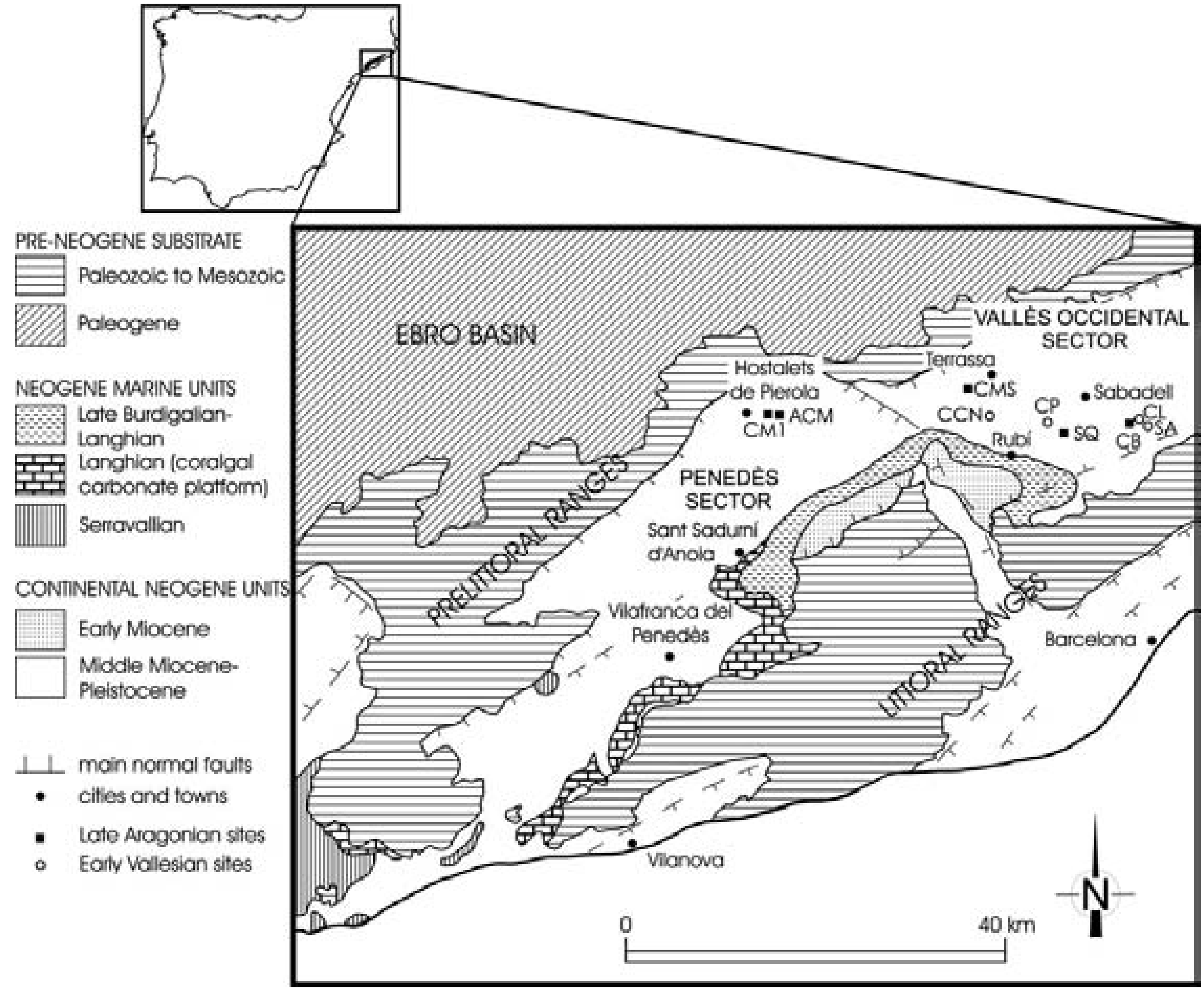

Figure 1. Geographical map showing the location of the Vallès-Penedès Basin within the Iberian Peninsula (top left), and schematic geological map of this basin, showing the main geological units and the several palaeontological sites discussed in this paper (modified from Casanovas-Vilar *et al*. 2008a). Abbreviations: ACM, Abocador de Can Mata; CB, Castell de Barberà; CCN, Creu Conill; CL, Can Llobateres 1; CM1, Can Mata 1; CMS, Can Missert; CP, Can Poncic; SA, Santiga; SQ, Sant Quirze.

Auditory bulla invading the mastoid. Shallow and long mandible, with a very high and verticalized symphysis. Sinuous and high mandibular corpus (highest at the level of p4), with a shallow, large and a U-shaped genial flange at the level of the postcanine diastema (only well developed in adults). Two mental foramina on the upper part of the flange. Posteriorly curved angular process. Posteriorly directed condyloid process that does not surpass the alveolar level. Slightly lingually curved coronoid process. Very deep masseteric fossa. Dentition characterized by sabre-like upper canines, with mesial and distal crenulated borders, and labial and lingual vertical grooves, as well as incisor-like lower canines. Labiolingually compressed cheek-teeth with crenulated borders. Tetracuspid P3. P4 with preparastyle and without protocone, with two main roots and a variously developed or fused vestigial mesiolabial root. M1 vestigial and partially hidden by P4. All lower teeth distolingually oriented relative to the mandibular corpus. Reduced p3 with two fused roots or a single root. Tetracuspid p4. m1 with two main asymmetric cusps and without metaconid.

Differential diagnosis. *Albanosmilus* differs from afrosmilin genera in a series of derived features of the Barbourofelini, such as: lack of P2 and p2; poorer development of the lingual portion of P3; P4 with a well-developed preparastyle and without protocone; lack of metaconid and talonid in m1; longer P4 relative to p4; longer m1 relative to p4; greater development of the genial flange; and the presence of notch in m1. Amongst barbourofelins, *Albanosmilus*

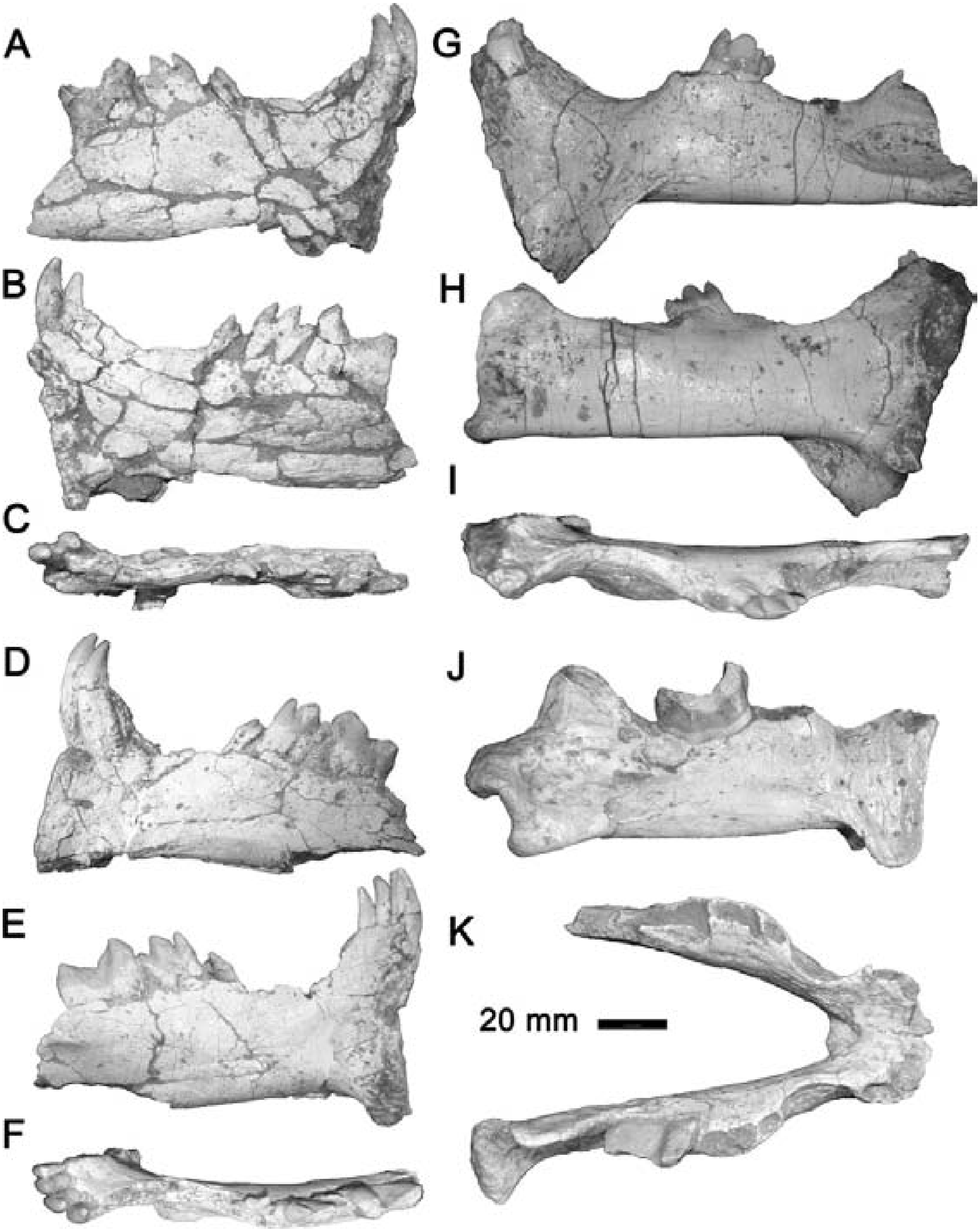

Figure 2. Mandibular remains of *Albanosmilus jourdani* from the Vallès-Penedès Basin. **A–C,** R partial hemimandible with i1–m1 (IPS46487a) in **A,** labial, **B,** lingual and **C,** occlusal views. **D–F,** L partial hemimandible with i1–m1 (IPS46487b) in **D,** labial, **E,** lingual and **F,** occlusal views. **G–I,** L partial hemimandible with partial c1 and p4 (IPS54866) in **G,** labial, **H,** lingual and **I,** occlusal views. **J, K,** Partial mandible with R m1 (IPS36393), in **J,** right labial and **K,** occlusal views.

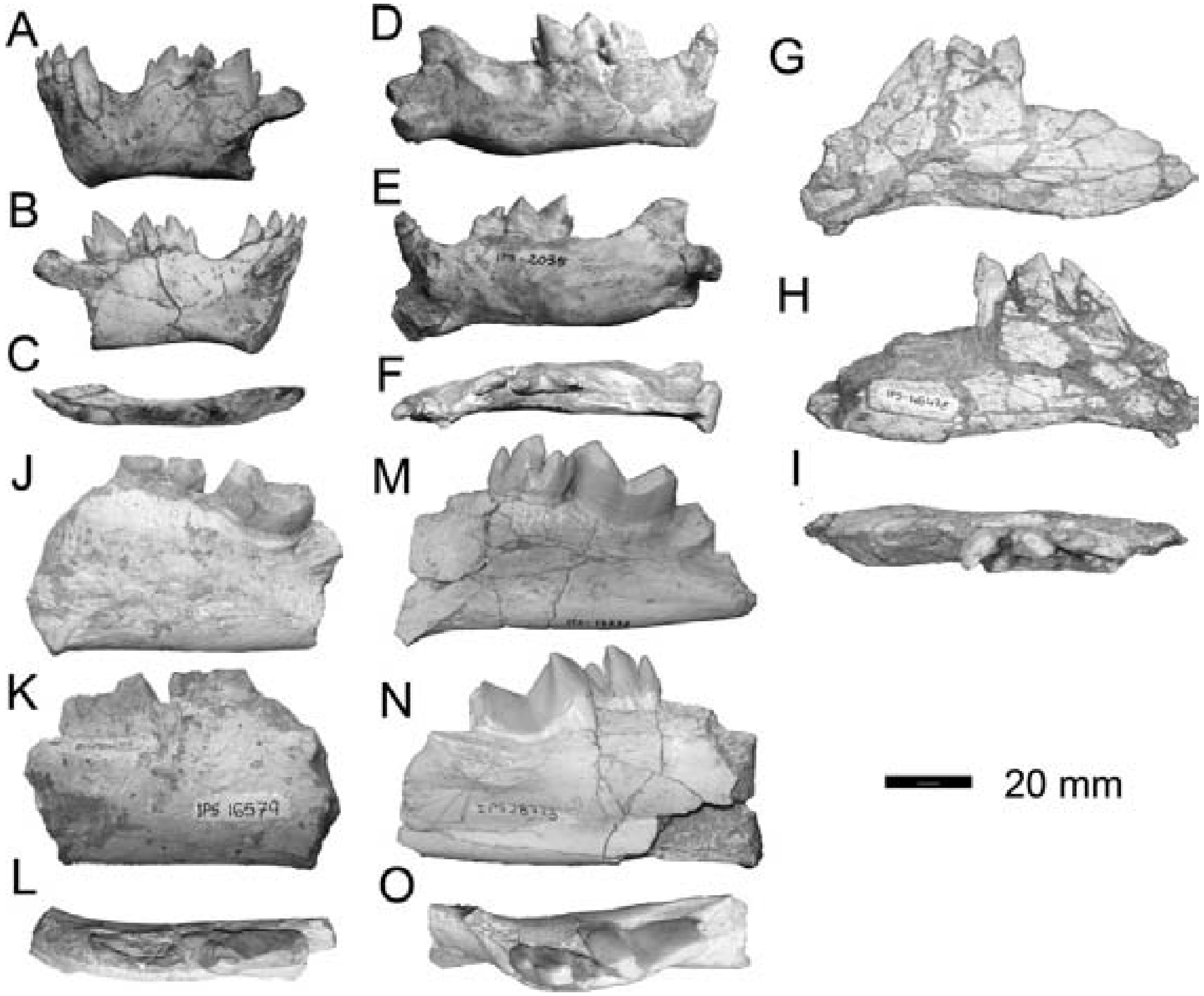

Figure 3. Mandibular remains of *Albanosmilus jourdani* from the Vallès-Penedès Basin. **A–C,** L partial hemimandible with di1–dp4 (IPS41943) in **A,** labial, **B,** lingual and **C,** occlusal views. **D–F,** R partial hemimandible with di3 and dp3–dp4 (IPS2035) in **D,** labial, **E,** lingual and **F,** occlusal views. **G–I,** L mandibular fragment with dp3 (partial) and dp4 (IPS46478) in **G,** labial, **H,** lingual and **I,** occlusal views. **J–L,** L mandibular fragment with p4–m1 (IPS16579) in **J,** labial, **K,** lingual and **L,** occlusal views. **M–O,** L mandibular fragment with p4–m1 (IPS28723) in **M,** labial, **N,** lingual and **O,** occlusal views.

differs from *Sansanosmilus* in a series of derived features shared with *Barbourofelis*, including: larger size; more reduced p3; P4 with a more developed parastyle and a well-developed preparastyle; more frequent reduction or lack of p3, lacking a mesial cusp and displaying a double fused or single root; lack of a metaconid, and presence of an expanded paraconid, in m1; longer P4 relative to p4, and longer m1 relative to p4; absolutely longer carnassials and relatively broader p4; presence of orbital closure by means of a postorbital bar; larger infraorbital foramen; excavated masseteric insertion; broader palate; higher and thinner mandibular symphysis; and more distally positioned anterior crest of the flange. Finally, *Albanosmilus* differs from *Barbourofelis* by the following features: presence of a mesial cingulum cusp in P3 (i.e. presence of a four-cusped P3); lack of metaconid in m1; and c1 larger than i3.

Albanosmilus jourdani (Filhol, 1883)
(Figs. 2–10)

1883 *Machairodus jourdani* Filhol; 57, pl. 4, figs 3–5.
1885 *Hyaenictis germanica* Fraas; 319, pl. 4, fig. 2a,b (*partim*).
1887 *Hyaenictis germanica* Fraas; Depéret: 127, pl. 13, fig. 4, pl. 14, figs 2, 3.
1888 *Hyaenictis germanica* Fraas; Schlosser: 435.
1892 *Machairodus jourdani* Filhol; Depéret: 18, pl. 1 fig. 1.
1901 *Machairodus jourdani* Filhol; Boule: 569.
1907 *Machairodus jourdani* Filhol; Roman: 61, pl. 3, fig. 8.
1929 *Albanosmilus jourdani* (Filhol); Kretzoi: 1306.
1943a *Albanosmilus jourdani* (Filhol); de Villalta Comella & Crusafont Pairó: 122, figs 29–30, pl. 13, figs 5–5c, 6.
1943a *Albanosmilus jourdani* var. *andresi* de Villalta Comella & Crusafont Pairó: 127, figs 31–35, pl. 12,

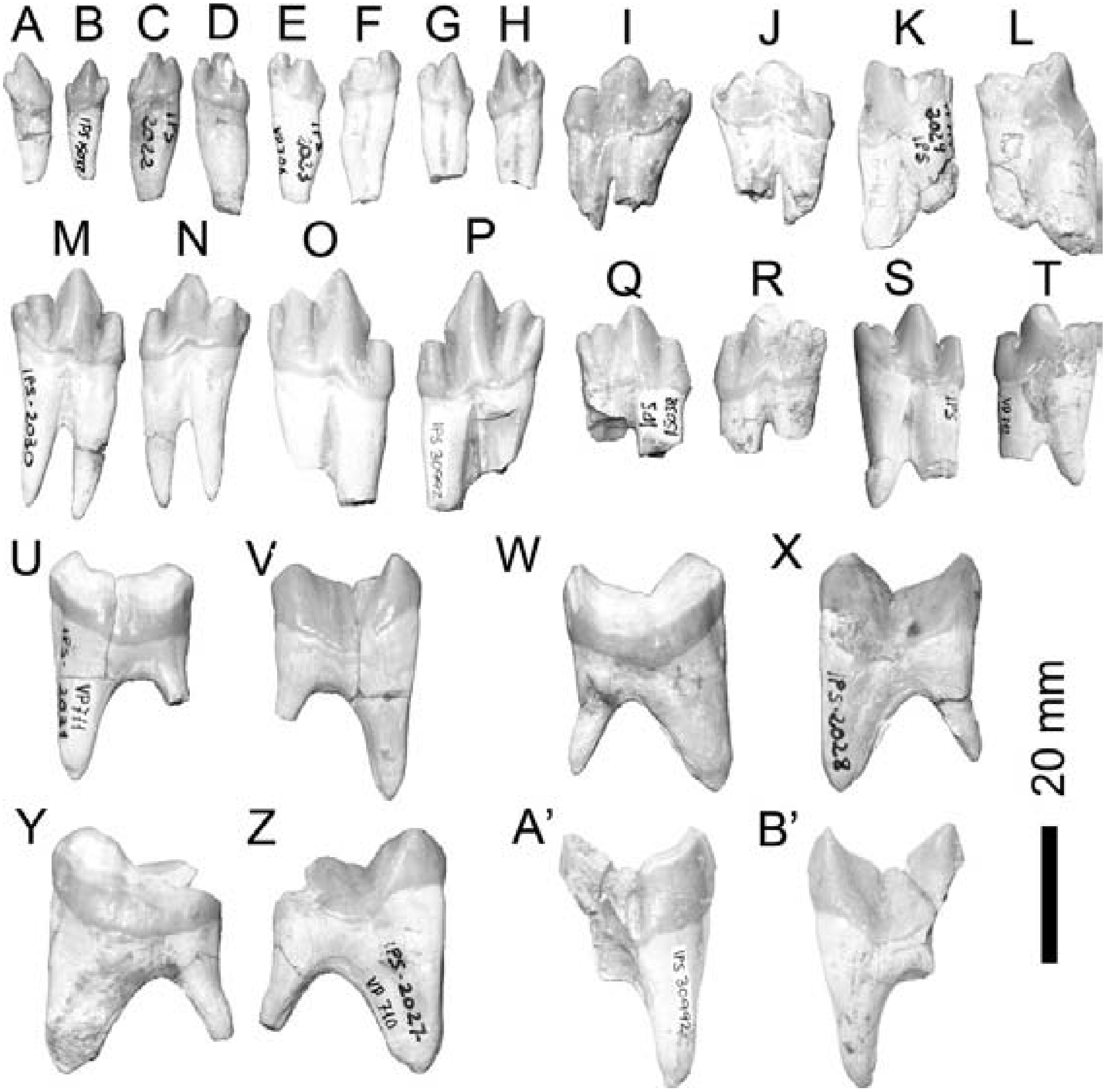

Figure 4. Isolated lower cheek teeth of *Albanosmilus jourdani* from the Vallès-Penedès Basin. **A, B,** R p3 (IPS15037) in A, labial and **B,** lingual views. **C, D,** L p3 (IPS2022) in **C,** labial and **D,** lingual views. **E, F,** L p3 (IPS2023) in **E,** labial and **F,** lingual views. **G, H,** R p3 (IPS30992.2) in **G,** labial and **H,** lingual views. **I, J,** R p4 (IPS31259) in **I,** labial and **J,** lingual views. **K, L,** R p4 (IPS2029) in **K,** labial and **L,** lingual views. **M, N,** L p4 (IPS2030) in **M,** labial and **N,** lingual views. **O, P,** R p4 (IPS30992.3) in **O,** labial and **P,** lingual views. **Q, R,** L p4 (IPS15038) in **Q,** labial and **R,** lingual views. **S, T,** L p4 (IPS2021) in **S,** labial and **T,** lingual views. **U, V,** R m1 (IPS2031) in **U,** labial and **V,** lingual views. **W, X,** L m1 (IPS2028) in **W,** labial and **X,** lingual views. **Y, Z,** R m1 (IPS2027) in **Y,** labial and **Z,** lingual views. **A′, B′,** R m1 (IPS30992.4) in **A′,** labial and **B′,** lingual views.

figs 1–1b, 2–2a, 3–3a, 4–4a, 5–5a, 6–6a, 7–7a, pl. 13, figs 1–1a, 2–2a, 3–3a, 4.

1943b *Albanosmilus jourdani* (Filhol); de Villalta Comella & Crusafont Pairó: 37, figs 1–4, pl. 1, figs 1–6, pl. 2, figs 1–7, pl. 3, figs 1–13.

1951 *Albanosmilus jourdani* (Filhol); Viret: 96.

1961 *Sansanosmilus palmidens* Blainville; Ginsburg: 154 (*partim*).

1973 *Sansanosmilus jourdani* (Filhol); Heizmann: 58, figs 17d, 18a–c.

1973 *Albanosmilus jourdani* (Filhol); Crusafont-Pairó & Ginsburg: 38, figs 3–5.

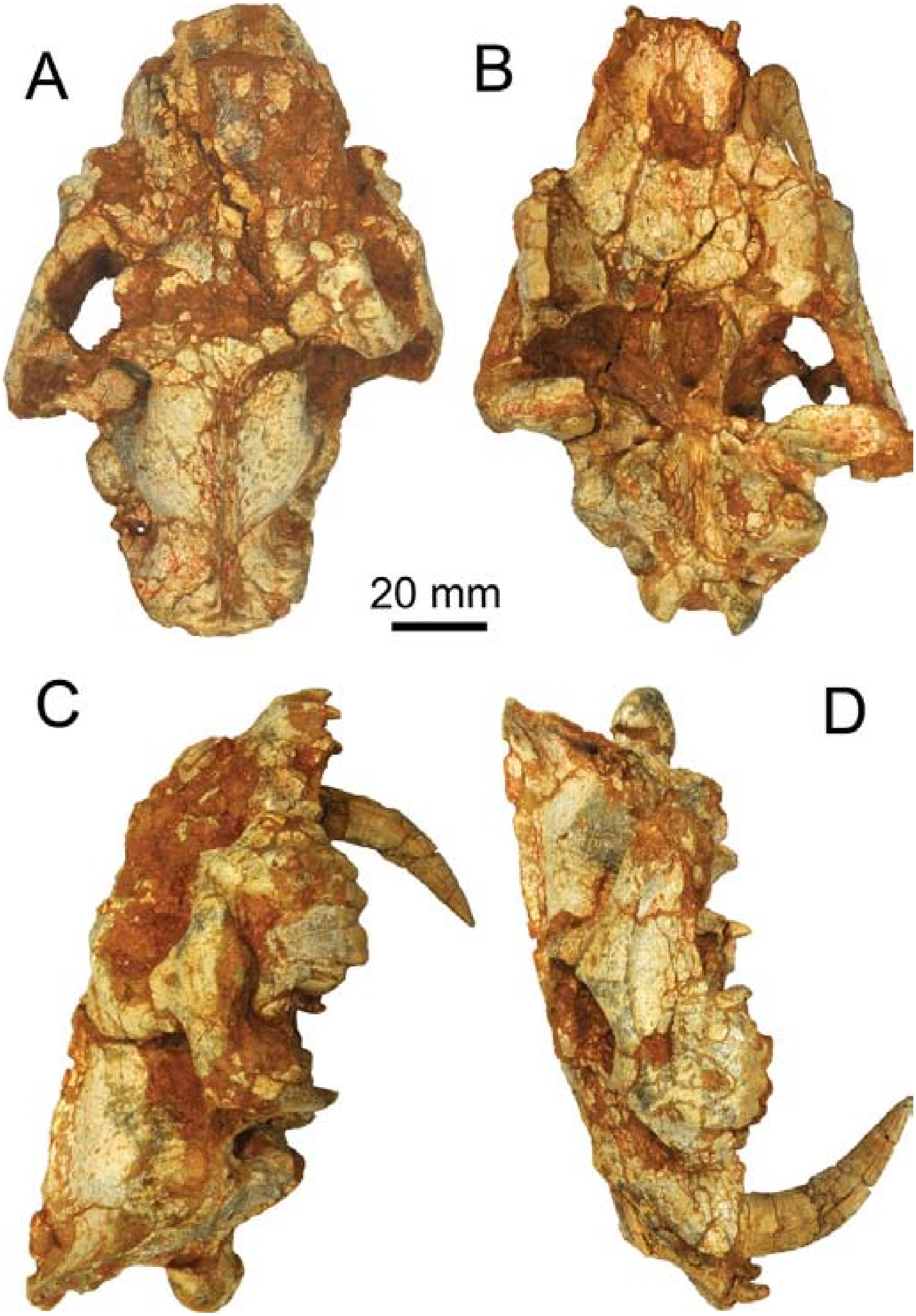

Figure 5. **A–D,** cranium of *Albanosmilus jourdani* (IPS49575) from ACM/C8-B/C in **A,** upper, **B,** basal, **C,** right lateral and **D,** left lateral views.

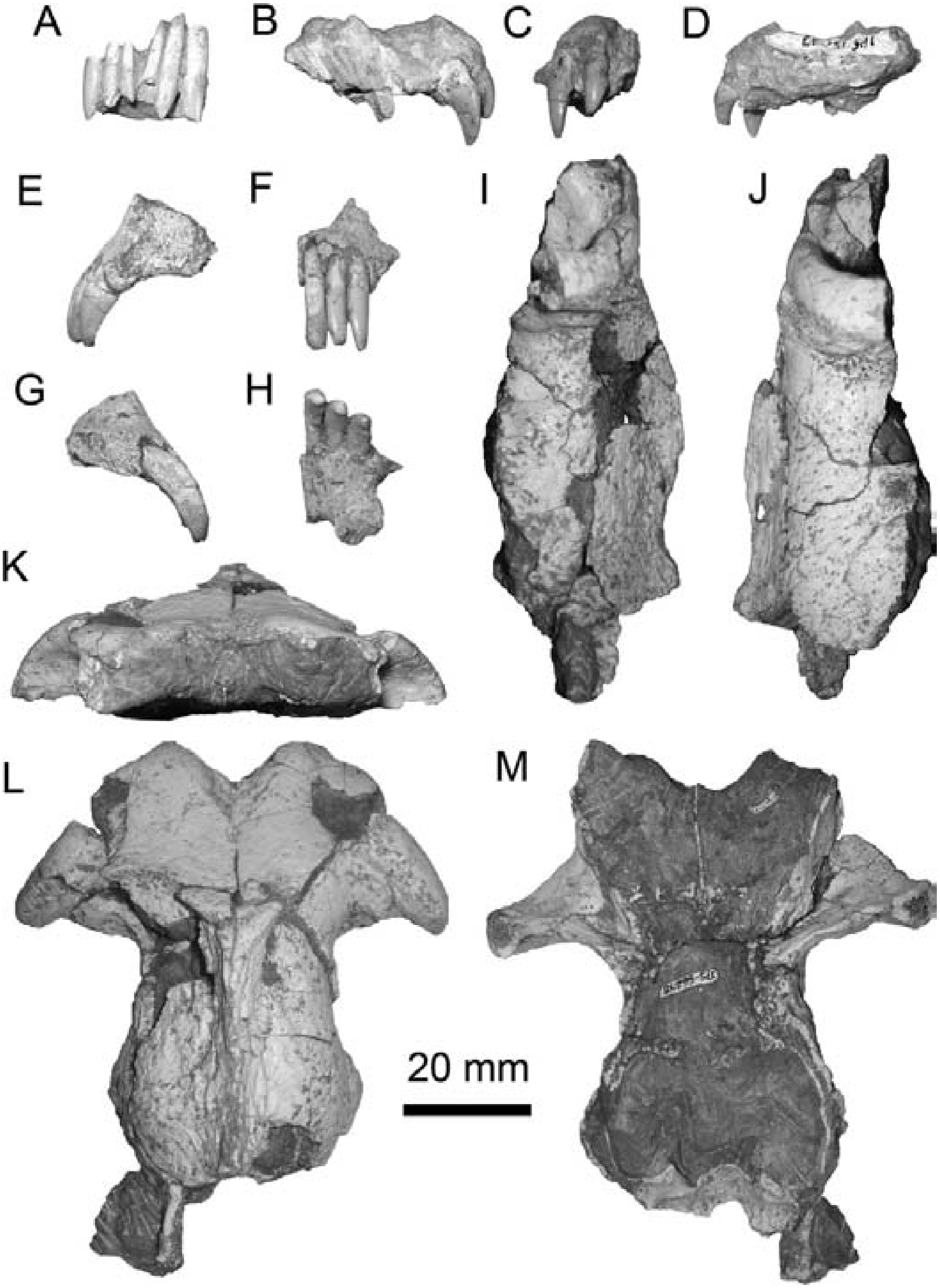

Figure 6. Cranial remains of *Albanosmilus jourdani* from the Vallès-Penedès Basin. **A,** upper incisors (IPS15034) in frontal view. **B–D,** R partial palate (IPS15040) in **B,** right lateral, **C,** frontal and **D,** medial views. **E–H,** L premaxillary fragment with I1–I3 (PS46487d) in **E,** lateral, **F,** frontal, **G,** medial and **H,** palatal views. **I–M,** calvarium IPS56248 in **I,** left lateral, **J,** right lateral, **K,** frontal, **L,** upper and **M,** basal views.

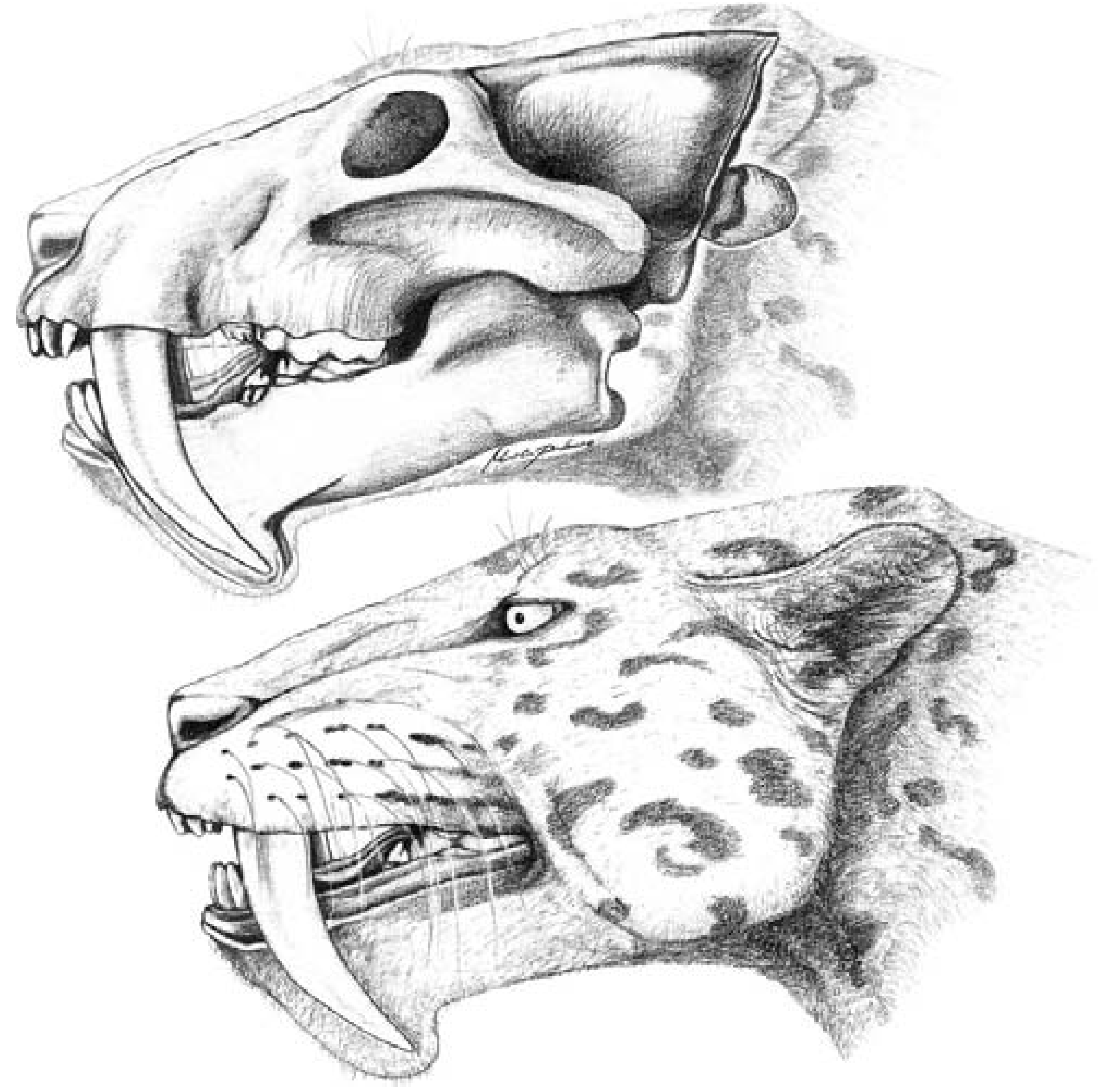

Figure 7. Reconstruction of the skull and the life appearance of *Albanosmilus jourdani* on the basis of the Vallès-Penedès remains. Original artwork by Marta Palmero.

1976 *Grivasmilus jourdani* (Filhol); Crusafont Pairó & Kurtén: 5.

1981 *Sansanosmilus jourdani* (Filhol); Ginsburg *et al*.: 391, fig. 11, pl. 2, figs 4, 5.

1982 *Sansanosmilus jourdani vallesiensis* de Beaumont & Crusafont-Pairó: 51, 61, pl. 3, fig. 1, pl. 4, figs 1–8.

1997 *?Barbourofelis vallesiensis* (de Beaumont & Crusafont-Pairó); Geraads & Güleç: 373.

2004 *Sansanosmilus vallesiensis* de Beaumont & Crusafont-Pairó; Morlo *et al*.: 53.

2006 *Sansanosmilus jourdani* (Filhol, 1883); Morlo: 341, figs 1D–G, 2A–D.

2009 *Sansanosmilus vallesiensis* de Beaumont & Crusafont; Nagel: 606, fig. 1A–D.

2010 *Sansanosmilus jourdani* (Filhol, 1883); Robles *et al.*: 266, figs 2, 3.

Emended diagnosis. As for genus.

Remarks. According to Morlo (2006), *Albanosmilus jourdani* may differ from *A. whitfordi* in a more reduced lower incisor region, the more posterior orientation of the mesial crest of the flange, and the more posteriorly extended dorsal aspect of the symphysis. Such differences, however, have not been substantiated (Tseng *et al.* 2010), and as far as it can be ascertained on the basis of available features, *A. whitfordi* can be only distinguished from the type species of the genus by the slightly larger size of the dentition (Fig. 11).

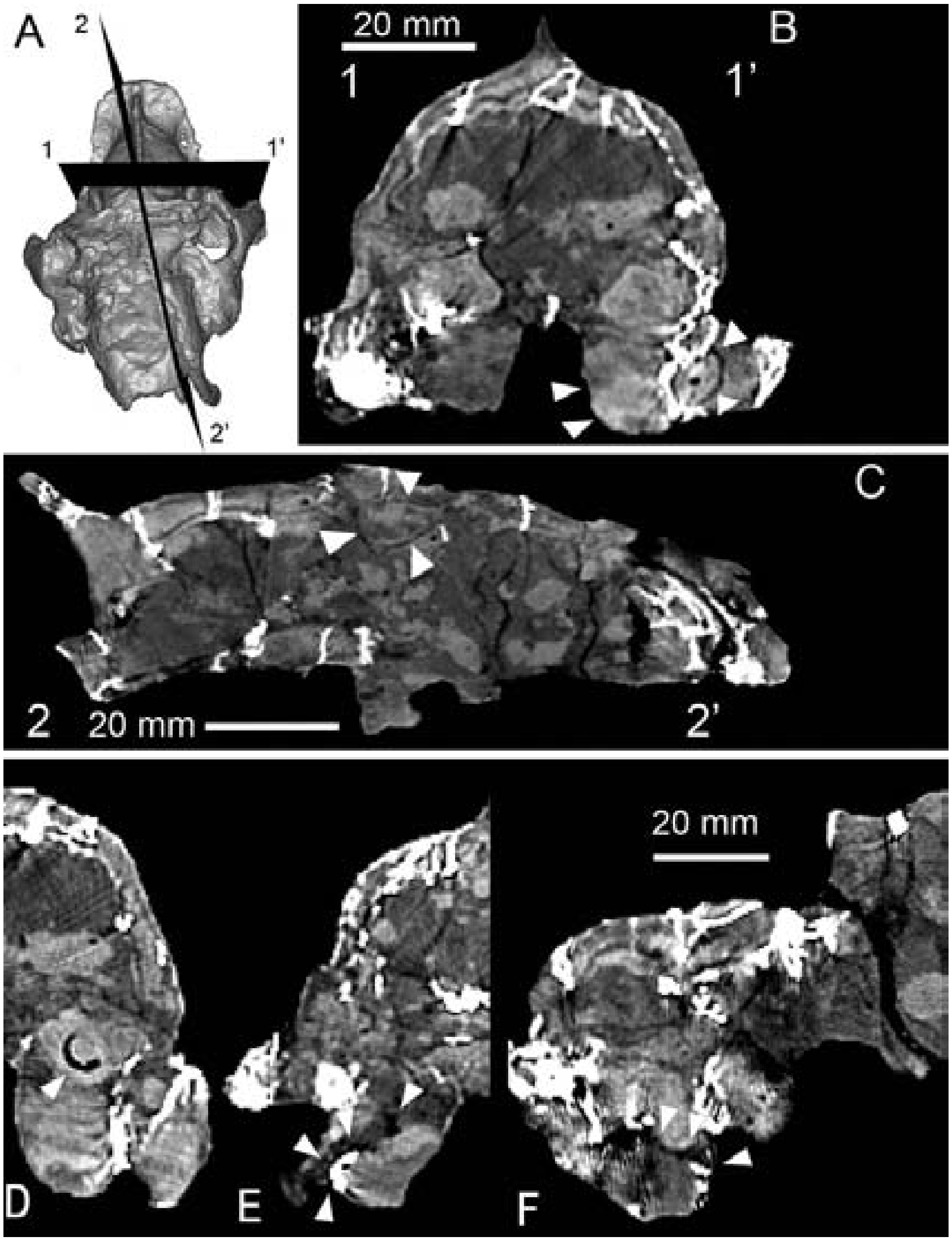

Figure 8. A, Virtual image of the cranium of *Albanosmilus jourdani* (IPS49575) showing the planes corresponding to the computed tomography sections shown in B and C; **B,** coronal section 1–1′ (orthogonal to the sagittal plane) through the mastoid processes and 4.3 mm from the posteriormost end of the occipital condyles; white arrows indicate the extension of the auditory bulla, which invades the mastoid; **C,** oblique section 2–2′ (deviated 30° from the sagittal plane); white arrows indicate the extension of the frontal sinus; **D,** coronal section of the left side of the cranium showing part of the cochlea (indicated by an arrow); **E,** coronal and **F,** parasagittal sections of the right side showing the course of the internal auditory meatus (indicated by arrows).

Holotype. Muséum d'Histoire Naturelle de Lyon No. 1384, R mandibular fragment with p4–m1 (Filhol 1883, pl. 4, figs 3–5).

Type locality. La Grive-Saint-Alban M (Saint-Alban-de-Roche, Isère, France).

Measurements. See Table 2 for dental measurements and Table 3 for dental proportions.

Age and distribution. MN6 to MN9, Europe and Turkey. In the Iberian Peninsula, known from MN7 to MN9, with a well-dated stratigraphical range of 11.9 to 9.7 Ma in the Vallès-Penedès Basin.

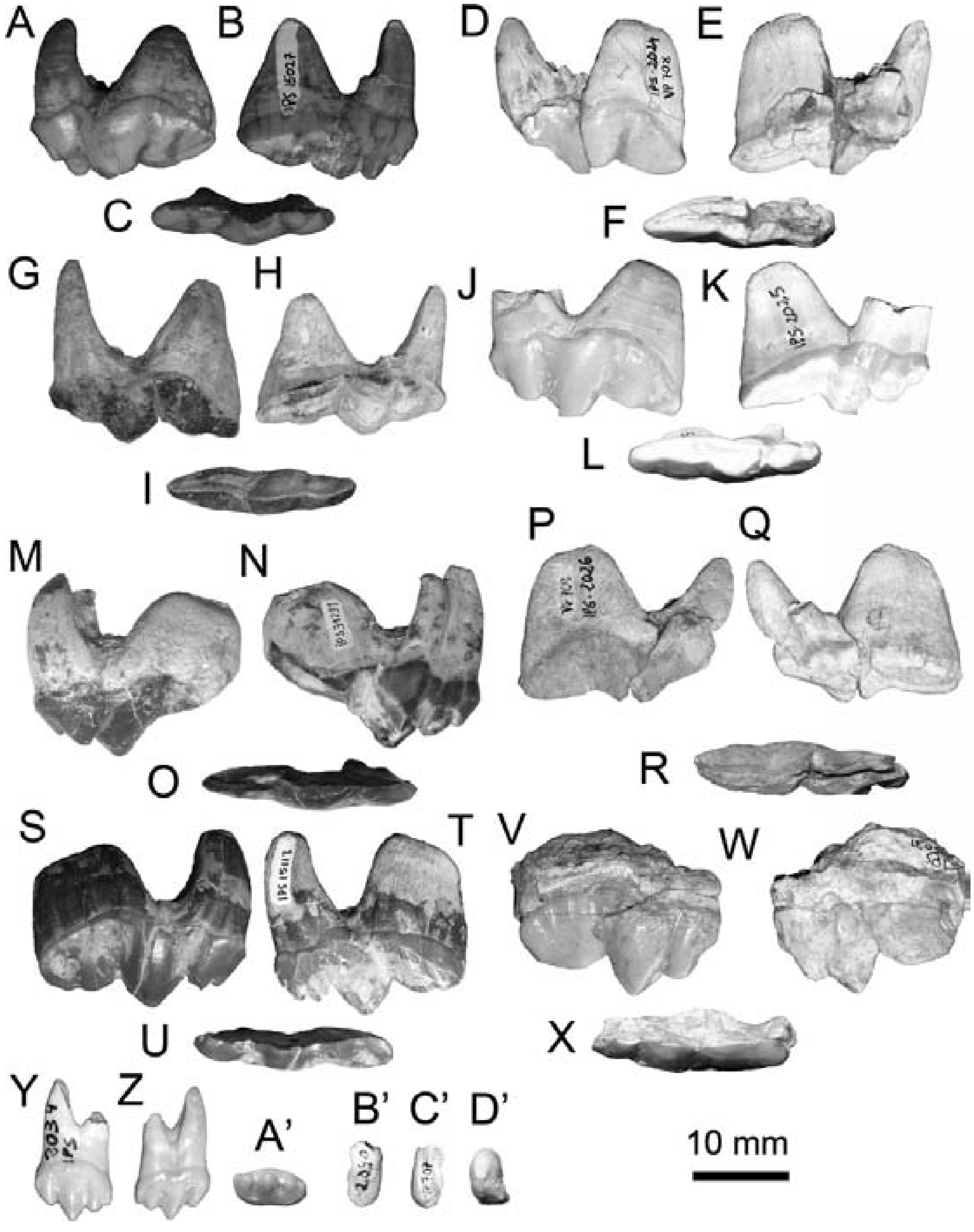

Figure 9. Isolated upper cheek teeth of *Albanosmilus jourdani* from the Vallès-Penedès Basin. **A–C,** L P4 (IPS15027) in **A,** labial, **B,** lingual and **C,** occlusal views. **D–F,** L P4 (IPS2024) in **D,** labial, **E,** lingual and **F,** occlusal views. **G–I,** L P4 (IPS2025) in **G,** labial, **H,** lingual and **I,** occlusal views. **J–L,** L P4 (IPS54950) in **J,** labial, **K,** lingual and **L,** occlusal views. **M–O,** L P4 (IPS31231) in **M,** labial, **N,** lingual and **O,** occlusal views. **P–R,** R P4 (IPS2026) in **P,** labial, **N,** lingual and **O,** occlusal views. **S–U,** R P4 (IPS15113) in **S,** labial, **T,** lingual and **U,** occlusal views. **V–X,** R P4 (IPS15031) in **V,** labial, **W,** lingual and **X,** occlusal views. **Y–A′**, L P3 (IPS2034) in **Y,** labial, **Z,** lingual and **A′,** occlusal views. **B′–D′**, L M1 (IPS2040) in **B′**, labial, **C′**, lingual and **D′**, occlusal views.

Table 3. Cranial and mandibular measurements (in mm) of *Albanosmilus jourdani* from ACM.

	Cranium				
Record No.	LC	WC	WPC	WP	WCO
IPS49575	207.7	150	66	114.6	44.8
IPS56248	—	108	—	—	—
	Mandible				
Rec. No.	LM	WM	WM1	WF	LS
IPS46487a	—	12.9	—	—	50.3
IPS36393	128.0	14.2	24.6	28.7	—
IPS46487b	—	12.3	—	37.8	50.1
IPS54866	—	15.0	27.2	62.0	63.8
IPS13233	—	15.2	25.9	—	—
IPS16579	—	14.3	26.0	—	—
IPS41943	—	6.9	19.5	—	28.0
IPS2035	—	11.2	19.6	—	—
IPS46478	—	11.8	—	—	—

For abbreviations of measurements see Material and methods.

Description

The craniodental remains of *Albanosmilus jourdani* from the Vallès-Penedès Basin described in this paper are reported in Table 1. This sample includes many isolated teeth as well as several partial mandibles, an almost complete cranium, and a calvarium. The remains catalogued under IPS46487 (a to d, including the right and left hemimandibles, as well as left premaxillary and maxillary fragments) were found associated and probably belong to the same individual. When the remains from the different sites are considered together, all of the permanent dentition is available for description, whereas for the deciduous dentition, only the lower teeth can be described. All available teeth display some degree of wear, on the lingual portion of the crown in the upper teeth, and on the labial portion in the lower ones.

Mandible. The morphology of the mandible can be ascertained on the basis of several available mandibular specimens (Figs 2, 3). The most informative adult specimens are the following: two partial hemimandibles from the same individual IPS46487 (Fig. 2A–F), which preserve the symphyseal suture but lack the rami; partial hemimandible IPS54866, which more completely preserves the corpus but similarly lacks the gonial region and the ramus; partial mandible IPS36393, which preserves the complete symphysis and, on the right side, the complete corpus and ramus (including the mandibular condyle and the coronoid process). Furthermore, there are two available infantile partial hemimandibles: IPS41943 (Fig. 3A–C), which displays the symphyseal suture and part of the corpus; and IPS2035 (Fig. 3D–F), which is damaged on the symphyseal region but completely preserves the rest of the corpus and the ramus (including the condyle and the coronoid process).

Overall, the mandible is long and low, with a high corpus and a very high symphysis, but a very low mandibular ramus. The symphysis is straight and very vertical. The corpus displays a sinuous shape in dorsal view, and reaches its maximum height at the level of p4. There is a long postcanine diastema. Below the latter, there is a shallow genial flange under the mesial portion of the c1 crown, displaying a marked, U-shaped crest that ends under the mesial portion of the p3 crown. On the labial side of the corpus, there are two mental foramina situated on the upper part of the flange: one under p3, and the other under i3. The anterior portion of the ramus begins just behind m1, where there is a large and deep messeteric fossa.

There is a posteriorly curved angular process, which projects beyond the lower level of the corpus, and a large and robust, curved condyloid process, which is horizontally situated and projects posteriorly without surpassing the alveolar level. The ramus is low, but higher than the corpus, due to the presence of a slightly mesiolingually curved coronoid process, which projects well above the alveolar level.

The infantile mandibles display a similar overall morphology to the adult ones, but are more slender, and show a lesser development of the genial flange. Their morphology can be described on the basis of three partial hemimandibles IPS41943 (Fig. 3A–C), IPS2035 (Fig. 3D–F) and IPS46478 (Fig. 3G–I). The infantile mandibular corpus displays a sinuous shape in occlusal view from the mandibular symphysis to the coronoid process, and is relatively higher than the adult one. The symphysis is high, being very vertical. There is a diastema between dc1 and the first deciduous premolar, as in the adult hemimandibles. At the level of the diastema on the labial side of the corpus, there are two mental foramina situated close to one another, as can be seen in IPS41943. No flange can be discerned in any of the available juvenile mandibles. The ramus is low and curved distally, beginning just behind dp4, except in IPS2035, which in occlusal view displays an elongated fossa that corresponds to the distal portion of the unerupted m1. The coronoid process, only preserved in IPS2035, is as high as the dp4 protocone, further displaying in labial view a slight mesiodistal crest. The masseteric fossa, visible in IPS2035, is shallower than in the adult specimens.

Cranium. Cranial anatomy can be best assessed on the basis of the almost complete cranium IPS49575 (Fig. 5A–D). This specimen shows some lateral distortion, and the orbital and zygomatic regions are better preserved on the left than on the right side. In addition, the nasals and frontals are badly damaged, although the morphology of this area can be determined using the calvarium IPS56248 (Fig. 6I–M). The morphology of the skull and external appearance of this taxon have been reconstructed (Fig. 7) on the basis of these two cranial specimens, as well as the mandibular specimens described above. Given the degree of deformation in IPS49575, some corrections have been made in the reconstruction, particularly regarding the posterior portion and orientation of the orbit. In turn, the internal anatomy of IPS49575 has been examined using several radiographical sections derived by computed tomography (Fig. 8).

The cranium is very brachycephalic, with an overall triangular shape on its anterior moiety in dorsal view. The muzzle is short, broad and robust, with a moderately prognathic premaxilla. The latter is swollen at the level of the canine. The palate is short, decreasing in breadth from P4 towards C1. It displays two deep fossae below P4 and M1. The naso-frontal region is broad and flat. There is a large and oval infraorbital foramen, situated above P3. There is a large postcanine fossa, excavated under the zygomatic from the mesial portion of P4, which reaches its maximum depth above the carnassial. There is a relatively large frontal sinus that is posteriorly situated (Fig. 8C). The orbits are elliptical and situated obliquely with respect to the parasagittal plane. They are posteriorly closed by a postorbital process that joins the jugal process, forming a robust postorbital bar. The zygomatic arches are very robust, reaching maximum lateral expansion posteriorly. The neurocranium is narrow compared to the splanchnocranium, and shows a marked postorbital constriction. There is a high and continuous sagittal crest; anteriorly, this crest bifurcates to form two crests that run along the posterior border of the postorbital bar until reaching the zygomatic arch. Posteriorly, the sagittal crest reaches the robust and well-defined nuchal (occipital) crests, which extend downwards until reaching the mastoid processes. The small parietals are inflated and display a rough surface with numerous pits. The occipitals also display a roughened and single surface inclined inwards, which contains the two occipital condyles. At the base of each condyle, a shallow, elongated and comma-shaped fossa is present, the deepest part of which would correspond to the condylar foramen. In ventral view, the sutures between the basisphenoid, pterygoid and the occipital cannot be discerned. The narrow occipital, situated between the auditory bullae, is excavated by two deep grooves that are separated by a thin crest. Although the auditory bullae are somewhat anteriorly situated, the mastoid processes, separated from the bullae by a shallow valley, are clearly more anteriorly situated relative to the rest of the basicranium (compared to felids and nimravids). There is a well-defined retroarticular process adjacent to the foramen ovale, the bulla being as high as the mastoid process and the retroarticular process. The basiphenoid and the pterygoid are narrow, and display two main foramina at the base of the bullae: the foramen rotundum, which is situated close to the bulla; and the foramen ovale, which is located close to the pterygoid-palatal crest. The latter is poorly preserved, although it appears straight and thin, displaying the choanae and the distal part of the palate. A subquadrangular fossa which ends at the level of distal P4 on the palate can be also discerned.

The CT scans enable description of the internal auditory region, although preservation and resolution are insufficient to describe all of the structures in detail. The auditory bulla is fully ossified, and its shape (mainly that of the hypotympanic chamber) changes along the anteroposterior axis, from subcircular posteriorly to more subtriangular anteriorly. The anterior and medial walls of the bulla are almost perpendicular to the basisphenoid plane, whereas the posterior wall is more obliquely inclined. It is not possible to separate the ectotympanic from the entotympanic portion on the ossified surface of the bulla, although the corresponding chambers can be internally recognized. In the posterior portion of the bulla, the epitympanic chamber (caudal entotympanic mastoid invasion of Hunt (1987), or caudal entotympanic mastoid chamber of Joeckel & Stavas (1996)) can be distinguished, thereby showing that the bulla invades the mastoid (Fig. 8B). The roof of this chamber is slightly convex, showing a subcircular profile in transverse section, with maximum mediolateral and dorsoventral diameters of 10.6 and 12.0 mm, respectively. In turn, the main (ectotympanic) chamber of the middle ear measures 13.6 mm mediolaterally, and 18.2 mm dorsoventrally. In the anterior portion of the ectotympanic chamber there is a small structure, approximately 3 mm in anteroposterior length, which apparently corresponds to the proseptum, although a detailed description is precluded by preservation. The auditory notch is not visible externally, but on the CT scans a canal interpreted as the auditory meatus can be discerned on both sides. The most external part of the meatus is located on the anterior part of the valley that separates the bulla from the mastoid. From this point, the meatus (Fig. 8E, F) runs inwards in a posterodorsal direction (with an inclination of about 50° in a coronal plane, and of about 24° in a parasagittal plane). The right and left petrosal bones are visible in the CT scans, being stoutly built and situated at the posterior moiety of the bullae. They display a quadrangular section in coronal view, becoming smaller posteriorly, and do not recess deeply into the basicranium. The cochlea can be clearly discerned in the anterior part of the right petrosal (Fig. 8D), which mainly lies on the top of the bullae, whereas the most posterior portion of the petrosal is twisted towards the inner portion of the remaining temporal bone.

Deciduous lower dentition. No upper deciduous teeth are available, but the whole lower deciduous dentition can be described on the basis of the three partial infantile hemimandibles (IPS41943, IPS46478 and IPS2035), together with the isolated dp3 IPS43115. The three lower infantile incisors are asymmetrical, uniradiculate, and slightly labiolingually oriented, increasing in size from di1 to di3. The crown of di1 is not preserved in any of the three available infantile hemimandibles. The crown of di2 is labiolingually compressed and displays an asymmetrical profile in labial/lingual views. It has three cuspids of different size, the main cuspid being central, the smallest situated in the distal portion of the crown, and the mid-sized being mesially positioned close to the base of the crown. dc1 is uniradiculate and labiolingually compressed, only displaying a single main cuspid. This tooth displays an asymmetrical triangular profile in labial/lingual views, showing two (mesial and lingual) crenulated crests that run from crown base up to the apex.

The dp3 is biradiculate and displays a labiolingually compressed, tetracuspid crown, showing in labial/lingual views an asymmetrical triangular profile with the cusps twisted in a distolingual direction. A small but distinct cuspid is mesially situated close to the base of the crown, linked to the main cuspid that is situated at crown mid-length. Slightly distally next to the latter there is a third, smaller but well-defined cuspid. A fourth well-defined and more distal cuspid, similar in size to the mesialmost one, is separated from the third cuspid by a narrow notch. dp4, like the preceding tooth, is biradiculate and displays a labiolingually compressed crown, differing from dp3 in the presence of only three well-defined cuspids. The mesial one (paraconid) is separated from the main cuspid (protocone) by a shallow notch, which can be only observed on the labial side of IPS2035. The protocone, situated on the mid-distal portion of the crown, is higher than the paracone. This tooth displays a well-defined talonid with a single cuspid, which is lower than the other two, being separated from the protocone by a shallow depression.

Lower dentition. Besides the available partial mandibles and mandibular fragments (Figs 2, 3), there are many isolated lower teeth (Fig. 4), which enable us to describe the whole lower dentition. The mandibular specimens nonetheless show that all the lower teeth are distolingually oriented with respect to the corpus.

The three incisors are asymmetrical, unicuspid and uniradiculate, increasing in size from i1 to i3. The i1 is spatulate, whereas i2 and i3 display a labiolingually curved crown that is more caniniform than in the preceding incisor. All lower incisors display two narrow, more or less symmetrical crenulations on the lingual side, which run from the crown apex (in mesial and distal directions) towards its base; additional crenulations can be observed on the lingual side of some specimens. On the distal side of i1 there is a contact facet against i2, which is also visible on the distal aspect of the crown-contact facet against i3, and in some specimens also a wear facet (against the upper incisors) on the labial side. The i3 similarly displays a contact facet with i2 on the mesial side of the crown, as well as a small contact facet against c1 on the basalmost portion of the distal side of the crown.

The c1 is a moderately high and labiolingually compressed, incisor-like tooth (Fig. 2A–F). This tooth is implanted somewhat more posteriorly than the incisor row, and its crown does not protrude from the occlusal level as defined by the incisors, showing a relatively long diastema behind.

There are two premolars. The p3 (Fig. 4A–H) displays a labiolingually compressed crown, which is asymmetrical and triangular in lingual/labial view. The crown of this tooth is usually tricuspid, although it is bicuspid in some specimens (IPS46487a and IPS46487b). Similarly, p3 frequently displays two fused roots (IPS46487a, b, IPS2022, IPS2023), although in some specimens there is a single root (IPS28723). The three cuspids are pointed and curved distolingually. The mesial cuspid protrudes the least and can sometimes be absent (IPS46487a and IPS46487b), although when present it is distinct and well defined. This mesial cuspid is linked to the main, most protruding one, situated at about mid-crown length, by a fine crenulated cristid, whereas the distal cuspid is also connected to the main one by another crenulated cristid. Nevertheless, the main cuspid is separated from the two others by two corresponding (mesial and distal) notches, which are narrow and short on the labial side, but much broader and deeper on the lingual side. This tooth further displays a discontinuous lingual cingulid close to the crown base at the level of the mesial and distal cuspulids.

The p4 (Fig. 4I–T) is a biradiculate tooth with a labiolingually compressed and tetracuspid crown that is much longer than in p3. The two roots are slightly curved distally, further being partially fused with one another on their basal portion. The cuspids are pointed and distolingually curved, with the main one (protoconid) being situated slightly in the mesial portion of the crown. The mesial cuspid is low but well defined, being separated from the protoconid by a narrow notch. In all available specimens there is a fine crenulated lingual cingulid around the protoconid close to the crown base, which merges with a straight crenulated cristid that usually runs from the apex of this cuspid towards the base of the crown (this cristid is absent in IPS2021). The mesial cuspid is linked to the protoconid by a fine and crenulated cristid that runs in a mesiodistal direction. The protoconid is much larger than the remaining cuspids, thus conferring to the p4 crown an asymmetrical profile in labial/lingual views. The protoconid is separated from the third cuspid by well-defined lingual and labial vertical notches, the lingual notch being broader and deeper than the distal notch, further ending closer to the crown base. The third cuspid, which is less protuberant than the protoconid but higher than the mesial cuspid, is situated in the distal portion of the crown, together with the fourth cuspid that is situated on the distalmost portion of the crown. This distal cuspid is smaller and less protuberant than the preceding cuspid, being separated from it by two (labial and lingual) short notches. In addition to the lingual cingulid portion around the protoconid, there is also a crenulated lingual cingulid at the level of the third and fourth cuspids close to the crown base.

There is a single lower molar, the carnassial or m1 (Fig. 4U–B′). This is a biradiculate tooth with a labiolingually compressed crown that apparently displays two main cuspids (protoconid and paraconid), although there is no available unworn specimen showing the intact occlusal morphology of this tooth. The two roots are unfused, the mesial being much stouter than the distal root. The paraconid, situated on the mesial moiety of the crown, is linked to the crown base by a fine crenulated cristid that runs in a mesial direction, as well as by another fine crenulated cristid that runs in distally towards the protoconid, which is situated in the distal moiety of the crown. On the lingual wall, the crown displays a conspicuous concavity, whereas on the labial side there is a much shallower depression, which may be absent or worn out in some specimens. All available specimens possess a flat, continuous and very vertical wear facet against P4 along all the labial aspect of the crown, although this facet does not reach the crown base in any specimen.

Upper dentition. In addition to the teeth preserved in the cranium IPS49575 (Fig. 5) and some (pre)maxillary fragmentary specimens (Fig. 6), the morphology of the upper permanent dentition can be described on the basis of numerous isolated specimens (Figs 9, 10).

The three incisors (Figs 5B–D, 6A–H) are uniradiculate, with a unicuspid and labiolingually compressed crown. They increase in size from I1 to I3. The I1 displays a subtle crenulated crest on the distal portion of the crown, and contact facets can be discerned on both the mesial and distal sides of the crown. The I2 displays a more marked crenulated crest on the distal portion of the crown than the preceding incisor, running from the apex to the base of the crown. Subtle contact facets can be observed on the mesial and distal sides of the basal portion of the crown. The I3 crown is higher than that of the preceding incisors, and displays a more caniniform morphology, in being more asymmetrical and somewhat curved distally. Like I2, this tooth also shows a distally positioned, crenulated crest running from the apex to the base of the crown.

The C1 (Fig. 10) displays a sabre-like morphology, with a very labiolingually compressed and high crown that displays convex mesial and concave distal profiles. The C1 crown further displays crenulations along the mesial and distal margins from base to apex, as well as two vertical, shallow grooves along its labial and lingual sides.

There are two premolars, which display a labiolingually compressed crown with a sharp occlusal morphology. The P3 (Fig. 9Y–A′) is a small, biradiculate tooth with a tetracuspid crown. The cusps are well defined and linked to one another by a subtle crenulated crest. The most mesial cusp, which is the least protuberant, displays a crenulated cingulum around its lingual basal aspect. The main cusp, which is by far the most protuberant, is positioned about mid-crown length, and is separated from the concomitant cusps by two (mesial and distal) notches, which are shallow on the labial side and deeper on the lingual side. The third cusp is somewhat smaller but slightly more protuberant than the mesial cusp, whereas the fourth cusp, being situated in the distalmost portion of the crown, is the smallest and least distinct.

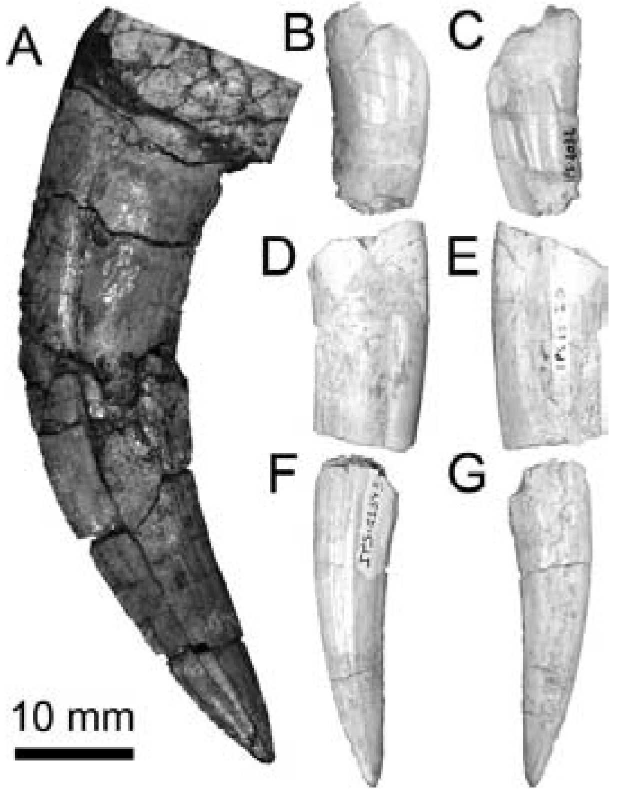

Figure 10. Canines of *Albanosmilus jourdani* from the Vallès-Penedès Basin. **A,** L C1 (IPS49575) in labial view. **B, C,** R C1 crown fragment (IPS2032) in **B,** labial and **C,** lingual views. **D, E,** R C1 crown fragment (IPS15120) in **D,** labial and **E,** lingual views. **F, G,** L C1 apical crown fragment (IPS11343) in **F,** labial and **G,** lingual views.

The upper carnassial or P4 (Fig. 9A–X) displays a long and labiolingually compressed crown. Some specimens (Fig. 9G–I, O–T) are biradiculate, showing a single and stout distal root, as well as a double fused or even single root, which is much more slender than the mesial one. Other specimens (Fig. 9D–F, J–L, P–R) are triradiculate, showing a vestigial mesiolingual root that is distinct from the main mesial one. Apparently, P4 originally displayed four main cusps; however, no unworn specimens are available to demonstrate the occlusal morphology. As no protocone can be discerned on the lingual moiety of the crown, this cusp

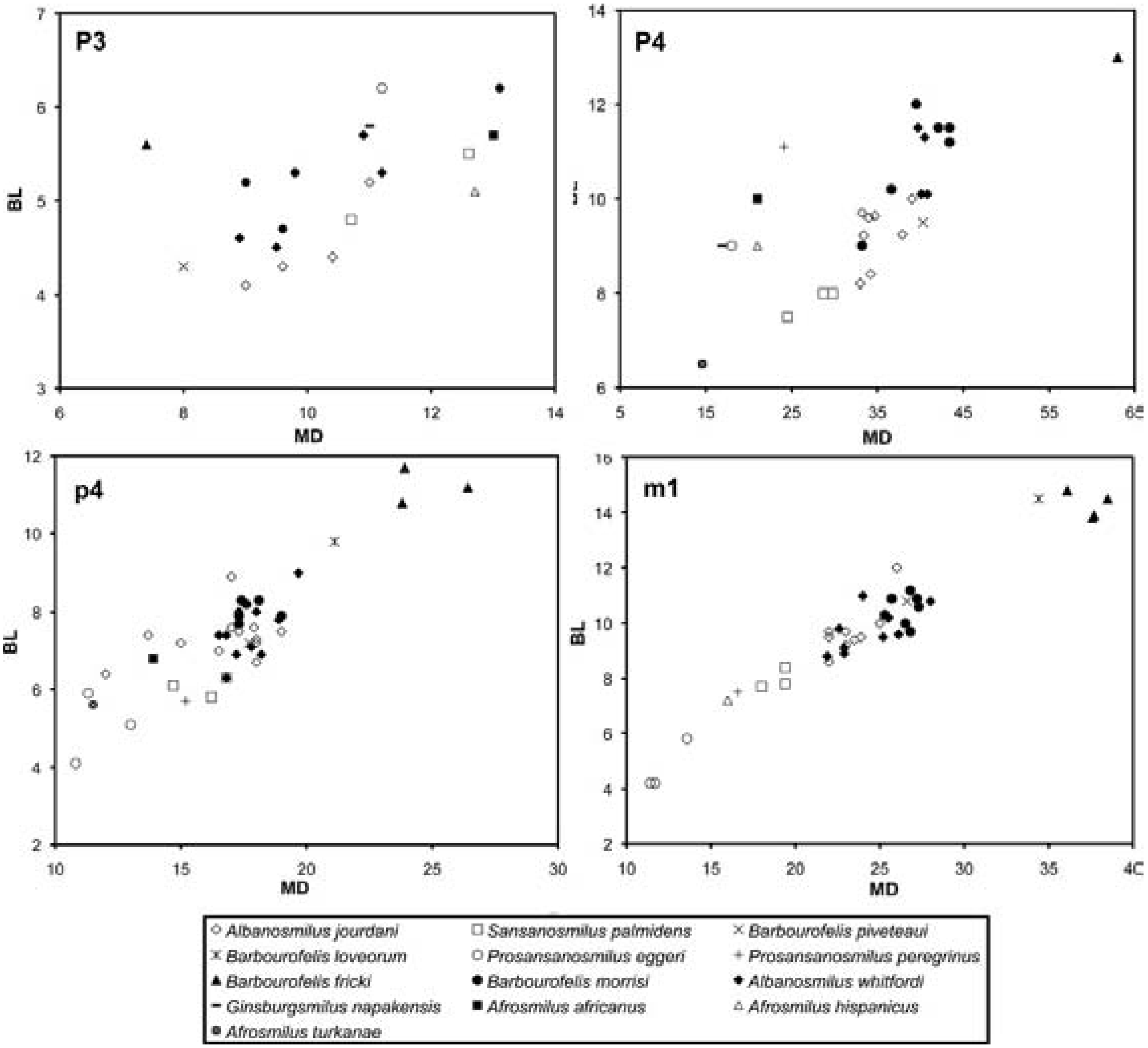

Figure 11. Dental proportions (crown width versus length) of the P3, P4, p4 and m1 of *Albanosmilus jourdani* from the Vallès-Penedès Basin compared to other barbourofelids from African, North American, Asian and European localities. See Material and methods for the references employed to depict these graphics.

may have been originally absent or, if present and eroded by wear, it must have been very small or vestigial. The paracone is the main cusp of this tooth, being situated on the labial moiety of the crown in a slightly mesial position with respect to mid-crown length, and separated from the adjacent cusps by two (mesial and distal) short and narrow, moderately distinct vertical notches at least on the labial crown wall. On the mesial portion of the crown, there are two smaller and lower cusps, the more protuberant parastyle and the more mesially situated preparastyle, which are separated from one another by a shallow groove. Finally, the elongated metacone is situated on the distal portion of the crown, being constituted by two small cuspules that are separated from one another on the labial side of the crown by a shallow groove.

There is a single molar, M1 (Fig. 9B′–D′), which is a small, low-crowned, unicuspid, uniradiculate vestigial tooth. Unlike the premolars, it is not labiolingually compressed but displays a broader rather than long crown. The position of M1 with regard to P4 is somewhat variable, being situated distally in some specimens (IPS49575) and more mesially (IPS15031) in others.

Dental proportions. The dental size and proportions of *Albanosmilus jourdani* regarding P3, P4, p4 and m1

(Fig. 11) overlap to some degree with those of *S. palmidens*, *A. whitfordi* and *B. morrisi*. However, whereas the former displays a smaller dental size regarding P4, p4 and m1, both *A. whitfordi* and *B. morrisi* tend to display slightly larger teeth than *A. jourdani*.

Cladistic analysis

The cladistic analysis of the Barbourofelidae performed in this study yielded 36 most parsimonious cladograms with a tree length of 86 steps, CI = 0.72, RI = 0.82 and RC = 0.59. The strict consensus and 50% majority rule consensus, together with support metrics, are shown in Fig. 12.

Discussion

Morphological comparisons and taxonomic attribution

The material of *Albanosmilus jourdani* described in this paper fits the diagnostic features of Barbourofelidae reported by Morlo *et al*. (2004): (1) plesiomorphic dental formula 3131/3131; (2) markedly compressed, sabre-toothed C1 with crenulations on, at least, their posterior border, and with vertical grooves; (3) strong relationships between the eruption of C1 with the development of other sabre-toothed features, particularly the presence of a mandibular flange; (4) no mesial cusp in p3 – except in *S. palmidens*, this tooth is tricuspid (Filhol 1890; Ginsburg 1961), further being sometimes absent in *A. jourdani* – but distinct and sometimes large distal accessory cusp in p3 and p4; (5) relatively high protoconid in m1 (at least in early genera such as *Prosansanosmilus* and *Afrosmilus*); (6) slightly to strongly curved (sinuous) mandibular corpus; and (7) fully ossified bulla with a short proseptum on its anteromedial portion. It also displays several derived features indicating that *A. jourdani* belongs to the tribe Barbourofelini, including (Schultz *et al*. 1970; Morales *et al*. 2001): (1) all teeth serrated; (2) deep excavation on the maxilla above P4; (3) distolingually oriented lower teeth; and (4) well-defined parastyle in P4.

The position of the Vallès-Penedès barbourofelin material at the genus and species level, however, is uncertain. The scarcity of fossil remains of Eurasian barbourofelids has hampered for many years the clarification of their taxonomic status, as well as their phylogenetic relationships (see below). In Eurasia, barbourofelins are represented by relatively scarce cranial and mandibular remains, customarily attributed to *Sansanosmilus* and sometimes also to *Barbourofelis* (Filhol 1883; Ginsburg 1961; Geraads & Güleç 1997; Morlo 2006). In North America, however, there are several barbourofelin species customarily attributed to *Barbourofelis* whose cranial and mandibular anatomy is

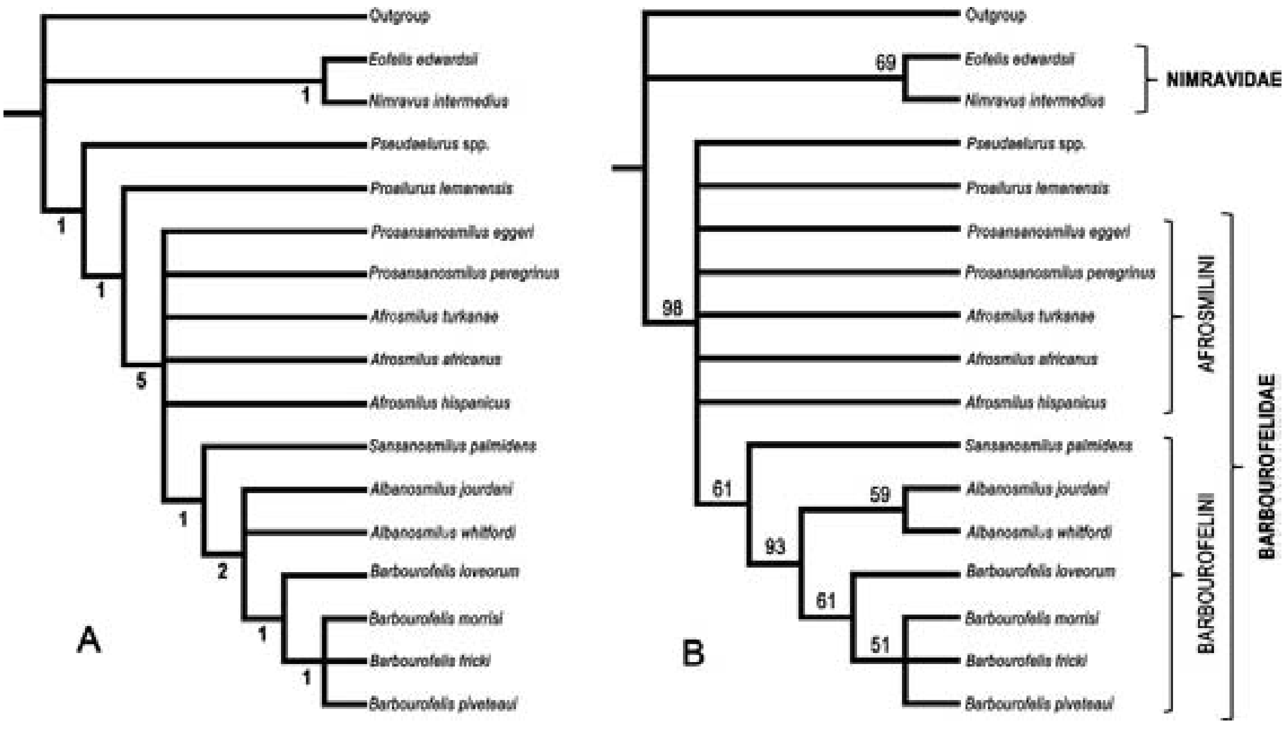

Figure 12. Results of the cladistic analysis (see text for further details). The data matrix employed is available in the Online Supplementary Material (Table 1). **A,** strict consensus of 36 most parsimonious cladograms, with numbers below nodes indicating Bremer indices. **B,** bootstrap 50% majority rule consensus, with numbers above nodes indicating bootstrap values.

generally better known (Schultz *et al*. 1970; Baskin 1981; Bryant 1988; Bryant 1991; Naples & Martin 2000; Baskin 2005; Tseng *et al*. 2010). Thus, whereas the taxonomic distinction between *S. palmidens* and *S. jourdani* has been well established for years at least at the species level (de Beaumont & Crusafont 1982; Morlo 2006), the phylogenetic position and taxonomic status of other Eurasian barbourofelins, particularly *Sansanosmilus vallesiensis* and *Barbourofelis piveteaui*, has remained unclear or poorly justified. The new craniodental material described here fits the morphology of the material previously attributed to *Sansanosmilus jourdani* or *S. vallesiensis*, but indicates that the latter nominal taxa cannot be distinguished at the species or subspecies level (the latter being a junior subjective synonym of the former), further showing several cranial features that were previously unknown and which warrant a distinction at the genus level when compared to the type species of the genus, *S. palmidens*.

Regarding synonyms at the species level, de Villalta Comella & Crusafont Pairó (1943a) erected the 'variety' *Albanosmilus jourdani* var. *andresi* on the basis of material from the Vallès-Penedès locality of SQ. Purported differentiating features from *A. jourdani* from La Grive included a larger P4 with more elaborated roots, which is here interpreted as intraspecific variation and thus devoid of taxonomic value (such a possibility was also taken into account by de Villalta Comella & Crusafont Pairó 1943b, although they were inclined to dismiss it). According to the *International Code of Zoological Nomenclature* (ICZN 1999), a name originally published as a variety before 1961 is deemed to be subspecific unless the authors explicitly or implicitly considered it to be infraspecific (Article 45.6.4), which is not the case here. Therefore, *Albanosmilus jourdani andresi* de Villalta Comella & Crusafont Pairó, 1943a is a nomenclaturally valid subspecies name, here considered a junior subjective synonym of *A. jourdani* (Filhol, 1883).

A similar situation applies to *Sansanosmilus vallesiensis*, which was originally erected by de Beaumont & Crusafont-Pairó (1982) as a subspecies of *S. jourdani*, i.e. *S. jourdani vallesiensis*, on the basis of material from several Vallès-Penedès localities (SA, CL1, CP and CB). These authors noted subtle differences between the Vallesian remains and the Aragonian remains (from the Vallès-Penedès locality of SQ, as well as the type locality and Steinheim), and on this basis they proposed a distinct subspecies status for the former. In spite of the lack of clear diagnostic criteria, this taxon was subsequently considered to be a distinct species (Geraads & Güleç 1997; Nagel 2009), being assigned to either *Sansanosmilus* (Nagel 2009) or, tentatively, *Barbourofelis* (Geraads & Güleç 1997). According to Nagel (2009), *S. vallesiensis* can be distinguished from *S. jourdani* by the larger size of the former, the larger m1 protoconid as compared to the paraconid, and the larger p4. However, when the Vallesian material from the Vallès-Penedès Basin is compared to the new and much more complete Aragonian remains, which fits well with that of the nominotypic subspecies from other European localities, no significant differences can be found in dental morphology, size, mandibular flange development, or shape of the symphysis and mandibular corpus. Accordingly, it is considered here that *Albanosmilus jourdani vallesiensis* (de Beaumont & Crusafont-Pairó, 1982) is also a junior subjective synonym of *A. jourdani* (Filhol, 1883).

Regarding the validity of *Albanosmilus* Kretzoi, 1929 as a distinct genus, before considering its taxonomic status, it is necessary to discuss several nomenclatural issues. The genera *Albanosmilus* and *Sansanosmilus* were originally erected by Kretzoi (1929) in the same publication, with *A. jourdani* from La Grive and *S. palmidens* from Sansan being their respective type species. A generic distinction was maintained for many years by several authors (de Villalta Comella & Crusafont Pairó 1943a, b; Viret 1951; de Villalta & Crusafont 1952; Ginsburg 1961; Schultz *et al*. 1970; Crusafont-Pairó & Ginsburg 1973), although following the original proposal of synonymy by Simpson (1945), other authors considered them to be synonyms, particularly from the 1970s onwards (e.g. Heizmann 1973; Ginsburg *et al.* 1981; de Beaumont & Crusafont-Pairó 1982; Geraads & Güleç 1997; Morales *et al*. 2001; Morlo *et al.* 2004; Morlo 2006; Nagel 2009; Robles *et al.* 2010). de Villalta & Crusafont (1952) proposed a new genus, *Grivamilus*, as a replacement name for *Albanosmilus*. Although these authors did not employ the binomen *Grivasmilus jourdani* (only employed by Crusafont-Pairó & Kurtén 1976), it is implicit from their work that they referred to *Machairodus jourdani* Filhol, 1883 as its type species. As such, it seems to us that the proposal of this genus name, in spite of being unnecessary, is nomenclaturally valid. It should be taken into account that, when considering synonyms, the priority between *Sansanosmilus* and *Albanosmilus* must be determined on the basis of the First Reviewer (ICZN 1999, Article 24.2), which in this case is Simpson (1945), who favoured *Sansanosmilus*, thereby making *Albanosmilus* its junior subjective synonym. However, when *Sansanosmilus palmidens* and *Albanosmilus jourdani* are not considered congeneric, then *Albanosmilus* is available for the genus including the latter species, so that the genus name *Grivamilus* Crusafont-Pairó & Kurtén, 1976, proposed on the basis of the same type species, must be considered a junior objective synonym of *Albanosmilus* Kretzoi, 1929, and a potential junior subjective synonym of *Sansanosmilus* (only if a single genus is recognized).

From a taxonomic viewpoint, the remains of *Albanosmilus jourdani* described in this paper differ from those of *Sansanosmilus palmidens*, the type species of the genus, in several craniodental features, such as: (1) the overall larger dental size of the former (particularly regarding the carnassials); (2) more reduced p3, usually (but not always) without a distinct mesial cusp; (3) the lack of metaconid in m1; (4) differences in dental proportions, such as the longer P4 relative to p4; (5) the more distal position of the mesial crest of the genial flange; (6) the larger infraorbital foramen; (7) the excavated masseteric insertion; (8) the broader palate; and (9) the presence of orbital closure due to the presence of a complete postorbital bar. Taken together, these differences warrant classifying '*S.*' *jourdani* into a genus distinct from *S. palmidens*. One possibility would be to classify the former into the genus *Barbourofelis*, as previously done by Geraads & Güleç (1997) for *S. vallesiensis* (although tentatively). However, the cladistic analysis performed in this paper shows that many of the distinguishing features of *A. jourdani* with respect to *S. palmidens* are synapomorphies of an *Albanosmilus* + *Barbourofelis* clade, with *S. palmidens* displaying a more basal position amongst the Barbourofelini. On the other hand, *A. jourdani* lacks several derived features of the *Barbourofelis* clade (at least when '*B.*' *whitfordi*, here transferred into *Albanosmilus*, is excluded), which would include several North American species as well as the Turkish *B. piveteaui*. We therefore conclude that the most reasonable taxonomic alternative is to classify '*S.*' *jourdani* into a different genus from both *Sansanosmilus* (only for *S. palmidens*) and *Barbourofelis*, thus formally resurrecting *Albanosmilus* Kretzoi, 1929 as a valid, polytypic genus. The close similarities between *A. jourdani* and *A. whitfordi* had been previously noted by several researchers (Schultz *et al*. 1970; de Beaumont & Crusafont 1982; Morlo 2006), being originally attributed to *?Albanosmilus* by Kitts (1957), subsequently to *Sansanosmilus* by Mawby (1965), and later on tentatively transferred to *Barbourofelis* by Schultz *et al*. (1970). Although Morlo (2006) noted some differences between *S. jourdani* and *A. whitfordi* (see our differential diagnosis), most recently Tseng *et al*. (2010) published additional remains of this taxon that do not conclusively substantiate such differences. The new remains of *A. jourdani* described in this paper further strengthen the similarities in mandibular morphology with *A. whitfordi* (see Morlo 2006; Tseng *et al*. 2010), as well as in dental size and proportions regarding both the upper and lower dentition (Fig. 11), although *A. whitfordi* tends to show on average a larger dental size. Given these slight differences in dental size, coupled with their different distribution areas, it seems reasonable to maintain these two taxa as distinct species, at least until more complete material of *A. whitfordi* enables a more detailed taxonomic assessment in the future.

Phylogenetic relationships and palaeobiogeographical implications

The cladistic analysis performed in this paper (Fig. 12) supports the monophyly of Barbourofelidae, which has been widely accepted (Baskin 1981; Neff 1983; Hunt 1987; Bryant 1991; Martin 1998; Joeckel *et al*. 2002; Peigné 2001; Morlo *et al*. 2004). However, it should be taken into account that *Ginsburgsmilus*, putatively the most plesiomorphic barbourofelid (Morlo *et al*. 2004; Morlo 2006), has not been included in the analysis due to excessive missing data. In the past, some analyses recovered a sister-group relationship between Barbourofelidae and Nimravidae (Bryant 1991), but the more recent analysis by Morlo *et al*. (2004) yielded poor support for this. The latter view is further strengthened by numerous craniodental features that enable the distinction of barbourofelids from nimravids, including the possession of a fully ossified bulla invading the mastoid, the lack of postglenoid foramen, and the presence of a weak ridge on the posterior margin of the genial flange (for further details see Bryant 1991; Morlo *et al*. 2004). It has been proposed instead that barbourofelids might be more closely related to felids (Morales *et al*. 2001). The analysis performed in this paper, however, was devised in order to decipher the phylogenetic relationships of the Barbourofelini, and hence the taxa included are not representative enough to evaluate the phylogenetic relationships of the Barbourofelidae with regard to other carnivorans.

Moreover, the distinction between barbourofelids and felids has been substantiated by differences in basicranial anatomy (Tedford 1978), with the former displaying, for example, a horizontal proseptum more mesially situated than in *Proailusurus* and *Pseudaelurus* (Morlo *et al*. 2004). Unfortunately, basicranial features are unknown in the most plesiomorphic barbourofelids (Afrosmilini), which precludes including them in the cladistic analysis to test the phylogenetic relationships between felids and barbourofelids.

Geraads & Güleç (1997) previously performed a cladistic analysis devised to infer the internal phylogeny of Barbourofelidae. Our analysis differs from theirs by incorporating the new data available for *Albanosmilus jourdani*, in including additional characters and taxa that have been subsequently employed by Morlo *et al*. (2004), and in refining the character coding of the various *Barbourofelis* species and *A. whitfordi*. As already stated, our results strongly support barbourofelid monophyly (bootstrap support = 98, Bremer index = 5), but regarding the internal phylogeny of Barbourofelidae, neither the strict consensus (Fig. 12A) nor the bootstrap 50% majority rule consensus (Fig. 12B) resolve the relationships between the several afrosmilin taxa (*Prosansanosmilus* spp. and *Afrosmilus* spp.). Our results nevertheless support barbourofelin monophyly (bootstrap support = 61, Bremer index = 1), and further indicate that *Sansanosmilus* s.s. (i.e. *S. palmidens*) is the basalmost barbourofelin, with the *Barbourofelis* + *Albanosmilus* clade being quite strongly supported (bootstrap support = 93, Bremer index = 2). Although the internal phylogeny of *Barbourofelis* s.s. is not fully resolved, this clade is recovered as monophyletic (bootstrap support = 61, Bremer index = 1), with *B. loveorum* as its basalmost species (with the clade including the remaining *Barbourofelis* species showing a bootstrap support of 51 and a Bremer index of 1). Finally, our analysis is unable to resolve conclusively whether *A. whitfordi* is more closely related to *A. jourdani* than to the *Barbourofelis* clade, since a monophyletic *Albanosmilus* spp. clade is recovered by the bootstrap 50% majority rule consensus (Fig. 12B) with a bootstrap value of 59, but not by the strict consensus (Fig. 12A).

Our results roughly agree with those of Geraads & Güleç (1997, fig. 2), which were based on fewer characters and taxa. These authors, however, did not distinguish *A. jourdani* as a distinct genus (their *Sansanosmilus* s.l. being clearly paraphyletic), and further considered '*?B.*' *vallesiensis* as a distinct species more closely related to *Barbourofelis* spp. than to *A. jourdani*. Geraads & Güleç (1997) also considered that '*B.*' *whitfordi* would be the most plesiomorphic *Barbourofelis* species, although the scarcity of material by that time precluded a formal inclusion in their phylogenetic analysis. The subsequent description of additional material of this species (Tseng *et al*. 2010) and the direct study of specimens housed at the AMNH allowed us to include this taxon in our cladistic analysis. The failure of our analysis to resolve completely the phylogenetic relationships between *Albanosmilus* spp. and *Barbourofelis* s.s. in part stems from the fact that *A. whitfordi* and *A. jourdani* do not differ in a single character (other than missing data) from the matrix. From a taxonomic viewpoint the attribution of *A. whitfordi* to *Barbourofelis* is not justified, because the former shows none of the derived features that distinguish *Barbourofelis* s.s. from *Albanosmilus*. Accordingly, we reallocate *A. whitfordi* to the latter genus, which is weakly favoured by our cladistic results, despite recognizing that a closer relationship between *A. whitfordi* and *Barbourofelis* s.s. would be sounder on palaeobiogeographical grounds.

Geraads & Güleç (1997) and Morlo (2006) hypothesized that a European species of *Sansanosmilus* dispersed into North America close to the Middle/Late Miocene boundary, giving rise to the North American *Barbourofelis* clade, although the scarcity of Asian material supposedly precluded finding a good intermediate species. However, the close similarities between *A. jourdani* and *A. whitfordi*, together with their more basal position relative to *Barbourofelis* s.s. suggest that no such intermediary is required. When our phylogenetic results are combined with biochronological and palaeobiogeographical information, the hypothesis is favoured that *A. jourdani* (or an unknown species closely related to it) migrated from Eurasia into North America, giving rise to *A. whitfordi* and the *Barbourofelis* clade. The validity of this hypothesis is independent of the taxonomic attribution of *A. whitfordi* at the genus level, and is further strengthened by the record of *A. jourdani* in Asia (Wang *et al*. 2003). In Eurasia *A. jourdani* is recorded from 11.9 to 9.7 Ma (this study), whereas in North America *A. whitfordi* is recorded from 12 to 8.4 Ma (Tseng *et al.* 2010). This suggests that the dispersal of barbourofelids into North America did not take place during the Middle/Late Miocene transition (as previously argued by Geraads & Güleç 1997), but rather during the late Middle Miocene (> 12.0 Ma), since both *A. whitfordi* and *B. morrisi* are already recorded by this date (Tseng *et al*. 2010). This is in accordance with the previous hypothesis of Qiu (2003, fig. 2.1) that the dispersal of barbourofelids from Eurasia into North America took place between 15 and 11 Ma. In Eurasia, *A. jourdani* survived until the early Vallesian, coexisting with the newly arrived machairodontine felids such as *Machairodus* sp. in CL1 (Crusafont-Pairó & Kurtén 1976) and in Sinap locality 64 (Morlo 2006), soon afterwards to become extinct. In North America, however, *A. jourdani* would have given rise to the most derived barbourofelins, further coexisting with the derived felid *Nimravides* sp. from the Middle to Late Miocene (Baskin 1981; Morlo 2006).

Although our analysis fails to resolve fully the internal phylogeny of *Barbourofelis* s.s., it confirms the previous results of Geraads & Güleç (1997) that *B. loveorum* seems to be its most basal species, whereas *B. piveteaui* from Turkey is deeply nested among North American *Barbourofelis*. These authors formally classified the Turkish barbourofelin into *Barbourofelis*, but favoured the view that this taxon represented an independent development of a *Barbourofelis*-like dental morphology. Although conceivable, we see no particular reason for advocating such evolutionary convergence or parallelism instead of an additional dispersal event of *Barbourofelis* from North America into Eurasia. Finally, the palaeobiogeographical history of the Barbourofelini is further complicated by the finding of an advanced barbourofelid in the Late Miocene of Africa. Thus, Tsujikawa (2005) reported a cranium with damaged dentition of a large barbourofelid from the Namurungule Formation in Kenya (*c.*10–7.5 Ma). Initially attributed to Machairodontinae by Tsujikawa (2005), Werdelin & Peigné (2010) identified it as an undetermined barbourofelid that might belong to the genus *Sansanosmilus*. If confirmed, the presence of *Sansanosmilus* s.l. in Africa could have significant implications for the known biogeographical history of the Barbourofelinae. Nevertheless, it should be taken into account that additional intercontinental faunal dispersals and range extension events took place between Africa and Eurasia during the Late Miocene, so that the presence of *Sansanosmilus* in Africa by this time would not contradict available evidence indicating a Eurasian origin for *Sansanosmilus*.

Summary and conclusions

All the barbourofelin (Barbourofelidae: Barbourofelini) craniodental material available from the Vallès-Penedès Basin (NE Iberian Peninsula), obtained from several late Middle to Late Miocene localities, is described and attributed to *Albanosmilus jourdani*, a species that was previously attributed to the genus *Sansanosmilus*. In addition to isolated teeth and dentognathic remains (some described by previous authors), the newly described material includes a complete cranium, a calvarium and several mandibles, which taken together allow a more complete description of this species. On this basis, it is concluded that *Albanosmilus*, considered during the last decades to be a junior subjective synonym of *Sansanosmilus*, must be considered a distinct genus, with *Grivasmilus* being its objective junior synonym. Accordingly, an emended diagnosis of *Albanosmilus*, together with a differential diagnosis with regard to other barbourofelins, is provided. The nominal taxa *Albanosmilus jourdani andresi* and *Sansanosmilus jourdani vallesiensis* (the latter considered a distinct species of *Sansanosmilus* or even tentatively of *Barbourofelis*) are considered subjective junior synonyms of *Albanosmilus jourdani* s.s., which is the type species of the genus. The North American species previously known as *Barbourofelis whitfordi* is also attributed to *Albanosmilus*. A cladistic phylogenetic analysis of Barbourofelidae, which incorporates previously published data for other barbourofelids as well as the data provided by the newly described remains of *A. jourdani*, supports the monophyly of Barbourofelidae and Barbourofelini, with *Sansanosmilus palmidens* being the basalmost member of this tribe, and the *Barbourofelis* s.s. clade being further supported. It is currently unclear whether *Albanosmilus whitfordi* is more closely related to *Barbourofelis* s.s. than to *A. jourdani*, although the latter alternative is favoured by our results. Moreover, from a taxonomic viewpoint, attribution of *A. whitfordi* to *Barbourofelis* is not warranted on the basis of available morphologic evidence. From a palaeobiogeographical viewpoint, the results of the cladistic analysis indicate that North American barbourofelins originated following a dispersal event of *Albanosmilus* from Eurasia during the late Middle Miocene, with the Turkish *B. piveteaui* probably representing a later dispersal event from North America into Eurasia.

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Supplementary Material

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References

Agustí, J., Cabrera, L. & Moyà-Solà, S. 1985. Sinopsis estratigráfica del Neógeno de la fosa del Vallés-Penedés. *Paleontogia i Evolució*, **18**, 57–81.

Agustí, J., Köhler, M., Moyà-Solà, S., Cabrera, L., Garcés, M. & Parés, J. M. 1996. Can Llobateres: the pattern and timing of the Vallesian hominoid radiation reconsidered. *Journal of Human Evolution*, **31**, 143–155.

Agustí, J., Cabrera, L., Garcés, M. & Parés, J. M. 1997. The Vallesian mammal succession in the Vallès-Penedès basin (northeast Spain): Paleomagnetic calibration and correlation with global events. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **133**, 149–180.

Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O. & Parés, J. M. 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. *Earth-Science Reviews*, **52**, 247–260.

Agustí, J., Casanovas-Vilar, I. & Furió, M. 2005. Rodents, insectivores and chiropterans (Mammalia) from the late Aragonian of Can Missert (Middle Miocene, Vallès-Penedès basin, Spain). *Geobios*, **38**, 575–583.

Alba, D. M. & Moyà-Solà, S. 2012. A new pliopithecid genus (Primates: Pliopithecoidea) from Castell de Barberà (Vallès-Penedès Basin, Catalonia, Spain). *American Journal of Physical Anthropology*, **147**, 88–112.

Alba, D. M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Robles, J. M., Rotgers, C., Furió, M., Angelone, C., Köhler, M., Garcés, M., Cabrera, L., Almécija, S. & Obradó, P. 2006. Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l'Anoia, Cataluña), una sucesión de localidades del Aragoniense superior (MN6 y MN7+8) de la cuenca del Vallès-Penedès. Campañas 2002–2003, 2004 y 2005. *Estudios Geológicos*, **62**, 295–312.

Alba, D. M., Galindo, J., Casanovas-Vilar, I., Robles, J. M., Moyà-Solà, S., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Rotgers, C., Furió, M. & Angelone, C. 2007. La intervenció paleontològica a la nova fase del dipòsit controlat de Can Mata (Els Hostalets de Pierola, Anoia): campanyes 2002–2003, 2004 i 2005. *Tribuna d'Arqueologia*, 2006, 7–33.

Alba, D. M., Robles, J. M., Rotgers, C., Casanovas-Vilar, I., Galindo, J., Moyà-Solà, S., Garcés, M., Cabrera, L., Furió, M., Carmona, R. & Bertó Mengual, J. V. 2009. Middle Miocene vertebrate localities from Abocador de Can Mata (els Hostalets de Pierola, Vallès-Penedès Basin, Catalonia, Spain): An update after the 2006–2008 field campaigns. *Paleolusitana*, **1**, 59–73.

Alba, D. M., Moyà-Solà, S., Malgosa, A., Casanovas-Vilar, I., Robles, J. M., Almécija, S., Galindo, J., Rotgers, C. & Bertó Mengual, J. V. 2010a. A new species of *Pliopithecus* Gervais, 1849 (Primates: Pliopithecidae) from the Middle Miocene (MN8) of Abocador de Can Mata (els Hostalets de Pierola, Catalonia, Spain). *American Journal of Physical Anthropology*, **141**, 52–75.

Alba, D. M., Carmona, R., Bolet, A., Robles, J. M., Casanovas-Vilar, I., Furió, M., Sanisidro, Ó., Rifà, E., Balaguer, J., Checa, L., Luján, À. H., Tomàs, M. & Moyà-Solà, S. 2010b. Intervención paleontológica en la Autovía Orbital de Barcelona B-40, tramo Olesa de Montserrat – Viladecavalls: Resultados preliminares. *Cidaris*, **30**, 51–59.

Alba, D. M., Moyà-Solà, S. & Almécija, S. 2011a. A partial hominoid humerus from the middle Miocene of Castell de Barberà (Vallès-Penedès Basin, Catalonia, Spain). *American Journal of Physical Anthropology*, **144**, 365–381.

Alba, D. M., Casanovas-Vilar, I., Robles, J. M. & Moyà-Solà, S. 2011b. Parada 3. El Aragoniense superior y la transición con el Vallesiense: Can Mata y la exposición paleontológica de els Hostalets de Pierola. *Paleontologia i Evolució*, (Mem. Espec. 6), 95–109.

Alba, D. M., Casanovas-Vilar, I., Robles, J. M., Marmi, J. & Moyà-Solà, S. 2011c. New paleontological excavations at the Late Miocene site of Can Llobateres 1 (Vallès-Penedès Basin, NE Iberian Peninsula): preliminary results of the 2010 campaign. Pp. 35–43 in A. Pérez-García, F. Gascó, J. M. Gasulla & F. Escaso (eds) *Viajando a mundos pretéritos*. Ayuntamiento de Morella, Morella.

Alba, D. M., Casanovas-Vilar, I., Moyà-Solà, S. & Robles, J. M. 2011d. Parada 4. El Vallesiense inferior y su transición con el Vallesiense superior: Can Llobateres. *Paleontologia i Evolució*, (Mem. Espec. 6), 111–123.

Alberdi Alonso, M. T. 1981. *Paleoecología del yacimiento del Neógeno continental de Los Valles de Fuentidueña (Segovia)*. Fundación Juan March, Madrid, 58 pp.

Álvarez-Sierra, M. A., Calvo, J. P., Morales, J., Alonso-Zarza, A., Azanza, B., García Paredes, I., Hernández Fernández, M., Van der Meulen, A. J., Peláez-Campomanes, P., Quiralte, V., Salesa, M. J., Sánchez, I. M. & Soria, D. 2003. El tránsito Aragoniense-Vallesiense en el área de Daroca-Nombrevilla (Zaragoza, Spain). *Coloquios de Paleontología*, (Vol. Ext. 1), 25–33.

Andrews, C. W. 1914. On the Lower Miocene vertebrates from British East Africa, collected by Dr. Felix Oswald. *Quarterly Journal of the Geological Society of London*, **70**, 163–186.

Azanza, B., **Alonso-Zarza, A. M.**, **Álvarez-Sierra, M. A.**, **Calvo, J. P.**, **Fraile, S.**, **García-Paredes, I.**, **Gómez, E.**, **Hernández-Fernández, M.**, **Van der Meulen, A.**, **De Miguel, D.**, **Montoya, P.**, **Morales, J.**, **Murelaga, X.**, **Peláez-Campomanes, P.**, **Perez, B.**, **Quiralte, V.**, **Salesa, M. J.**, **Sánchez, I. M.**, **Sánchez-Marco, A.** & **Soria, D.** 2004. Los yacimientos de vertebrados continentales del Aragoniense superior (Mioceno Medio) de Toril, Cuenca de Calatayud-Daroca. *Geo-Temas*, **6**, 271–274.

Barbour, E. H. & **Cook, H. J.** 1915. A new saber-toothed cat from Nebraska. *Nebraska Geological Survey*, **4**, 235–238.

Bartrina, M. T., Cabrera, L., Jurado, M. J., Guimerà, J. & Roca, E. 1992. Evolution of the central Catalan margin of the Valencia trough (western Mediterranean). *Tectonophysics*, **203**, 219–247.

Baskin, J. A. 1981. *Barbourofelis* (Nimravidae) and *Nimravides* (Felidae) with a description of two new species from the late Miocene of Florida. *Journal of Mammalogy*, **62**, 122–139.

Baskin, J. A. 2005. Carnivora from the late Miocene Love Bone Bed of Florida. *Bulletin of the Florida Museum of Natural History*, **62**, 122–139.

Beaumont, G. de & **Crusafont-Pairó, M.** 1982. Les Félidés (Mammifères, Carnivores) du Vallésien du Vallès, Catalogne, Espagne. *Archives des Sciences Genève*, **35**, 41–64.

Bernor, R. L., Kordos, L., Rook, L., Agustí, J., Andrews, P., Armour-Chelu, M., Begun, D. R., Cameron, D. W., Damuth, J., Daxner-Hock, G., de Bonis, L., Fejfar, O., Fessaha, N., Fortelius, M., Franzen, J., Gasparik, M., Gentry, A., Llenas, M., Meszáros, L., Müller, P., Renne, P., Rocek, Z., Sen, S., Scott, R., Szyndlar, Z., Topál, G., Ungar, P. S., Utescher, T., **Van Dam, J. A.**, **Werdelin, L. & Ziegler, R.** 2002. Recent advances on multidisciplinary research at Rudabánya, Late Miocene (MN9), Hungary: a compendium. *Palaeontographica Italica*, **89**, 3–36.

Blainville, H. M. D. de 1843. *Ostéographie ou description iconographique comparée du squelette et du système dentaire des Mammifères récents et fossils pour servir de base à la zoologie et à la géologie. Tome II. —Secundatès*. J. B. Baillière et Fils, Paris, 718 pp.

Boule, M. 1901. Révision des espèces européennes de *Machairodus*. *Bulletin de la Société Géologique de France*, **4**, 551–573.

Bowdich, T. E. 1821. *An analysis of the natural classifications of Mammalia, for the use of students and travellers*. J. Smith, Paris.

Bremer, K. 1994. Branch support and tree stability. *Cladistics*, **10**, 295–304.

Bryant, H. N. 1988. Delayed eruption of the deciduous upper canine in the sabertoothed carnivore *Barbourofelis lovei* (Carnivora, Nimravidae). *Journal of Vertebrate Paleontology*, **8**, 295–306.

Bryant, H. N. 1991. Phylogenetic relationships and systematics of the Nimravidae (Carnivora). *Journal of Mammalogy*, **72**, 56–78.

Cabrera, L. & **Calvet, F.** 1990. Sequential arrangement of the Neogene sedimentary record in the Vallés-Penedés and Valls-Reus half grabens. Iberian margins, NE Spain. *Terra Abstracts*, **2**, 1–110.

Cabrera, L. & **Calvet, F.** 1996. Onshore Neogene record in NE Spain: Vallès-Penedès and El Camp grabens (NW Mediterranean). Pp. 97–105 in P. F. Friend & C. Dabrio (eds) *Tertiary Basins of Spain*. Cambridge University Press, Cambridge.

Cabrera, L., Calvet, F., Guimerà, J. & Permanyer, A. 1991. El registro sedimentario miocénico en los semigrabens del Vallès-Penedès y de El Camp: organización secuencial y relaciones tectónican-sedimentación. *I Congreso Grupo Español del Terciario, Libro-Guía Excursión 4*, 132 pp.

Cabrera, L., Roca, E., Garcés, M. & de Porta, J. 2004. Estratigrafía y evolución tectonosedimentaria oligocena superior-neógena del sector central del margen catalán (Cadena Costero-Catalana). Pp. 569–573 in J. A. Vera (ed.) *Geología de España*. Sociedad Geológica de España-Instituto Geológico y Minero de España, Madrid.

Carmona, R., Alba, D. M., Casanovas-Vilar, I., Furió, M., Garcés, M., Bertó Mengual, J. V., Galindo, J., & Luján, Á. H. 2011. Intervención paleontológica en la serie del Mioceno Superior del Ecoparc de Can Mata (cuenca del Vallès-Penedès, NE de la pennsula Ibérica). Pp. 65–74 in A. Pérez-García, F. Gascó, J. M. Gasulla, & F. Escaso (ed.) *Viajando a mundos pretéritos*. Ayuntamiento de Morella, Morella, Spain.

Casanovas-Vilar, I., Furió, M. & Agustí, J. 2006. Rodents, insectivores and paleoenvironment associated to the first-appearing hipparionine horses in the Vallès-Penedès Basin (Northeastern Spain). *Beiträge zur Paläontologie*, **30**, 89–107.

Casanovas-Vilar, I., Alba, D. M., Almécija, S., Robles, J. M., Galindo, J. & Moyà-Solà, S. 2008a. Taxonomy and paleobiology of the genus *Chalicomys* Kaup, 1832 (Rodentia, Castoridae), with the description of a new species from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, Spain). *Journal of Vertebrate Paleontology*, **28**, 851–862.

Casanovas-Vilar, I., Alba, D. M., Moyà-Solà, S., Galindo, J., Cabrera, L., Garcés, M., Furió, M., Robles, J. M., Köhler, M. & **Angelone, C.** 2008b. Biochronological, taphonomical and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae). *Journal of Human Evolution*, **55**, 589–603.

Casanovas-Vilar, I., Garcés, M., Robles, J. M. & **Moyà-Solà, S.** 2011a. An updated chronology for the Miocene hominoid radiation in Western Eurasia. *Proceedings of the National Academy of Sciences, USA*, **108**, 5554–5559.

Casanovas-Vilar, I., Alba, D. M., Robles, J. M. & **Moyà-Solà, S.** 2011b. Registro paleontológico continental del Mioceno de la cuenca del Vallès-Penedès. *Paleontologia i Evolució*, (Mem. Espec. 6), 55–80.

Chen, G. F. & **Wu, W. Y.** 1976. Miocene mammals from Jiulongkou, Cixian, Hebei Province. *Vertebrata PalAsiatica*, **14**, 6–15. [In Chinese].

Crusafont, M. & **Truyols, J.** 1954. *Catálogo paleomastológico del Mioceno del Vallés-Penedés y de Calatayud-Teruel*. Segundo Cursillo Internacional de Paleontología. Museu de la Ciudad de Sabadell, Sabadell, 25 pp.

Crusafont-Pairó, M. & **Ginsburg, L.** 1973. Les carnassiers fossiles de Los Valles de Fuentidueña (Ségovie, Espagne). *Bulletin du Muséum National d'Histoire Naturelle, Paris*, **3**, 19–45.

Crusafont-Pairó, M. & **Golpe-Posse, J. M.** 1974a. Nuevos yacimientos del Terciario continental del N. E. de España. *Acta Geológica Hispánica*, **9**, 81–83.

Crusafont-Pairó, M. & **Golpe-Posse, J. M.** 1974b. Asociación de *Anchitherium* Mey., 1834, con *Hipparion* Christ, 1832, en el Alto Mioceno del Vallés. *Boletín de la Real Sociedad Española de Historia Natural (Geología)*, **72**, 75–93.

Crusafont Pairó, M. & **Kurtén, B.** 1976. Bears and bear-dogs from the Vallesian of the Vallès-Penedès basin, Spain. *Acta Zoologica Fennica*, **144**, 1–29.

Depéret, C. 1887. Recherches sur la succession des faunes des Vertébrés miocènes de la Vallée du Rhône. *Archives du Muséum d'Histoire Naturelle de Lyon*, **4**, 45–319.

Depéret, C. 1892. La faune de Mammifères miocènes de La Grive-Saint-Alban (Isère) et de quelques autres localités du bassin du Rhône. Documents nouveaux et révision générale. *Archives du Museum d'Histoire Naturelle de Lyon*, **5**, 1–93.

Farris, J. S. 1989. The retention index and the rescaled consistency index. *Cladistics*, **5**, 417–419.

Filhol, H. 1872. Sur les Carnassiers et les Chéiroptères dont on trouve les débris fossiles dans les gisements de phosphorite de Caylux, Frégols, Concots. *Comptes Rendus de l'Académie des Sciences Paris*, **75**, 92–94.

Filhol, H. 1879. Étude des mammifères fósiles de Saint-Gerand-le-Puy (Allier). *Annales des Sciences Géologiques*, **10**, 1–252.

Filhol, H. 1883. Notes sur quelques Mammifères fossiles de l'époque miocène. *Archives du Muséum d'Histoire Naturelle de Lyon*, **3**, 1–97.

Filhol, H. 1890. *Études sur les Mammifères fossiles de Sansan*. G. Masson, Paris, 319 p.

Fortelius, M. (coord.). 2011. *Neogene of the Old World Database of Fossil Mammals (NOW)*. University of Helsinki [updated at http://www.helsinki.fi/science/now/], last accessed March 2011.

Fraas, O. 1885. Beiträge zur Fauna von Steinheim. *Jahreshefte des Vereins für vaterländische Naturkunde in Würtemberg*, **41**, 313–326.

Fraile, S., Pérez, B., De Miguel, I. & **Morales, J.** 1997. Revisión de los Carnívoros presentes en los yacimientos del Neógeno español. Pp. 77–80 in J. P. Calvo & J. Morales (eds) *Avances en el conocimiento del Terciario Ibérico*. UCM-CSIC, Madrid.

Garcés, M., Agustí, J., Cabrera, L. & **Parés, J. M.** 1996. Magnetostratigraphy of the Vallesian (late Miocene) in the Vallès-Penedès Basin (northeast Spain). *Earth and Planetary Science Letters*, **142**, 381–396.

Geraads, D. & **Güleç, E.** 1997. Relationships of *Barbourofelis piveteaui* (Ozansoy, 1965), a Late Miocene nimravid (Carnivora, Mammalia) from Central Turkey. *Journal of Vertebrate Paleontology*, **17**, 370–375.

Gervais, P. 1850 (1848–1852). *Zoologie et paléontologie françaises. Tome I*. Arthus Bertrand, Paris, 271 pp.

Gibert, J. M. de & **Casanovas-Vilar, I.** 2011. Contexto geológico del Mioceno de la cuenca del Vallès-Penedès. *Paleontologia i Evolució*, (Mem. Espec. 6), 39–45.

Ginsburg, L. 1961. La faune des carnivores miocènes de Sansan (Gers). *Mémoires du Muséum National d'Histoire naturelle*, **9**, 1–190.

Ginsburg, L. 1978. *Syrtosmilus syrtensis*, n. gen., n. sp., felidé machairodontiforme du Burdigalien de Libye. *Comptes Rendus Sommaire de la Société Géologique de France*, **2**, 73–74.

Ginsburg L. 1999. Order Carnivora. Pp. 109–148 in G. E. Rössner & K. Heissig (eds) *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München.

Ginsburg, L. 2001. Les faunes de mammifères terrestres du Miocène moyen des Faluns du bassin de Savigné-sur-Lathan (France). *Geodiversitas*, **23**, 381–394.

Ginsburg, L., Morales, J. & **Soria, D.** 1981. Nuevos datos sobre los carnívoros de Los Valles de Fuentidueña (Segovia). *Estudios Geológicos*, **37**, 383–415.

Golpe-Posse, J. M. 1974. Faunas de yacimientos con suiformes en el Terciario español. *Paleontología y Evolución*, **8**, 1–87.

Heizmann, E. P. J. 1973. Die Carnivoren des Steinheimer Beckens. B. Ursidae, Felidae, Viverridae sowie Ergänzungen und Nachträge zu den Mustelidae. *Palaeontographica*, (Suppl. 8), 1–95.

Heizmann, E. P. J, Ginsburg, L. & **Bulot, C.** 1980. *Prosansanosmilus peregrinus*, ein neuer machairodontider Felide aus dem Miocän Deutschlands und Frankreichs. *Stuttgarter Beiträge zur Naturkunde B*, **58**, 1–27.

Hunt, R. M. 1987. Evolution of the aeluroid Carnivora: significance of auditory structure in the nimravid *Dinictis*. *American Museum Novitates*, **2886**, 1–74.

International Commission on Zoological Nomenclature (ICZN). 1999. *International Code of Zoological Nomenclature. Fourth Edition*. The International Trust for Zoological Nomenclature, London.

Joeckel, R. M. & **Stavas, J. M.** 1996. New insights into the cranial anatomy of *Barbourofelis fricki* (Mammalia, Carnivora). *Journal of Vertebrate Paleontology*, **16**, 585–591.

Joeckel, R. M., Peigné, S., Hunt, R. M. & **Skolnick, R. L.** 2002. The auditory region and nasal cavity of Oligocene Nimravidae (Mammalia: Carnivora). *Journal of Vertebrate Paleontology*, **22**, 830–847.

Kitts, D. B. 1957. A Pliocene vertebrate fauna from Ellis County, Oklahoma. *Oklahoma Geological Survey Circular*, **45**, 1–24.

Kretzoi, M. 1929. Materialen zur phylogenetischen Klassification der Aeluroideen. *10th International Zoological Congress, Budapest*, **1927**, 1293–1355.

Kretzoi, M. 1945. Bemerkungen über das Raubtiersystem. *Annales Historico-Naturale, Museum Nationale Hungaricum*, **38**, 59–83.

Kurtén, B. 1976. Fossil Carnivora from the late Tertiary of Bled Douarah and Cherichira, Tunisia. *Notes du Service Géologique de Tunisie*, **42**, 177–214.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. Holmiae, Laurentii Salvii, 824 pp.

Martin, L. D. 1980. Functional morphology and the evolution of cats. *Transactions of the Nebraska Academy of Sciences*, **8**, 141–154.

Martin, L. D. 1984. Phyletic trends and evolutionary rates. *Carnegie Museum of Natural History Special Publication*, **8**, 526–538.

Martin, L. D. 1998. Nimravidae. *Pp.* 228–235 in C. M. Janis, K. M. Scott & L. L. Jacobs (eds) *Evolution of Tertiary mammals of North America, Vol. 1: Terrestrial carnivores, ungulates, and ungulatelike mammals.* Cambridge University Press, New York.

Mawby, J. E. 1965. Machairodonts from the late Cenozoic of the Panhandle of Texas. *Journal of Mammalogy*, **46**, 573–587.

McKenna, M. C. & **Bell, S. K.** 1997. *Classification of Mammals above the Species Level*. Columbia University Press, New York, 631 pp.

Mein, P. & **Ginsburg, L.** 2002. Sur l'âge relatif des différents dépôts karstiques miocènes de La Grive-Saint-Alban (Isère). *Cahiers scientifiques*, **2**, 7–47.

Morales, J., Salesa, M. J., Pickford, M. & **Soria, D.** 2001. A new tribe, new genus and two new species of Barbourofelinae (Felidae, Carnivora, Mammalia) from the Early Miocene of East Africa and Spain. *Transactions of the Royal Society of Edinburgh*, **92**, 97–102.

Morales, J., Pickford, M. & **Soria, D.** 2007. New carnivoran material (Creodonta, Carnivora and Incertae sedis) from the Early Miocene of Napak, Uganda. *Paleontological Research*, **11**, 71–84.

Morlo, M. 2006. New remains of Barbourofelidae (Mammalia, Carnivora) for the Miocene of southern Germany: implications for the history of barbourofelid migrations. *Beiträge zur Paläontologie*, **30**, 339–346.

Morlo, M, Peigné, S. & **Nagel, D.** 2004. A new species of *Prosansanosmilus*: implication for the systematic relationship of the family Barbourofelidae new rank (Carnivora, Mammalia). *Zoological Journal of the Linnean Society*, **140**, 43–61.

Moyà-Solà, S., Köhler, M., Alba, D. M., Casanovas-Vilar, I., Galindo, J., Robles, J. M., Cabrera, L., Garcés, M., Almécija, S. & **Beamud, E.** 2009. First partial face and upper dentition of the Middle Miocene hominoid *Dryopithecus fontani* from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, NE Spain): taxonomic and phylogenetic implications. *American Journal of Physical Anthropology*, **139**, 126–145.

Nagel, D. 2009. The early Vallesian vertebrates of Atzelsdorf (Late Miocene, Austria). 10. Carnivora. *Annalen des Naturhistorischen Museums in Wien*, **111A**, 605–618.

Naples, V. L. & **Martin, L. D.** 2000. Restoration of the superificial facial musculature in nimravids. *Zoological Journal of the Linnean Society*, **129**, 55–81.

Neff, N. A. 1983. *The basicranial anatomy of the Nimravidae (Mammalia: Carnivora): character analyses and phylogenetic inferences*. Unpublished PhD thesis, The City University of New York, 660 pp.

Ozansoy, F. 1965. Étude des gisements continentaux et des Mammifères du Cénozoique de Turquie. *Mémoires de la Société Géologique de France*, **102**, 1–92.

Peigné, S. 2001. A primitive nimravine skull from the Quercy fissures, France: implications for the origin and evolution of Nimravidae (Carnivora). *Zoological Journal of the Linnean Society*, **132**, 401–410.

Peigné, S. 2003. Systematic review of European Nimraviane (Mammalia, Carnivora, Nimravidae) and the phylogenetic relationships of Palaeogene Nimravidae. *Zoologica Scripta*, **32**, 199–229.

Peigné, S. & **de Bonis, L.** 2003. Juvenile cranial anatomy of Nimravidae (Mammalia, Carnivora): biological and phylogenetic implications. *Zoological Journal of the Linnean Society*, **138**, 477–493.

Peigné, S., Salesa, M. J., Antón, M. & **Morales, J.** 2006. New data on carnivores from the Middle Miocene (Upper Aragonian, MN6) of Arroyo del Val area (Villafeliche, Zaragoza Province, Spain). *Estudios Geológicos*, **62**, 359–374.

Qiu, Z. 2003. Dispersals of Neogene carnivorans between Asia and North America. *Bulletin of the American Museum of Natural History*, **279**, 18–31.

Qiu, Z. & **Qiu, Z.** 1995. Chronological sequence and subdivision of Chinese Neogene mammalian faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **116**, 41–70.

Robles, J. M., Alba, D. M., Carmona, R., Rotgers, C., Galindo, J., Balaguer, J., Almécija, S. & **Moyà-Solà, S.** 2010. Nuevos hallazgos de *Sansanosmilus jourdani* (Filhol 1883) (Carnivora: Barbourofelidae) del Mioceno medio de la serie estratigráfica del Abocador de Can Mata (cuenca del Vallès-Penedès, Barcelona, España). *Cidaris*, **30**, 265–271.

Robles, J. M., Alba, D. M., Casanovas-Vilar, I., Galindo, J., Cabrera, L., Carmona, R. & **Moyà-Solà, S.** 2011. On the age of the paleontological site of Can Missert (Terrassa, Valllès-Penedès Basin, NE Iberian Peninsula). Pp. 339–346 in A. Pérez-García, F. Gascó, J. M. Gasulla & F. Escaso (eds) *Viajando a mundos pretéritos*. Ayuntamiento de Morella, Morella.

Roca, E. & **Desegaulx, P.** 1992. Geological evolution and vertical movement analysis of the Valencia Trough area (western Mediterranean). *Marine and Petroleum Geology*, **9**, 167–185.

Roca, E. & **Guimerà, J.** 1992. The Neogene structure of the eastern Iberian margin: structural constraints on the crustal evolution of the Valencia Trough (Western Mediterranean). *Tectonophysics*, **203**, 203–218.

Roman, F. 1907. *Le Neogène continental de la la basse Vallée du Tage (rive droite). 1e partie*. Memoires de la Comission du Service Géologique de Portugal, Lisbonne, 88 pp.

Rotgers, C. & **Alba, D. M.** 2011. The genus *Anchitherium* (Equidae: Anchitheriinae) in the Vallès-Penedès Basin (Catalonia, Spain). Pp. 347–354 in A. Pérez-García, F. Gascó, J. M. Gasulla & F. Escaso (eds) *Viajando a mundos pretéritos*. Ayuntamiento de Morella, Morella.

Sabol, M., Joniak, P. & **Holec, P.** 2004. Succession(-s) of mammalian assemblages during the Neogene – a case study from the Slovak part of the Western Carpathians. *Scripta Facultatis Scientiarum Naturalium Universitatis Masarykiane Brunensis*, **31–32**, 65–84.

Schlosser, M. 1888. Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Credonten und Carnivoren des europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen aussereuropäischen Verwandten, 1. Teil. *Beiträge zur Paläontologie Österreich-Ungarns und des Orients, Mojisisovics*, **6**, 1–224.

Schmidt-Kittler, N. 1987. The Carnivora (Fissipedia) from the Lower Miocene of East Africa. *Palaeontographica A*, **197**, 85–126.

Schultz, C. B., Schultz, M. R. & **Martin, L. D.** 1970. A new tribe of saber-toothed cats (Barbourofelini) from the Pliocene of North America. *Bulletin of the University of Nebraska State Museum*, **9**, 1–31.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, **85**, 1–350.

Smith, J. B. & **Dodson, P.** 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology*, **23**, 1–12.

Strong, E. E. & **Lipscomb, D.** 2005. Character coding and inapplicable data. *Cladistics*, **15**, 363–371.

Swofford, D. 2003. *PAUP* 4.0*. Sinauer Associates, Sunderland, Massachusetts.

Tedford, R. H. 1978. History of dogs and cats. A view from the fossil record. Pp. 1–10 in *Nutrition and management of dogs and cats*. Ralston Purina Co, St. Louis.

Tomàs, M., Alba, D. M., Sanisidro, Ó., Bolet, A. & **Checa, L.** 2010. Los perisodáctilos del Mioceno superior de la Autovía Orbital de Barcelona B-40, tramo Olesa de Montserrat – Viladecavalls (cuenca del Vallès-Penedès). *Cidaris*, **30**, 317–323.

Tseng, Z. J., Takeuchi, G. T. & **Wang, X.** 2010. Discovery of the upper dentition of *Barbourofelis whitfordi* (Nimravidae, Carnivora) and an evolution of the genus in California. *Journal of Vertebrate Paleontology*, **30**, 244–254.

Tsujikawa, H. 2005. The updated Late Miocene large mammal fauna from Samburu Hills, northern Kenya. *African Study Monographs, Supplement*, **32**, 1–50.

Villalta Comella, J. F. de & **Crusafont Pairó, M.** 1943a. Los vertebratos del Mioceno continental de la cuenca Vallés-Pénédés (provincia de Barcelona). I. Insectívoros. II. Carnívoros. *Boletín del Instituto Geológico y Minero de España*, **56**, 145–336.

Villalta Comella, J. F. de & **Crusafont Pairó, M.** 1943b. *Contribución al conocimiento de* Albanosmilus jourdani *Filhol*. Consejo Superior de Investigaciones Científicas, Madrid, 44 pp.

Villalta, J. F. de & **Crusafont, M.** 1952. *Grivasmilus* remplaçant *Albanosmilus* (= *Sansanomilus*). *Comptes Rendus des Seances de la Société Géologique de France*, **14**, 308–309.

Viranta, S. & **Werdelin, L.** 2003. Carnivora. Pp. 178–193 in M. Fortelius, J. Kappelman, R. L. Bernor & S. Sen (eds) *Geology and Paleontology of the Miocene Sinap Formation, Turkey*. Columbia University Press, New York.

Viret, J. 1951. Catalogue critique de la faune des mammifères miocènes de la Grive Saint-Alban (Isère). 1ère partie: Chiroptères, Carnivores, Edentés pholidotes. *Nouvelles Archives du Museum d'Histoire Naturelle de Lyon*, **3**, 1–104.

Wang, X., Qiu, Z. & **Opdyke, N.D.** 2003. Litho-, bio-, and magnetostratigraphy and paleonvironment of Tunggur Formation (Middle Miocene) in Central Inner Mongolia, China. *American Museum Novitates*, **3411**, 1–31.

Werdelin, L. 2005. The Carnivora of Rudabánya (MN 9, Late Miocene, Hungary). *Palaeontographia Italica*, **90**, 163–180.

Werdelin, L. & **Peigné, S.** 2010. Carnivora. Pp. 603–657 in L. Werdelin & W. J. Sanders (eds) *Cenozoic Mammals of Africa*. University of California Press, Berkeley.

Table 4. Cladistic data matrix employed in this paper, based on the characters previously employed by Geraads & Güleç (1997) and Morlo et al. (2004), and further including additional data based on published sources as well as on the new material of *Albanosmilus jourdani* described in this paper (see Materials and methods for further details). Notes: *Syrtosmilus syrtensis* and *Ginsburgsmilus napakensis* were excluded from the analysis. Abbreviations: **I**, inapplicable character; **?**, missing data.

Character	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I	0	0	0	0	0
Pseudaelurus spp.	0	?	0	0	0	0	0	0	1	0	1	2	1	2	1	1	1	0	0	3	1	1	0	?	?	0	0	0	0	I	0	0	0	0	0
Proailurus lemanensis	0	0	0	0	0	0	0	1	1	0	1	2	1	1	1	0	1	0	0	2	1	0	0	0	0	0	0	0	0	I	0	0	1	0	0
Eofelis edwardsii	1	?	1	0	1	0	0	1	0	0	1	0	1	2	1	0	2	0	1	3	1	1	0	0	?	?	?	0	0	I	?	?	1	0	2
Nimravus intermedius	1	1	1	0	1	0	0	0	0	0	4	1	3	3	1	0	2	0	1	3	1	0	?	?	?	0	0	0	0	I	0	0	0	0	0
Syrtosmilus syrtensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	2	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?
Prosansanosmilus eggeri	1	?	?	?	2	0	0	1	1	1	2	2	2	2	2	2	1	1	2	2	2	2	?	?	?	?	0	?	1	0	?	0	0	0	0
Prosansanosmilus peregrinus	1	?	2	?	?	?	?	?	2	1	3	3	?	?	2	2	1	1	2	2	2	2	?	?	?	?	?	0	1	0	0	0	0	0	0
Afrosmilus turkanae	?	?	?	?	2	2	?	0	1	0	2	2	?	?	2	0	1	1	2	2	3	2	?	?	?	?	?	1	0	0	?	?	0	1	?
Afrosmilus africanus	1	?	2	?	2	2	1	0	2	0	3	3	?	?	2	0	1	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	?	?	?
Afrosmilus hispanicus	1	?	2	?	2	2	?	0	2	1	3	2	?	?	?	?	?	1	2	2	3	?	?	?	?	?	?	?	?	?	?	?	?	1	0
Ginsburgsmilus napakensis	1	?	1	1	?	0	0	1	1	0	1	2	1	1	?	0	1	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Sansanosmilus palmidens	1	?	2	1	2	2	1	0	1	1	5	I	3	3	2	2	0	1	3	2	3	2	0	0	1	0	0	0	1	1	0	0	0	0	0
Barbourofelis loveorum	1	1	?	1	2	2	0	0	2	0	5	I	?	?	2	2	0	1	3	3	3	2	1	1	2	1	0	1	1	1	1	2	1	1	1
Barbourofelis fricki	1	?	2	1	2	2	0	0	2	1	5	I	3	?	2	2	0	1	3	3	3	2	1	1	2	1	1	1	1	2	1	2	1	1	1
Barbourofelis piveteaui	1	1	2	1	2	2	0	0	2	2	5	I	3	?	2	2	0	1	3	3	3	2	1	1	2	1	1	1	1	1	1	2	1	1	1
Barbourofelis morrisi	1	?	2	1	2	2	0	0	2	1	5	I	3	3	2	2	0	1	3	3	3	2	1	1	2	1	1	0	1	1	1	2	1	1	1
Albanosmilus jourdani	1	?	2	1	2	2	1	0	2	2	5	I	3	3	2	2	0	1	3	3	3	2	1	1	2	1	0	1	1	1	0	1	1	1	1
Albanosmilus whitfordi	1	?	2	1	2	2	1	0	2	2	5	I	?	?	2	2	0	1	3	3	3	2	?	1	2	1	0	1	1	1	0	1	1	1	1

Appendix 1

Collection numbers of riginal remains and good-quality casts of several North-American *Barbourofelis* species, housed at the American Museum of Natural History (AMNH; New York, USA) studied as comparison material:

Barbourofelis loveorum. AMNH 116920, left mandible with i3 and p4-m1 (cast).

Barbourofelis fricki. AMNH 61981, right m1; AMNH 61982, left partial mandible with i1-m1; AMNH 103202, left mandible with i1-m1 (cast); AMNH 108193, cranium and right hemimandible (cast of holotype).

B. whitfordi. AMNH 61856, partial cranium with left and right canine (partial) and P3-P4; AMMH 61858, left hemimandible with i2-m1; AMNH 69453, left partial maxilla with I1-I3, and partial canine and P4; AMNH 69454, right partial maxilla with I2-C1; AMNH 32798/80159, left hemimandible with i1-m1 (cast); AMNH 61844, right hemimandible with c1 and p3-m1; AMNH 61857, left partial mandible with i3-m1; AMNH 69455, right hemimandible with i1-m1; AMNH 14308, right hemimandible with p4-m1 (cast of the holotype specimen); AMNH 69456, right partial hemimandible with i2-m1; AMNH w/n (CLAR.C38A-210), left partial hemimandible with p4-m1

Barbourofelis morrisi. AMNH 25201, right hemimandible with i3-m1; AMNH 25202, right partial hemimandible with m1; AMNH 61850, partial cranium with left I1, partial canine and P3, and right P4; AMNH 61869, right partial hemimandible with m1; AMNH 61870, cranium with left P4 and right P3; AMNH 61875, cranium with right P3 and left P3-P4; AMNH 61878, left maxillary fragment with dP3-dP4 and P4 germ; AMNH 61889, right hemimandible with partial p4-m1; AMNH 61896, right hemimandible with p4-m1; AMNH 61900, right hemimandible with i1-i3 and p4-m1; AMNH 61962, right maxillary fragment with P3-P4; AMNH 61979, right maxilla with I1-I3 and P3; AMNH 61980, complete mandible with the whole dentition; AMNH 79999, cranium with the whole dentition (holotype).

Appendix 2

Character and character state definition for the data matrix (Online Supplementary Material, Table 1) employed in the cladistic analysis are reported below. Equivalences from the data matrices previously published by other authors are included within parentheses, by using the following abbreviations: **GG**, Geraads & Güleç (1997); **MEA**, Morlo *et al.* (2004).

#01 (=MEA01): Crenulations on the dentition. (0) absent; (1) present, at least on the distal border of the C1.

#02 (=MEA02): Size of dC1 relative to that of C1. (0) dC1 much smaller than C1; (1) dC1 moderately smaller than or nearly the size of C1.

#03 (=MEA03): Labiolingual compression of the C1. (0) very slightly compressed (length/breadth index smaller than 1.5); (1) markedly compressed (index between 1.5 and 1.8); (2) very compressed (index larger than 1.8).

#04 (=MEA04). Vertical grooves on the C1. (0) absent; (1) present.

#05 (=MEA05). P1. (0) present and reduced relative to P2; (1) very reduced, sometimes absent; (2) absent.

#06 (=MEA06). P2. (0) present and reduced relative to P3; (1) very reduced, sometimes absent; (2) absent.

#07 (=MEA07). P3, mesial cingulum cusp. (0) absent; (1) present. This is similar to Geraads & Güleç's (1997) character #05, which is based on the number of cusps in the P3 but recognized three different states.

#08 (=MEA08). P3, development of the lingual portion of the crown. (0) absent or nearly absent; (1) developed, the third root more or less clearly separate from the others.

#09 (=MEA09). P4, parastyle. (0) absent; (1) present and developed; (2) distinctly more developed than in state 1. This is similar to Geraad & Güleç's (1997) character #08, whereas their character #09 separately refers to the hypsodonty of this tooth.

#10 (=GG07, MEA10). P4, preparastyle. (0) absent; (1) present and small; (2) distinctly more developed than in state 1.

#11 (=GG06, MEA11). P4, protocone size. (0) large; (1) reduced compared to state 0; (2) about the size of the parastyle; (3) reduced, distinctly smaller than the parastyle; (4) markedly reduced, crest-like, no basin between protocone and paracone; (5) absent. Observations: Morlo *et al.* (2004) defined character state (5) as 'markedly reduced and applied against the paracone lingual wall', but did not apply this state to any taxon. Here we have redefined this character state as 'absent' and have scored as such the derived barbourofelids of the genera *Sansanosmilus*, *Albanosmilus* and *Barbourofelis*. To our knowledge, there is no unworn P4 showing whether these taxa displayed a reduced or absent protocone. It is nevertheless clear that, if present at all, the protocone must have been considerably reduced, since no trace of it can be found in all the available worn P4. The complete lack of protocone in the dP3 of *Barbourofelis loveorum* (see Bryant 1988) suggests that this would have been probably the case also for the P4.

#12 (=MEA12). P4, location of the protocone mesial border relative to the mesial border of the paracone/parastyle complex. (0) protocone mesially located; (1) protocone location variable, from state 0-1; (2) protocone mesial border across or slightly distal to the paracone border; (3) protocone distinctly distal to the paracone border. Observations: This character is scored as inapplicable in the derived barbourofelids *Sansanosmilus* and *Barbourofelis* because they presumably lacked a protocone in the P4 (see comments regarding #11); if present, the protocone would have been small and its position cannot be evaluated due to wear, so that alternatively these taxa may be scored as missing data, which would not make any difference regarding the cladistic analysis.

#13 (=GG10, MEA13). M1. (0) large-sized, with the ratio P4 length / M1 width much lower than 1.5; (1) reduced and transversely elongated, with the ratio around 1.5; (2) more reduced, with the ratio between 1.6 and 1.8; (3) extremely reduced, with the ratio higher than 1.8. Geraads & Güleç (1997) coded this character as missing data in *A. jourdani*, but we have coded it on the basis of the newly described material.

#14 (=MEA14). M1, development of the protocone and metacone. (0) metacone and protocone large; (1) the two cusps strongly reduced but with the protocone still prominent and the metacone distally projected; (2) protocone markedly reduced but still prominent, metacone completely reduced and not projected distally; (3) protocone extremely reduced and not prominent, metacone reduced but still distally projected.

#15 (=MEA15). p1. (0) present and reduced; (1) very reduced, sometimes absent; (2) vestigial or absent.

#16 (=MEA16). p2. (0) present and reduced; (1) very reduced, sometimes absent; (2) vestigial or absent.

#17 (=MEA17). p3-p4, distal accessory cusp. (0) present on p4 only; (1) present on p3 and p4; (2) absent.

#18 (=MEA18). m1 protoconid height. (0) protoconid relatively low; (1) protoconid relatively high.

#19 (=MEA19). Reduction of m1 talonid compared to that of metaconid. (0) no clear trend, metaconid and talonid display a similar reduction; (1) metaconid markedly more reduced than talonid; (2) talonid markedly more reduced than metaconid; (3) both absent. Observations: character state 3 has been added here in order to reflect the condition of barbourofelins.

#20 (MEA20). m1 metaconid. (0) large and little reduced compared to the paraconid; (1) markedly reduced compared to the paraconid; (2) very small; (3) vestigial or absent.

#21 (=MEA21). m1 reduction of talonid. (0) talonid long, distinctly more than 20% of total m1 length; (1) talonid short, between 10 and 20% of total m1 length; (2) talonid extremely reduced, forming only a small posterior bulge; (3) vestigial or absent.

#22 (=MEA22). m2. (0) present and reduced; (1) very reduced, sometimes absent; (2) absent.

#23 (=GG01). Orbit. (0) open; (1) closed.

#24 (=GG02). Infraorbital foramen. (0) medium-sized; (1) very large.

#25 (=GG03). Masseter insertion. (0) normal; (1) enlarged; (2) excavated.

#26 (=GG04). Palate at the level of P3-P4. (0) normal; (1) very broad.

#27 (=GG11). Position of M1. Polarity: (0) distal to P4; (1) medial to P4. Observations: Geraads & Güleç (1997) coded this character as missing data in *A. jourdani*, but we have coded it on the basis of the newly described material.

#28 (=GG12). Mandibular symphysis. (0) low and thick; (1) high and thin. Observations: Geraads & Güleç (1997) coded this character as missing data in *A. jourdani*, but we have coded it on the basis of the newly described material.

#29. Genial flange. (0) absent; (1) present. Newly added character.

#30 (=GG13). Genial flange size. (0) small; (1) long; (2) very long. This character is inapplicable in taxa scored as 0 for #29.

#31 (=GG14). c1. (0) larger than i3; (1) same size. Observations: Geraads & Güleç (1997) coded this character as missing data in *A. jourdani*, but we have coded it on the basis of the newly described material.

#32 (=GG18). Ratio P4 length / p4 length. (0) ratio lower than 1.85; (1) ratio between 1.95 and 2.1; (2) ratio higher than 2.25.

#33 (=GG19). Ratio p4 length / m1 length. (0) ratio higher than 0.85; (1) lower than 0.72.

#34 (=GG20). m1 paraconid. (0) normal; (1) expanded.

#35 (=GG21). m1 notch. (0) strong; (1) weak; (2) absent.

Notes: New character states for *Albanosmilus* and *Sansanosmilus* were based on Villalta Comella & Crusafont Pairó (1943a, b), Ginsburg (1961), Heizmann *et al.* (1980), Martin (1980, 1984), de Beaumont & Crusafont-Pairó (1982), Geraads & Güleç (1997) and this study. New character scores for *Barbourofelis* spp. were based on Schultz *et al.* (1970), Baskin (1981), Bryant (1988) and Tseng *et al.* (2010), as well as in the *Barbourofelis* material housed at the AMNH (see Appendix 1).

Chapter 7. New *Pseudaelurus* and *Styriofelis* remains (Carnivora: Felidae) from the Middle Miocene of Abocador de Can Mata (Vallès-Penedès Basin)

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General Palaeontology, Systematics, Evolution (Vertebrate Palaeontology)

New *Pseudaelurus* and *Styriofelis* remains (Carnivora: Felidae) from the Middle Miocene of Abocador de Can Mata (Vallès-Penedès Basin)

Nouveaux restes de Pseudaelurus *et* Styriofelis *(Carnivora : Felidae) du Miocène moyen de l'Abocador de Can Mata (Bassin de Vallès-Penedès)*

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ABSTRACT

New remains of felid jaws and teeth are described from several localities of the local stratigraphic series of Abocador de Can Mata (ca. 11.9 to 11.6 Ma, Middle Miocene; Vallès-Penedès Basin, Catalonia, Spain). Three different taxa are identified: *Styriofelis turnauensis*, *Pseudaelurus romieviensis* and *Pseudaelurus quadridentatus*. The described remains of *P. romieviensis* enable extending considerably the chronological range of this species in the Iberian Peninsula, in agreement with its record in the rest of Europe. Moreover, it is shown for the first time that *P. romieviensis* may possess a p2. The presence of this tooth therefore does not constitue a valid diagnostic feature to distinguish *P. romieviensis* from *P. quadridentatus*.

RÉSUMÉ

De nouveaux restes dentaires et mandibulaires de Félidés provenant de la série stratigraphique de l'Abocador de Can Mata (de 11,9 à 11,6 Ma, Miocène moyen ; bassin de Vallès-Penedès, Catalogne, Espagne) sont décrits. Trois taxons différents sont déterminés : *Styriofelis turnauensis*, *Pseudaelurus romieviensis* et *Pseudaelurus quadridentatus*. Les restes décrits de *P. romieviensis* permettent d'élargir considérablement le cadre chronologique de la présence de cette espèce dans la péninsule Ibérique, en accord avec sa représentation dans le reste de l'Europe. De plus, il est montré pour la première fois que *P. romieviensis* peut posséder une p2. La présence de cette dent ne constitue donc pas un caractère diagnostique valide permettant de distinguer *P. romieviensis* de *P. quadridentatus*.

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1. Introduction

The genus *Pseudaelurus* Gervais, 1850 (Carnivora: Felidae: Felinae), as understood in the traditional, broad sense (*Pseudaelurus* s.l.; see review in Werdelin et al., 2010) includes several species distributed across Europe (Ginsburg, 1999; Rothwell, 2003), North America (Rothwell, 2003) and, to a lesser extent, Asia (Rothwell, 2003), but not in Africa (Werdelin and Peigné, 2010) except for very scarce material from Saudi Arabia (Thomas et al., 1982). It should be taken into account, however, that *Pseudaelurus* s.l. is a clearly paraphyletic grouping (a grade instead of a clade), from which both the Felinae and the Machairodontinae evolved (Werdelin et al., 2010). The North American species of "*Pseudaelurus*" (see review in Rothwell, 2003) might have independently evolved there from a *Proailurus*-like ancestor, and in any case they do not seem to be ancestral to the subsequent radiations of either conical-toothed or saber-toothed cats (Werdelin et al., 2010).

In Europe, four species have been traditionally recognized (Heizmann, 1973; Ginsburg, 1983, 1999; Rothwell, 2003; Werdelin et al., 2010); they are, from smaller to larger size (see Rothwell, 2003, for further details on the nomenclatural history of the species names): *P. turnauensis* (Hoernes, 1882) (type locality: Göriach, Austria, MN5), including *P. transitorius* Depéret, 1892 (type locality: La Grive-Saint-Alban, MN7 + 8) as its junior subjective synonym (Beaumont, 1961; Rothwell, 2003; Werdelin et al., 2010); *P. lorteti* Gaillard, 1899 (type locality: La Grive-Saint-Alban, France, MN7 + 8); *P. romieviensis* (Roman and Viret, 1934) (type locality: La Romieu, France, MN4); and *P. quadridentatus* (Blainville, 1843) (type locality: Sansan, France, MN6), which is the type species of the genus and includes *P. marini* Villalta Comella and Crusafont-Pairó, 1943 (type locality: els Hostalets de Pierola) as its junior subjective synonym (Ginsburg et al., 1981).

The above-mentioned taxonomic scheme for European species of *Pseudaelurus* is untenable in the light of current phylogenetic views (Salesa et al., 2012; Turner et al., 2011; Werdelin et al., 2010;), according to which *P. quadridentatus* would lie at the origin of the true saber-toothed cats (subfamily Machairodontinae), whereas *P. lorteti* and *P. turnauensis* would be at the base of the conical-toothed cats (subfamilies Pantherinae and Felinae). For this reason, based on the more sabertooth-like features of *P. quadridentatus* (Beaumont, 1978), several authors (Beaumont, 1964, 1978; Ginsburg, 2002; Salesa et al., 2012) have favored the splitting of the European species of "*Pseudaelurus*" into several genera or subgenera. *Schizailurus* Viret, 1951 has been therefore employed at least for the two smaller species, *P. lorteti* (type species) and *P. turnauensis*, usually at the subgenus rank (Beaumont, 1961, 1978; Crusafont-Pairó and Ginsburg, 1973; Crusafont et al., 1955; Petter, 1976; Viret, 1951) but sometimes elevated to the genus level (Beaumont, 1964). However, as noted by Ginsburg (2002; see also Salesa et al., 2012; Werdelin et al., 2010), *Schizailurus* is an objective junior synonym of *Miopanthera* Kretzoi, 1938 (type species *P. lorteti*). Ginsburg (2002) therefore recognized a taxonomically valid, monotypic subgenus *Miopanthera*, while classifying *P. turnauensis* into another monotypic subgenus, *Styriofelis* Kretzoi, 1929, both originally erected as distinct genera. However, given the similarities between their respective types species, our recommendation is to consider *Miopanthera* as a subjective junior synonym of *Styriofelis* (Salesa et al., 2011, 2012; Werdelin et al., 2010), including both *S. lorteti* and *S. turnauensis*. Most recently, a new species, *Styriofelis vallesiensis* Salesa et al., 2012 from the MN10 of Spain was erected (Salesa et al., 2012). According to Ginsburg (2002), *P. romieviensis* should be maintained in the genus *Pseudaelurus*, given its ancestral status with regard to *P. quadridentatus* (Heizmann, 1973; Ginsburg, 2002). Such classification is provisionally followed here, although it should be taken into account that the phylogenetic status of *P. romieviensis* is uncertain, because the available material is scarce and fragmentary (Koufos, 2008, 2011; Salesa et al., 2012; Werdelin et al., 2010;).

The European genus *Styriofelis* was first represented by *S. turnauensis* (Werdelin et al., 2010), and its first appearance datum usually attributed to the MN3 (Werdelin et al., 2010), although in the Iberian Peninsula it has been already cited from the MN2 (Alcalá et al., 1990; see also

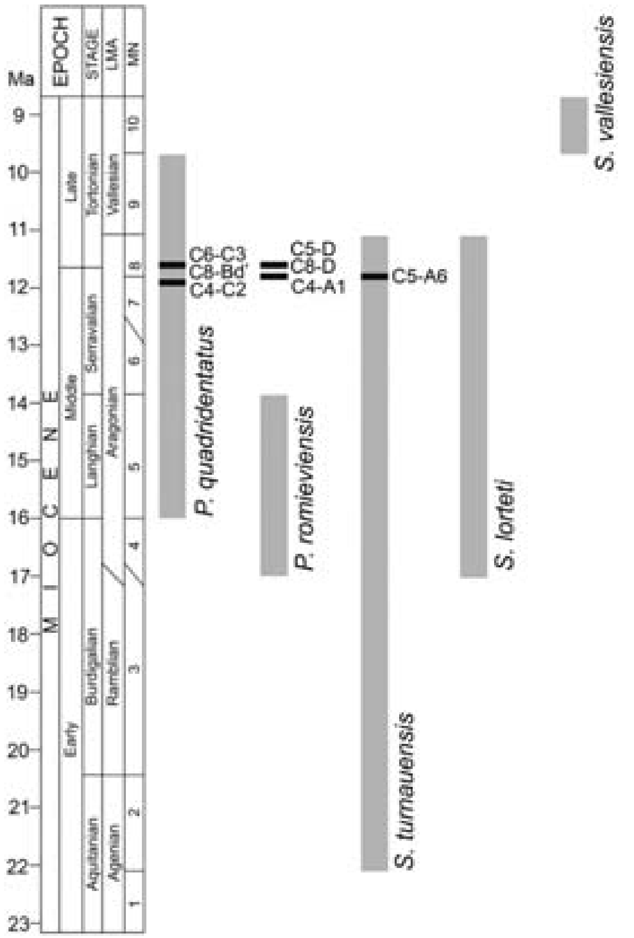

Fig. 1. Stratigraphic chart of *Pseudaelurus* spp. and *Sytriofelis* spp. in the Iberian Peninsula. Gray lines correspond to previously known ranges (see main text for references).

Fig. 1. Répartition stratigraphique de *Pseudaelurus* spp. et *Syriofelis* spp. dans la péninsule Ibérique. Les lignes grises correspondent aux répartitions connues précédemment (voir le texte principal pour les références).

our Fig. 1 and the Discussion for further details). In the MN4, both *S. lorteti* and the two species of *Pseudaelurus* are recorded. *Styriofelis lorteti* and *P. romieviensis* became extinct toward the end of the Middle Miocene (ca. 11.6 Ma), *S. turnauensis* and *P. quadridentatus* survived until the MN9 (Werdelin et al., 2010), and *S. turnauensis* was replaced by *S. vallesiensis* in the MN10 (Salesa et al., 2012). The previously known Iberian chronostratigraphic record of these taxa agrees with that in Europe, except that occurrences of *P. romieviensis* are very scarce and restricted to the MN4 and MN5 (Discussion). In this paper, we describe the unpublished remains of *Pseudaelurus* and *Styriofelis* from the Late Aragonian local stratigraphic series of Abocador de Can Mata, which had been preliminarily attributed to *Pseudaelurus* sp. (Alba et al., 2006b, 2009; Casanovas-Vilar et al., 2008) or *P.* cf. *quadridentatus* and *P.* cf. *turnauensis* by Alba et al. (2007).

2. Age and geological background

The fossil remains described in this paper come from several ACM localities (Alba et al., 2006a, 2006b, 2009, 2011), situated in the Vallès-Penedès Basin (NE Iberian Peninsula; Fig. 2). This basin is a NNE-SSW-oriented half-graben bordered by the Littoral and Pre-littoral Catalan Coastal Ranges, which was generated by the rifting of the NW Mediterranean region during the Neogene (Bartrina et al., 1992; Cabrera et al., 1991, 2004; Gibert and Casanovas-Vilar, 2011; Roca and Guimerà, 1992). Besides some Early and Middle Miocene shallow marine and transitional sequences, most of the basin infill consists of distal-marginal alluvial fan sediments with a rich fossil record of Early, late Middle and Late Miocene terrestrial vertebrates (Agustí et al., 1985; Casanovas-Vilar et al., 2011c).

The ACM localities are situated in the area of els Hostalets de Pierola, which is characterized by thick Middle to Late Miocene alluvial sequences that were deposited in the distal-to-marginal, inter-fan zones of the coalescing alluvial fan systems of els Hostalets de Pierola and Olesa (Moyà-Solà et al., 2009a). The age of the more than 250 paleontological localities from the 250-m-thick ACM series can be accurately estimated on the basis of lithostratigraphic, magnetostratigraphic and biostratigraphic correlation (Alba et al., 2009, 2011; Casanovas-Vilar et al., 2011a; Moyà-Solà et al., 2009a), corresponding to the MN7 and MN8 sensu Mein and Ginsburg (2002). In particular, the ACM series spans from ca. 12.5 to 11.4 Ma (Casanovas-Vilar et al., 2011a), and estimated interpolated ages can be provided for the several localities and most isolated remains on the basis of average local sedimentation rates for each

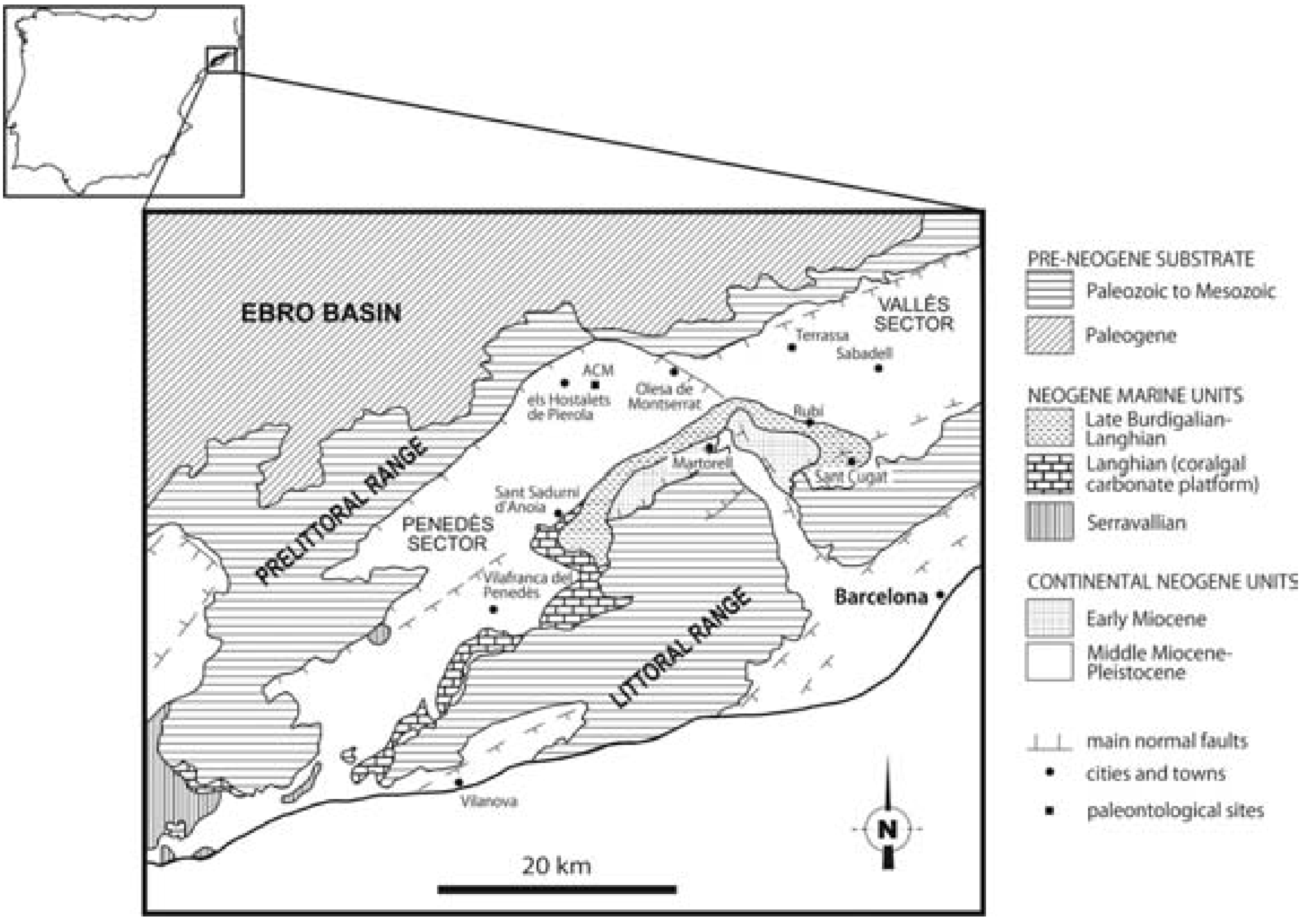

Fig. 2. Schematic geological map of the Vallès-Penedès Basin, showing the main geological units as well as the location of Abocador de Can Mata (ACM, black square). Modified from an original kindly provided by Isaac Casanovas-Vilar.

Fig. 2. Carte géologique schématique du bassin de Vallès-Penedès, montrant les principales unités géologiques, ainsi que la localisation de l'Abocador de Can Mata (ACM, carré noir). Modifié à partir d'un original aimablement fourni par Isaac Casanovas-Vilar.

subchron. The oldest ACM localities with felid remains are correlated to subchron C5r.3r; they include: C4-C2 (11.9 Ma, MN7 or MN8), C4-A1 (11.8 Ma, MN8), and C5-A6 (11.8 Ma, MN8). The remaining localities are correlated to subchron C5r.2n, including: C6-C3 and C8-Bd' (11.6 Ma, MN8). The several isolated felid remains from ACM subsectors C5-C and C8-B described in this paper are also correlated to the latter subchron, with an estimated age of 11.6 Ma (MN8).

3. Material and methods

3.1. Abbreviations

Measurements: L: mesiodistal length; B: buccolingual breadth.

Institutions and fossil collections: ICP: Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona; IPS: collections from the ICP.

Fossil sites: ACM: local stratigraphic series of Abocador de Can Mata; C4: Cell 4; C5: Cell 5; C6: Cell 6; C8: Cell 8.

3.2. Studied material and comparative sample

The fossil remains described in this paper (Figs. 3 and 4) are housed at the ICP. The comparative sample includes fossil remains from other European localities, on the basis of data taken from the literature.

3.3. Nomenclature and measurements

Dental nomenclature follows Salesa et al. (2012). Standard dental measurements (L and B) were measured (in mm) from the original specimens described in this paper, or taken from the literature for the comparative sample.

4. Systematic paleontology

Order: CARNIVORA Bowdich, 1821
Suborder: FELIFORMIA Kretzoi, 1945
Family: FELIDAE Fischer, 1817
Subfamily: FELINAE Fischer, 1817
Genus *Styriofelis* Kretzoi, 1929
Styriofelis turnauensis (Hoernes, 1882)
(Fig. 4Y–D')

Referred material: IPS41970, left mandibular fragment with m1 from ACM/C5-A6 (Fig. 4B'–D'); IPS42169, right m1 from ACM/C5-A6 (Y–A'). See dental measurements in Table 1.

Description and measurements: The mandibular corpus of IPS41970 is low and buccolingually inflated. It preserves the beginning of the masseteric fossa under the protoconid of the carnassial. The m1 of the two available specimens displays two main cuspids: the paraconid, which is mesially curved; and the protoconid, which is distally curved, slightly higher and mesiodistally wider than the paraconid, and separated from the latter by a distinct buccal notch and a deep lingual valley. There is also a small but distinct cuspulid, the metaconid, at the distalmost portion of the crown, being separated from the protoconid by a shallow groove.

Remarks: On the basis of m1 size, *S. turnauensis* can be readily distinguished from the larger *Pseudaelurus* species as well as from the smaller *Styriofelis vallesiensis* (Gaillard, 1899; Heizmann, 1973; Rothwell, 2001; see also our Fig. 5C; Villalta Comella and Crusafont-Pairó, 1943). In this regard, *S. lorteti* reaches larger sizes than *S. turnauensis*, but both species largely overlap so that no secure attribution to the latter species is warranted based on the small size of the described material from ACM alone. The ACM material, however, can be confidently attributed to *S. turnauensis* on the basis of m1 talonid, which like in *S. vallesiensis* is less developed than in *S. lorteti* (see Discussion for further details). The lack of m2 in IPS41970 further supports this attribution, since this tooth is variably present in *S. lorteti* (compare Ginsburg, 2002, fig. 18a and pl. 2 fig. 1a,b, with Heizmann, 1973, pl. 4, fig. 2a).

Genus *Pseudaelurus* Gervais, 1850
Pseudaelurus romieviensis (Roman and Viret, 1934)
(Figs. 3A–F, V–X, 4V–X, 3A–F)

Referred material: IPS29690, left C1 from ACM/C4-A1 (Fig. 4A–C); IPS29832, right C1 from ACM/C4-A1 (Fig. 4D–F); IPS41973, right partial hemimandible with c1-p4 from ACM/C5-C (Fig. 3D–F); IPS42063, left partial hemimandible with c1-m1 from ACM/C5-C (Fig. 3A–C), and presumably from the same individual as IPS41973, since they were found in close spatial association; IPS60891, right p4 from ACM/C8-B (Fig. 4V–X). See dental measurements in Table 1.

Description and measurements: Only two upper canines are available from the upper dentition. IPS29832 is only worn along the mesial edge of the crown, whereas IPS29690 also displays some apical and distal wear. The crown and root are uniformly curved in buccal/distal view, with the former being slightly higher than the root (buccal crown height of 28.5 mm vs. root height of 37.2 mm in IPS29832, and preserved buccal height of 27.4 mm vs. root height of 31.1 mm in IPS29690). The crown displays an elliptical occlusal contour that is buccolingually compressed (breadth/length index of 57-58%). The lingual side of the crown is rather flat, whereas the buccal one displays a more markedly convex occlusal contour. A distal crest with no crenulations can be discerned in both specimens from tip to base of the crown, whereas the mesial crest is worn away.

The mandibular corpus displays a constant depth along the whole dental arcade, and displays a high and straight symphysis. There are two mental foramina, at the level of the p2 and the p3. The ramus is high and displays a very deep masseteric fossa, which extends anteriorly just below m1 mid-length. The condyloid process is buccolingually broad and posteriorly curved, being shorter than the angular process, which is slightly curved mesiolingually. On the lingual side of the angular process, a thin crest runs in a mesiodistal direction from the mid-length of the masseteric fossa to the end of the angular process.

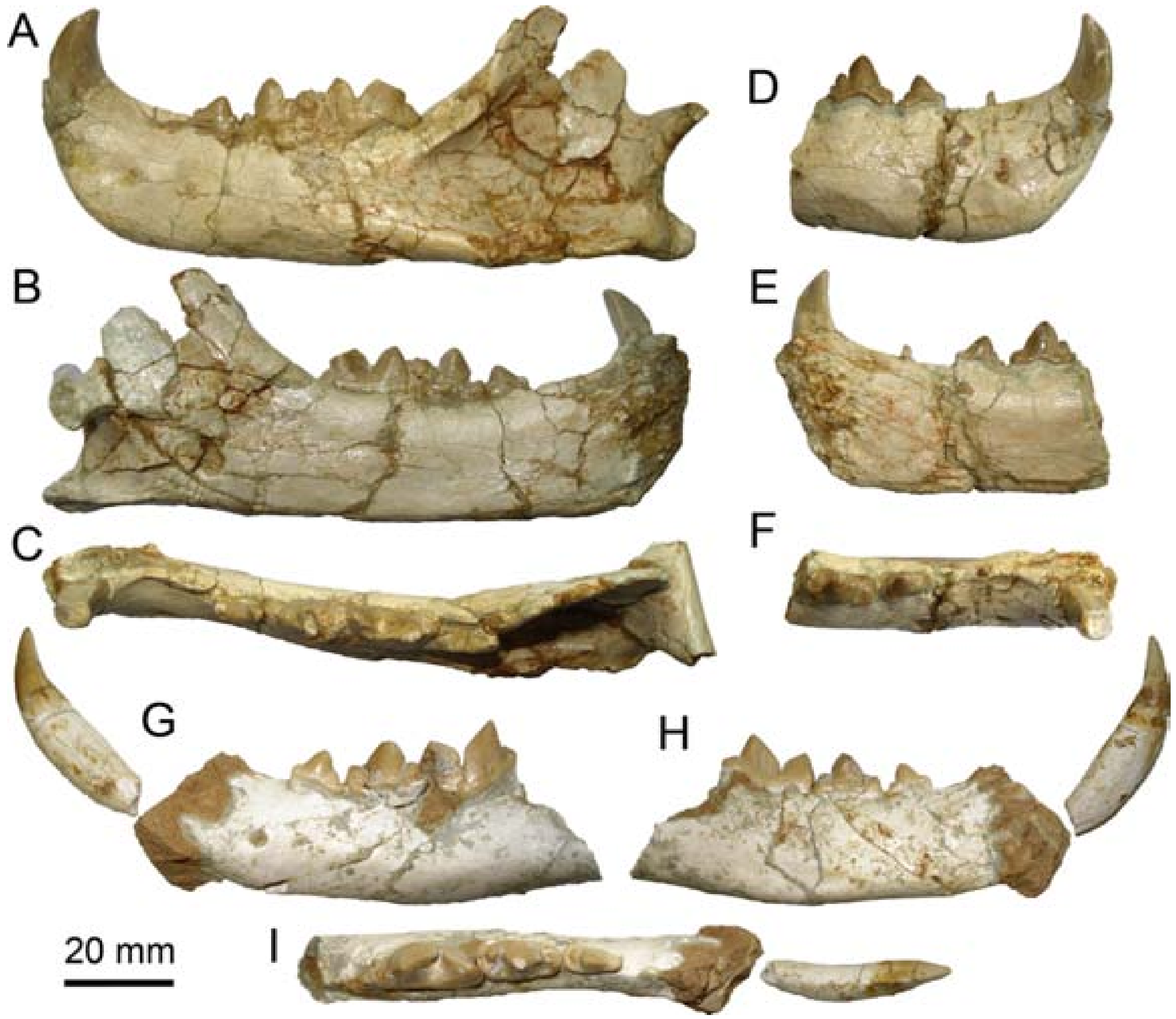

Fig. 3. Mandibular remains of *Pseudaelurus romieviensis* (**A–F**) and *Pseudaelurus quadridentatus* (**G–I**) from ACM. **A–C**: left partial hemimandible with c1-m1 IPS42063: **A**: buccal view; **B**: lingual view; **C**: occlusal view. **D–F**: right partial hemimandible with c1-p4 IPS41973: **D**: buccal view; **E**: lingual view; **F**: occlusal view. **G–I**: left partial hemimandible with c1-m1 IPS60892c: **G**: buccal view; **H**: lingual view; **I**: occlusal view.

Fig. 3. Restes mandibulaires de *Pseudaelurus romieviensis* (**A–F**) et *Pseudaelurus quadridentatus* (**G–I**) de l'ACM : **A–C** : hémimandibule gauche partielle avec c1-m1 IPS42063 : **A** : vue buccale ; **B** : vue linguale ; **C** : vue occlusale. **D–F** : hémimandibule droite partielle avec c1-p4 IPS41973 : **D** : vue buccale ; **E** : vue linguale ; **F** : vue occlusale. **G–I** : hémimandibule gauche partielle avec c1-m1 IPS60892c : **G** : vue buccale ; **H** : vue linguale ; **I** : vue occlusale.

With regard to the lower dentition, no lower incisors are preserved. The c1 crowns are quite worn (preserved buccal height 14.1 mm in IPS41973 and 15.3 mm in IPS42063). It displays a fine crest with no crenulations along its mesial portion, whereas dental wear can be observed on the distal side (so that no distal crest can be discerned). The two available specimens further display a contact facet with the i3 on the basalmost, mesial side of the crown. A uniradiculated and unicuspid p2 is present in IPS41973, whereas IPS42063 also displays the p2 alveolus but the crown is missing. The p2 crown is much smaller than those of the remaining postcanine teeth. The p2 is separated from the c1 by a long diastema (14.2 mm in IPS41973 and 12.7 mm in IPS42063), and from the p3 by a shorter one (8.3 mm and 5.4 mm, respectively). The p3 displays three cuspids, linked to each other by a fine cristid; the main cuspid (protoconid), situated at about mid-crown length, is higher than the remaining ones and displays an appreciable backward tilt; the mesial accessory cuspid is situated close to the crown base, whereas the distal accessory cuspid is situated on the middle of the talonid basin, which is lingually expanded and displays a faint distal cingulid close to the crown base. The also tricuspid p4 is larger than the p3 and displays a more asymmetric profile in buccal view (the protoconid is more distally inclined). The protoconid, situated at about mid-crown length, is the largest and most conspicuous cusp. The mesially accessory cuspid is small but nevertheless distinct, being separated from the protoconid by a conspicuous notch. The distal accessory cuspid, in turn, is separated from the protoconid by a

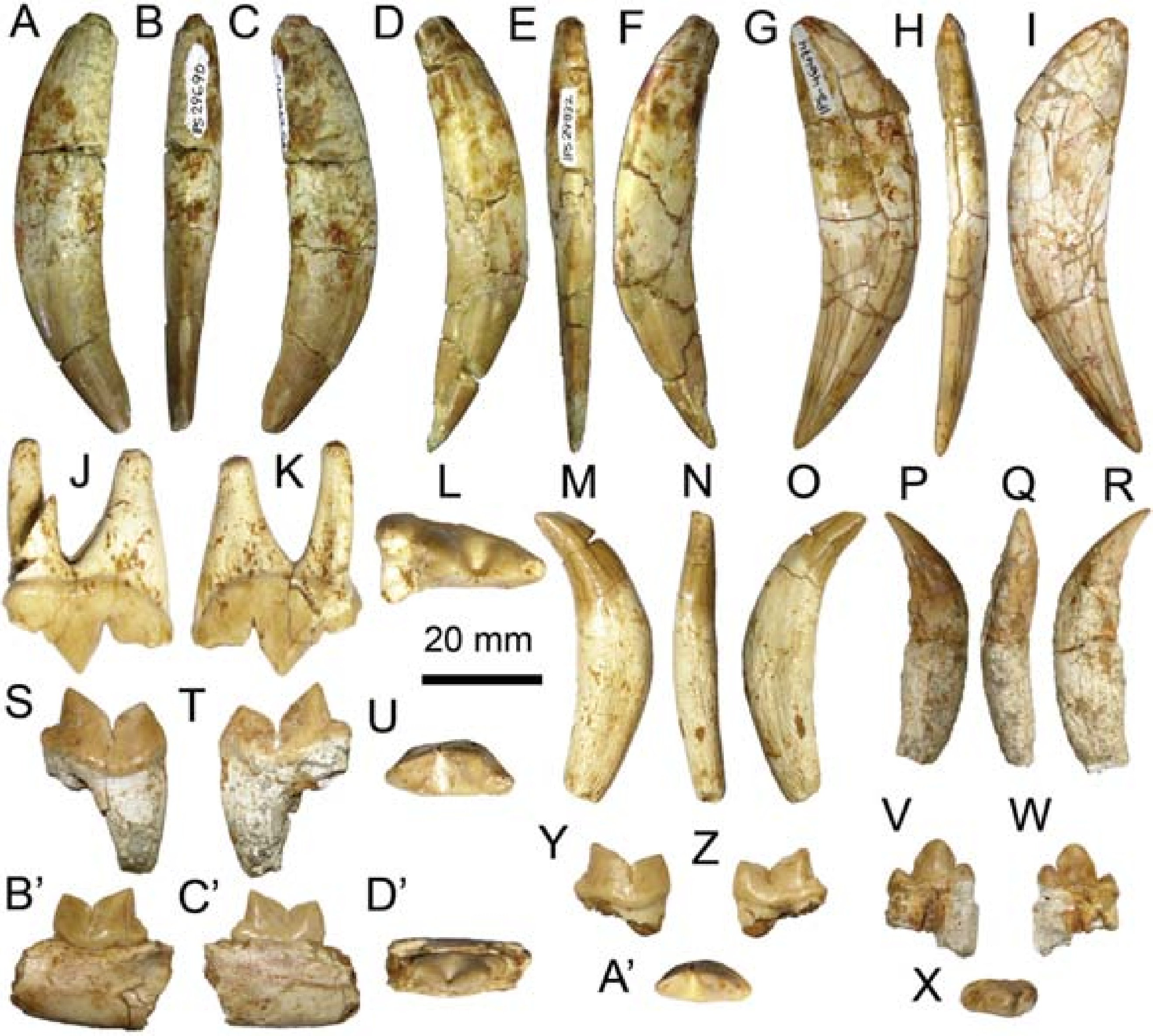

Fig. 4. Isolated dental remains of *Pseudaelurus romieviensis* (**A–F**, **V–X**), *Pseudaelurus quadridentatus* (**G–U**), and *Styriofelis turnauensis* (**Y–D'**): **A–C**: left C1 IPS29690: **A**: buccal view; **B**: distal view; **C**: lingual view. **D–F**: right C1 IPS29832: **D**: buccal view; **E**: distal view; **F**: lingual view. **G–H**: right C1 IPS46474: **G**: buccal view; **H**: distal view; **I**: lingual view. **J–L**: left P4 IPS54968: **J**: buccal view; **K**: lingual view; **L**: occlusal view. **M–O**: right c1 IPS50940: **M**: buccal view; **N**: distal view; **O**: lingual view. **P–R**: right c1 IPS60892a: **P**: buccal view; **Q**: distal view; **R**: lingual view. **S–U**: right m1 IPS60892b: **S**: buccal view; **T**: lingual view; **U**: occlusal view. **V–X**: right p4 IPS60891: **V**: buccal view; **W**: lingual view; **X**: occlusal view. **Y–A'**: right m1 IPS42169: **Y**: buccal view; **Z**: lingual view; **A'**: occlusal view. **B'–D'**: left mandibular fragment with m1 IPS41970: **B'**: buccal view; **C'**: lingual view; **D'**: occlusal view.

Fig. 4. Restes dentaires isolés de *Pseudaelurus romieviensis* (**A–F**, **V–X**), *Pseudaelurus quadridentatus* (**G–U**) et *Styriofelis turnauensis* (**Y–D'**) : **A–C** : C1 gauche IPS29690 : **A** : vue buccale ; **B** : vue distale ; **C** : vue linguale. **D–F** : C1 droite IPS29832 : **D** : vue buccale ; **E** : vue distale ; **F** : vue linguale. **G–H** : C1 droite IPS46474 : **G** : vue buccale ; **H** : vue distale ; **I** : vue linguale. **J–L** : P4 gauche IPS54968 : **J** : vue buccale ; **K** : vue linguale ; **L** : vue occlusale. **M–O** : c1 droite IPS50940 : **M** : vue buccale ; **N** : vue distale ; **O** : vue linguale. **P–R** : c1 droite IPS60892a : **P** : vue buccale ; **Q** : vue distale ; **R** : vue linguale. **S–U** : m1 droite IPS60892b : **S** : vue buccale ; **T** : vue linguale ; **U** : vue occlusale. **V–X** : p4 droite IPS60891 : **V** : vue buccale ; **W** : vue linguale ; **X** : vue occlusale. **Y-A'** : m1 droite IPS42169 : **Y** : vue buccale ; **Z** : vue linguale ; **A'** : vue occlusale. **B'–D'** : fragment mandibulaire gauche avec m1 IPS41970 : **B'** : vue buccale ; **C'** : vue linguale ; **D'** : vue occlusale.

buccal groove, and like in the p3 it is included within the talonid basin (although slightly towards the buccal side). Like in the preceding premolar, the talonid is lingually expanded and displays a better-developed distal cingulid close to crown base. The carnassial (m1) is larger than the remaining lower cheek teeth and displays an even more asymmetric profile in buccal view. This tooth bears two main trigonid cuspids (paraconid and protoconid) as well as a small but distinct metaconid at the distal end of the crown. The paraconid is obliquely-oriented towards lingual and separated from the protoconid by a broad buccal notch and a deep lingual valley. The partially-preserved protoconid (the apex is lacking) is distally situated, curved, and higher and mesiodistally longer than the paraconid, further begin separated from the talonid by a shallow buccal groove. No m2 is present.

Remarks: The isolated upper canines attributed to *P. romieviensis* fit well the measurements of two specimens

Table 1
Dental measurements of *Pseudaelurus* spp. and *Styriofelis turnauensis* from ACM localites.
Tableau 1
Mesures dentaires de *Pseudaelurus* spp. et *Styriofelis turnauensis* des localités de l'ACM.

Taxon	Site	Age (Ma)	Catalogue No.	Tooth	L	B
Styriofelis turnauensis	ACM/C5-A6	11.8 (MN8)	IPS41970	l m1	11.3	4.9
Styriofelis turnauensis	ACM/C5-A6	11.8 (MN8)	IPS42169	r m1	11.3	5.1
Pseudaelurus romieviensis	ACM/C4-A1	11.8 (MN8)	IPS29690	l C1	13.2	7.7
Pseudaelurus romieviensis	ACM/C4-A1	11.8 (MN8)	IPS29832	r C1	13.3	7.6
Pseudaelurus romieviensis	ACM/C5-C	11.6 (MN8)	IPS41973	r c1	7.4	7.7
Pseudaelurus romieviensis	ACM/C5-C	11.6 (MN8)	IPS41973	r p2	2.0	1.3
Pseudaelurus romieviensis	ACM/C5-C	11.6 (MN8)	IPS41973	r p3	9.5	4.8
Pseudaelurus romieviensis	ACM/C5-C	11.6 (MN8)	IPS41973	r p4	12.8	6.3
Pseudaelurus romieviensis	ACM/C5-C	11.6 (MN8)	IPS42063	l c1	7.8	9.1
Pseudaelurus romieviensis	ACM/C5-C	11.6 (MN8)	IPS42063	l p3	9.1	5.1
Pseudaelurus romieviensis	ACM/C5-C	11.6 (MN8)	IPS42063	l p4	12.8	6.3
Pseudaelurus romieviensis	ACM/C5-C	11.6 (MN8)	IPS42063	l m1	16.3	7.5
Pseudaelurus romieviensis	ACM/C8-B	11.6 (MN8)	IPS60891	r p4	13.8	6.3
Pseudaelurus quadridentatus	ACM/C4-C2	11.9 (MN7 or MN8)	IPS46474	r C1	15.2	6.5
Pseudaelurus quadridentatus	ACM/C6-C3	11.6 (MN8)	IPS50940	r c1	9.1	7.1
Pseudaelurus quadridentatus	ACM/C6-C3	11.6 (MN8)	IPS54968	l P4	22.4	10.5
Pseudaelurus quadridentatus	ACM/C8-Bd'	11.6 (MN8)	IPS60892a	r c1	9.0	6.5
Pseudaelurus quadridentatus	ACM/C8-Bd'	11.6 (MN8)	IPS60892b	r m1	18.0	7.8
Pseudaelurus quadridentatus	ACM/C8-Bd'	11.6 (MN8)	IPS60892c	l c1	9.1	6.6
Pseudaelurus quadridentatus	ACM/C8-Bd'	11.6 (MN8)	IPS60892c	l p3	9.7	4.8
Pseudaelurus quadridentatus	ACM/C8-Bd'	11.6 (MN8)	IPS60892c	l p4	13.9	6.7
Pseudaelurus quadridentatus	ACM/C8-Bd'	11.6 (MN8)	IPS60892c	l m1	18.0	7.9

B: buccolingual breadth; L: mesiodistal length; r: right; l: left.

of *P. romieviensis* from France (Ginsburg, 2002; see also our Fig. 5D), except for the fact that the ACM specimens are slightly more buccolingually compressed than those from France (breadth/length index 63–68%; Ginsburg, 2002). In contrast, the ACM C1 attributed to *P. romieviensis* are much smaller than those of *P. quadridentatus* from Spain (Ginsburg et al., 1981; see also our Fig. 5D), which are moreover much more buccolingually compressed (breadth/length index of 43–45%). An isolated upper canine from the MN9 of Sinap locality 12 (Turkey) was attributed to *P. quadridentatus* by Viranta and Werdelin (2003), but its proportions fit better with those of *P. romieviensis* (breadth/length index 63%).

With regard to the lower dentognathic material of *P. romieviensis* from ACM, it can be distinguished mainly from *P. quadridentatus* by the presence of a distinct and better-individualized metaconid on the m1 (Ginsburg et al., 1981; Roman and Viret, 1934; Salesa et al., 2012). The ACM material attributed to *P. romieviensis* can be further distinguished from *P. quadridentatus* by the somewhat smaller dental size (Heizmann, 1973; Roman and Viret, 1934; Rothwell, 2001), being in contrast larger than *Styriofelis* spp. (Gaillard, 1899; Heizmann, 1973; Rothwell, 2001; Salesa et al., 2012; see also Figs. 5B–D).

In the original diagnosis of this species, Roman and Viret (1934, p. 19) argued that, besides its smaller dental size, *P. romieviensis* also clearly differs from *P. quadridentatus* by the relatively slender mandibular corpus of the former. In fact, the holotype from La Romieu has a mandibular robusticity index (corpus height behind the m1/mesiodistal length of the m1 × 100) of 127.2%, which matches the figures computed for other material assigned to the same species, such as Baigneaux-en-Beauce (131.3%; data taken from Ginsburg, 2002) and IPS42063 from ACM (142.4%). In contrast, the material assigned to *P. quadridentatus* displays higher robusticity values: 163.3% for Sansan and 156.1% for La Grive-Saint-Alban (data taken from Gaillard, 1899; Ginsburg, 1961). Roman and Viret (1934, p. 19) further argued that *P. romieviensis* displays a p4 proportionally shorter than the m1, whereas the opposite condition is shown by the mandible of *P. quadridentatus* from Sansan. The holotype from La Romieu has an index of p4/m1 mesiodistal length of 76.7%, which is similar to the values displayed by the specimen of *P. romieviensis* from Baigneaux-en-Beauce (74.7%; data taken from Ginsburg, 2002) and IPS42063 from ACM (78.5%). In contrast, the material traditionally assigned to *P. quadridentatus* from Sansan, La Grive and Steinheim displays higher values (87.6%, 89.2% and 88.4%, respectively; data taken from Gaillard, 1899; Ginsburg, 1961; Heizmann, 1973).

More recently, Heizmann (1973) pointed out that the main diagnostic features of *P. romieviensis* would be the lack of p1 and p2, as well as the presence of a well-developed anterior accessory cuspid in the p4, according to specimens from La Romieu (MN4) and Baigneaux-en-Beauce (MN5). Koufos (2008), following Heizmann's (1973) criteria, further assigned a mandible from Antonios (Greece, MN4-MN5) to *P. romieviensis*. The ACM mandible IPS60892, attributed here to *P. romieviensis*, shows for the first time the presence of a p2 in this species. Moreover, this specimen displays a less developed anterior accessory cuspid in the p4, resembling the condition displayed by the mandible SO-6417 from Baigneaux-en-Beauce (Ginsburg, 2002, p. 131, fig. 19). Such differences are merely attributable to intraspecific variation, which is still insufficiently known due to the scarce record of this species.

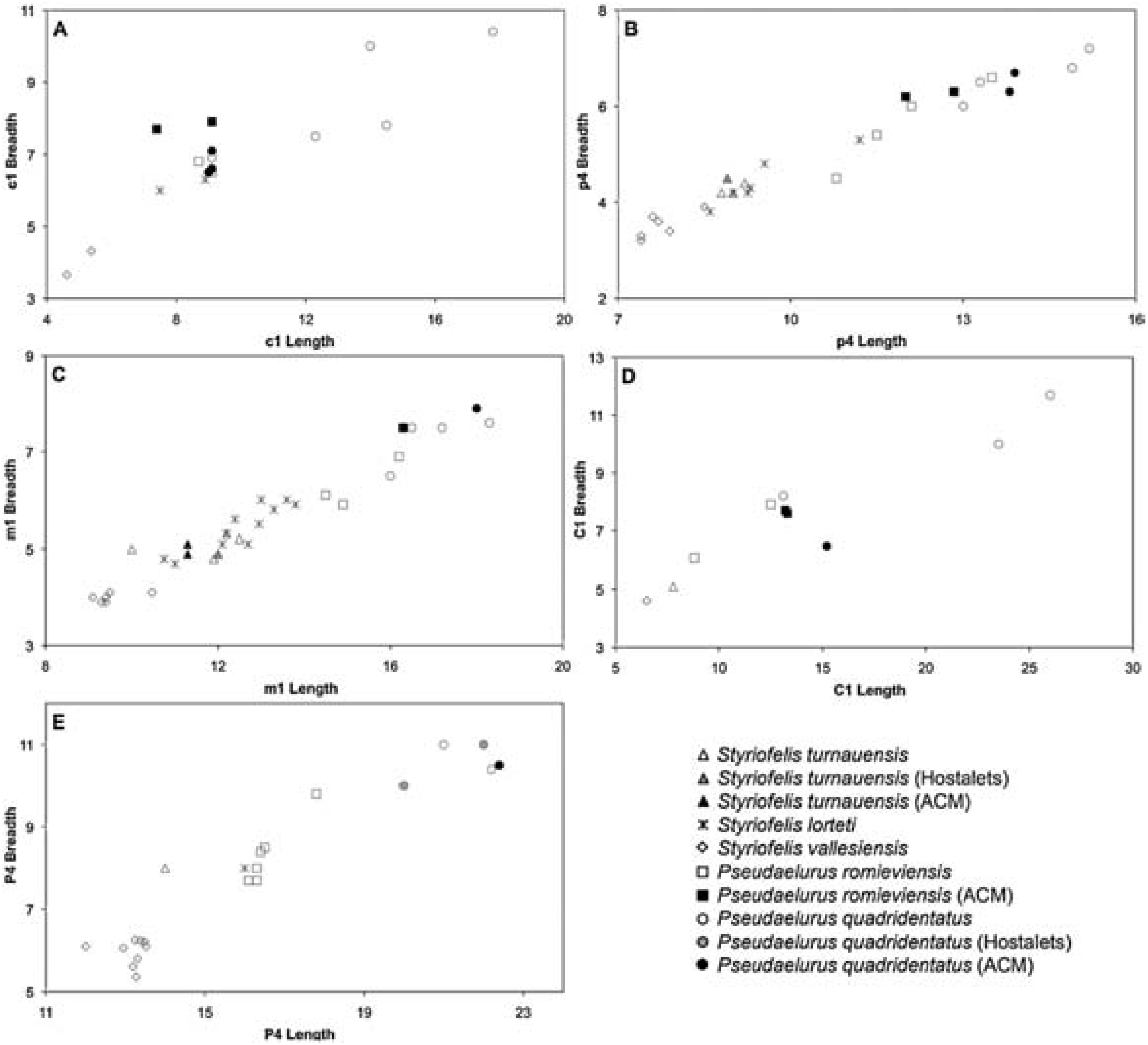

Fig. 5. Dental proportions of *Pseudaelurus* and *Styriofelis* from ACM, compared to other European localities: **A**, c1; **B**, p4; **C**, m1; **D**, C1; **E**, P4. Comparative data for *S. turnauensis* are from Vieux Collonges (Mein, 1958), Göriach (Thenius, 1949), La Grive-Saint-Alban (Gaillard, 1899; Ginsburg, 2002), Can Vila (Crusafont-Pairó, 1952; Villalta Comella and Crusafont-Pairó, 1943) and Sinap Formation (Viranta and Werdelin, 2003); for *S. lorteti*, from Artenay and Chilleurs-aux-Boix (Ginsburg, 2002), La Grive-Saint-Alban (Gaillard, 1899; Ginsburg, 1961) and Steinheim (Heizmann, 1973); for *S. vallesiensis*, from Batallones (Salesa et al., 2012); for *P. romieviensis*, from La Romieu (Roman and Viret, 1934), Vieux-Collonges (Mein, 1958, identified as *P.* aff. *quadridentatus*), Baigneaux-en-Beauce and Aérotrain (Ginsburg, 2002) and Antonios (Koufos, 2008); and for *P. quadridentatus*, from Göriach (Thenius, 1949), La Grive-Saint-Alban (Gaillard, 1899; Ginsburg, 1961), Steinheim (Heizmann, 1973), Hostalets Inferior (Villalta Comella and Crusafont-Pairó, 1943), Los Valles de Fuentidueña (Ginsburg et al., 1981), and Sinap Formation (Viranta and Werdelin, 2003).

Fig. 5. Proportions dentaires de *Pseudaelurus* et *Styriofelis* de l'ACM, comparées à d'autres localités européennes : **A**, c1 ; **B**, p4 ; **C**, m1 ; **D**, C1 ; **E**, P4. Les données de comparaison pour *S. turnauensis* proviennent de Vieux Collonges (Mein, 1958), Göriach (Thenius, 1949), La Grive-Saint-Alban (Gaillard, 1899; Ginsburg, 2002), Can Vila (Crusafont-Pairó, 1952; Villalta Comella et Crusafont-Pairó, 1943) et Sinap Formation (Viranta et Werdelin, 2003) ; pour *S. lorteti*, d'Artenay et Chilleurs-aux-Boix (Ginsburg, 2002), La Grive-Saint-Alban (Gaillard, 1899; Ginsburg, 1961) et Steinheim (Heizmann, 1973) ; pour *S. vallesiensis*, de Batallones (Salesa et al., 2012) ; pour *P. romieviensis*, de La Romieu (Roman et Viret, 1934), de Vieux-Collonges (Mein, 1958, identifié comme *P.* aff. *quadridentatus*), Baigneaux-en-Beauce et Aérotrain (Ginsburg, 2002) et Antonios (Koufos, 2008) ; et pour *P. quadridentatus*, de Göriach (Thenius, 1949), La Grive-Saint-Alban (Gaillard, 1899; Ginsburg, 1961), Steinheim (Heizmann, 1973), Hostalets Inferior (Villalta Comella et Crusafont-Pairó, 1943), Los Valles de Fuentidueña (Ginsburg et al., 1981), et Sinap Formation (Viranta et Werdelin, 2003).

Pseudaelurus quadridentatus (Blainville, 1843)
(Figs. 3G–I, P–R, 4G–O, S–U)

Referred material: IPS46474, right C1 from ACM/C4-C2 (Fig. 4G–I); IPS54968, left P4 from ACM/C6-C3 (Fig. 4J–L); IPS50940, right c1 from ACM/C6-C3 (Fig. 4M–O); IPS60892, left partial mandible with the p2 alveolus and the p3-m1 series (IPS60892c; Fig. 3G–I), associated isolated right c1 (IPS60892a; Fig. 3P–R) and isolated right m1 (IPS60892b; Fig. 4S–U) from a single individual from C8-Bd'. See dental measurements in Table 1.

Description: Regarding the upper dentition, only an isolated canine and a carnassial are available. The C1 is unworn, and although it is partially crushed at the basal level of the crown and most of the root, the overall shape of the tooth can be adequately evaluated and reliable crown measurements can be taken. In buccal/lingual view, this canine displays a somewhat concave distal contour and a more markedly convex mesial profile, the crown being slightly shorter (buccal crown height 31.9 mm) than the root (33.2 mm in length). The lingual crown aspect is quite flattened, whereas the buccal one is more convex, and the crown displays a buccolingually quite compressed occlusal profile (breadth/length index 43%). Two (mesial and distal) fine crests with no crenulations can be discerned from apex to cervix. The P4 displays three roots and a triangular occlusal profile with four main cusps. The protocone, quite worn and situated on the mesiolingual corner of the crown, is linked to the paracone (located at about the middle of the crown) by a fine crest of distobuccal direction. The paracone is the highest and better-individualized cusp. On the mesiobuccal corner of the crown, there is also a partially-worn unicuspid parastyle, which is linked to the paracone by a fine distolingual crest. The distal crown portion bears an elongated, somewhat sinuous and mesiodistally-aligned crest that corresponds to the metastyle, which ends at the distal end of the crown (where it is somewhat worn). The latter is separated from the paracone by a deep carnassial notch on the lingual side and by a similarly-deep but much broader valley on the buccal side.

The mandibular corpus is uniformly shallow along the whole dental arcade, and the symphysis is low, subvertical and with a straight profile. There are two mental foramina, at the level of the p2 and the p3. No lower incisors are preserved. The canine crowns are unworn (preserved buccal height 18.7 mm in IPS60892a and 18.3 mm IPS60892c) except for a contact facet against the i3 at the cervix, and display a fine crest without crenulations from tip to base on the lingual side. An alveolus for the p2 is present distally from the c1, being separated from the latter by a 5.4 mm-long diastema and from the p3 by a shorter diastema of 3.4 mm. The p3 displays three cuspids, the main one (protoconid) being situated at about mid-crown length and being clearly higher than the remaining ones. The mesial accessory cuspid is situated close to crown base, whereas the distal accessory cuspid is located slightly toward the buccal side of the talonid. The latter is lingually expanded and displays a weakly-developed distal cingulid close to the crown base. The p4 is longer, broader and higher than the p3, with a conspicuous protoconid that is similarly located at about mid-crown length, and two accessory cuspids. The mesial one is small but distinct, being separated from the protoconid by a groove. The similarly-sized distal accessory cuspid, in turn, is separated from the protoconid by a notch and is more clearly situated on the buccal portion of the talonid than in the p3. As in the latter, the talonid is lingually expanded and displays a weakly-developed but distinct distal cingulid close to the base of the crown. The carnassial (m1), larger than the remaining postcanine teeth, displays two main cuspids: the obliquely-oriented paraconid and the distally-curved protoconid. In buccal view, the paraconid is well developed both in length and height, so that the protoconid is only slightly more protruding than the former, from which it is separated by a narrow buccal notch and a deep lingual valley. The talonid, shorter and much lower than the trigonid, bears no well-individualized distal cuspid. There is no m2.

Remarks: The attribution of the described material from ACM to *P. quadridentatus* is justified by dental size, since the dentition of this species is larger than that of both *P. romieviensis* and *Styriofelis* spp. (Heizmann, 1973; Rothwell, 2001; see also our Fig. 5). Thus, although there is some overlap regarding m1 (Fig. 5C) and c1 (Fig. 5A), the size of both the P4 (Fig. 5E) and the p4 (Fig. 5B) enables a clear-cut distinction of *P. quadridentatus*—the c1 IPS50940 is attributed to *P. quadridentatus* because it falls very close in dental size and proportions to IPS60892a, which is associated to lower cheek teeth. Moreover, an attribution of the above-mentioned mandibular remains from ACM to *P. quadridentatus* is further confirmed by the morphology of the lower cheek teeth (more similar to *Styriofelis* spp.), including the shorter m1 talonid with a lesser-developed distal cuspid, as well as the lower-crowned and more inflated premolars, compared to *P. romieviensis* (Ginsburg, 1961, p. 141; Heizmann, 1973, p. 49, fig. 15). The morphology of the lower carnassials attributed to *P. quadridentatus* seems extremely variable on the basis of previously published material (Gaillard, 1899, pl. I, fig. 7; Ginsburg, 1961, pl. XII, fig. 4; Viret, 1951, pl. II, fig. 3). In particular, the reduction of the talonid and the absence of a distinct metaconid would be characteristic of *P. quadridentatus*, whereas the relative height and mesiodistal length between the paraconid and protoconid would be too variable to serve as a reliable taxonomic criterion. With regard to mandibular proportions, it is not possible estimate the mandibular robusticity of IPS60892, because the corpus is broken behind the m1. The p4/m1 length index for IPS60892 (77.8%) is however closer to the values usually reported for *P. romieviensis* than to those of *P. quadridentatus* (see the remarks section for *P. romieviensis* above).

Finally, in spite of being smaller than the upper canines of *P. quadridentatus* previously reported from Spain (Ginsburg et al., 1981; see also our Fig. 5D), the isolated C1 from ACM/C4-C2 is attributed to *P. quadridentatus* instead of *P. romieviensis* based on the somewhat larger size and especially the more buccolingually compressed occlusal profile of the former (breadth/length index of 43%, compared to 57–58% in the ACM specimens of *P. romieviensis*; see also the remarks regarding the latter species).

5. Discussion

5.1. Taxonomic attribution

Three different felid species are recorded at the ACM local stratigraphic series. The genus *Styriofelis* is recorded by a single species, *S. turnauensis*, which is identified from two lower carnassials mainly on the basis of dental size—smaller than in *Pseudaelurus* spp. and, with some overlap, than in *S. lorteti* (Gaillard, 1899), but larger than in *S. vallesiensis* (Salesa et al., 2012). This species attribution is further confirmed by the reduced development of the m1 talonid (including a short talonid relative to the trigonid, as well as a reduced albeit distinct distal cuspulid) compared to other felines (Crusafont-Pairó, 1952; Gaillard, 1899; Thenius, 1949; Villalta Comella and Crusafont-Pairó, 1943), including both *S. lorteti* and *Pseudaelurus* species. The reduced development of the m1 talonid is one of the various plesiomorphic dental characteristics shared by *S. turnauensis* and the younger species *S. vallesiensis* from the Vallesian and *Pristifelis attica* (Wagner, 1857) from the Turolian (Salesa et al., 2012). Other primitive features shared by these taxa, such as the robust P3 and the better-developed P4 paracone (Salesa et al., 2012) cannot be evaluated in the ACM material.

The genus *Pseudaelurus* is represented by more abundant remains at the ACM series, being attributed to either *P. romieviensis* or *P. quadridentatus*. The material attributed to the former of these species generally fits well its original diagnosis by Roman and Viret (1934; see also Heizmann, 1973), according to which *P. romieviensis* would be intermediate in size between *S. lorteti* and *P. quadridentatus*, being further characterized by short and high lower premolars, as well as by a lower carnassial with a well-developed talonid. The ACM remains, however, document for the first time the retention of a p2 in *P. romieviensis*; Heizmann (1973) included the lack of p2 in the diagnosis of this species, but the ACM material indicates that this feature is variable and hence does not serve as a taxonomic criterion to distinguish *P. romieviensis* from *P. quadridentatus*. Furthermore, the ACM material indicates that the development of the anterior accessory cuspid of the p4 is also variable in this taxon—thus contrasting with previous descriptions for this species (Heizmann, 1973; Koufos, 2008; Roman and Viret, 1934). In turn, the presence of *P. quadridentatus* among the ACM material is clearly justified by the larger dental size of this taxon as compared to *P. romieviensis*, as well as on the basis of several occlusal details—lesser-developed m1 talonid without a distinct metaconid, as well as lower-crowned and more inflated lower premolars, as compared to *P. romieviensis* (Ginsburg, 1961; Heizmann, 1973; Roman and Viret, 1934).

5.2. *The chronostratigraphic range of* Styriofelis *and* Pseudaelurus *in the Iberian Peninsula*

Some of the previous citations of *Pseudaelurus* sp. from the Iberian Peninsula could belong to either *Pseudaelurus* or *Styriofelis*; they include those from the MN5 of Somosaguas (Hernández Fernández et al., 2006; Salesa and Morales, 2000) and La Retama (Fraile et al., 1997; Morales et al., 1993), as well as those from the MN9 of Ballestar (Crusafont-Pairó and Golpe-Posse, 1974; Golpe-Posse, 1974, 1981). With these exceptions, the remaining published citations of *Pseudaelurus* s.l. from Iberia can be identified to the species level, thereby permitting us to compare the previously known chronostratigraphic ranges of the various species with the age of the new citations from ACM.

With regard to the genus *Styriofelis*, in the Iberian Peninsula it is represented by three different species. *S. lorteti* is restricted to the Aragonian, being recorded from the MN4 of Sant Mamet (Crusafont and Truyols, 1954; Crusafont et al., 1955) and Quinta do Pombeiro (Antunes, 1959, 2000), the MN5 of Moratines (Alberdi et al., 1984; Fraile et al., 1997; Morales and Soria, 1985; Peláez-Campomanes et al., 2003), Puente de Vallecas (Alberdi et al., 1984; Fraile et al., 1997; Morales and Soria, 1985; Peláez-Campomanes et al., 2003), Tarazona de Aragón (Astibia, 1987; Fortelius, 2012; identified as *P.* cf. *lorteti* by Fraile et al., 1997), Torrijos (Fortelius, 2012; identified as *P.* cf. *lorteti* by Fraile et al., 1997, and as *P. quadridentatus* by Aguirre et al., 1982 and Alberdi et al., 1984) and Chelas 1 (Antunes, 2000), the MN6 of La Barranca (Peigné et al., 2006) and Paracuellos 3 (Alberdi et al., 1984; Fraile et al., 1997; Morales and Soria, 1985; Peláez-Campomanes et al., 2003), and the MN7 + 8 of Toril 3A (Álvarez Sierra et al., 2003; Azanza et al., 2004). The lack of material of this species in the ACM, of course, might be attributable to insufficient sampling (given the amount of fossil remains recovered from the ACM, the small available sample of *Styriofelis* and *Pseudaelurus* indicates that these felids were quite rare). Nevertheless, this fact agrees well with the previous record of *S. lorteti* in the Vallès-Penedès Basin, which is restricted to the MN4 of Sant Mamet (Crusafont et al., 1955). Fraile et al. (1997) reported the presence of *S. lorteti* in both Hostalets de Pierola Inferior (MN7 + 8) and Superior (MN9), but the only previous citations (and available material) of *Styriofelis* from the area of els Hostalets correspond in fact to the MN7 of Can Vila (see below).

S. turnauensis, in contrast, is more frequently recorded than the preceding species within the Vallès-Penedès Basin. In the Iberian Peninsula as a whole, *S. turnauensis* is recorded from the MN2 of Loranca 1 and M (cited as *P. transitorius* by Alcalá et al., 1990 and Fraile et al., 1997), the MN3 of Sant Andreu de la Barca (Agustí and Galobart, 1998), Costa Blanca 1 (Fortelius, 2012), Horta da Tripas (Antunes, 1959, 2000), and Ágreda (Fraile et al., 1997, identified as *P. transitorius*), the MN3 or MN4 of Quinta do Narigaõ/Cristo Rei (Antunes, 2000), the MN4 of Can Canals and El Canyet (Fortelius, 2012), Artesilla (Fraile et al., 1997), and Quinta do Pombeiro/Quinta das Pedreiras (Antunes, 2000), the MN4? of La Vinya Vella in Esparreguera (Crusafont and Truyols, 1954; Crusafont et al., 1955; Golpe-Posse, 1974), the MN5 of Chelas 1 (Antunes, 2000), the MN7 of Can Vila (Crusafont-Pairó, 1952; Crusafont and Truyols, 1954; Villalta Comella and Crusafont-Pairó, 1943), the MN8 or MN9 of Castell de Barberà (Petter, 1976), and the MN9? of Serra d'en Camero in Sabadell (Crusafont-Pairó, 1952; Crusafont and Truyols, 1954). Previously, thus, *S. turnauensis* had been reported from several Vallès-Penedès localities, ranging from the MN3 to the MN8 and, probably, the Earliest Vallesian (MN9), and therefore the recognition of this taxon at the ACM agrees well with the chronostratigraphic range previously known for this species in this basin. Finally, an attribution to *S. turnauensis* agrees with the fact that the recently-described species, *S. vallesiensis*, is restricted to the MN10 of Batallones 1 and 3 (Salesa et al., 2012).

The Iberian records of the genus *Pseudaelurus*, in turn, mostly correspond to *P. quadridentatus*, which is recorded from the MN5 of Montejo de la Vega (Fraile et al., 1997; Mazo et al., 1998, 1999), Puente de Vallecas (Peláez-Campomanes et al., 2003) and Paracuellos 3 and 5 (Alberdi et al., 1984; Fraile et al., 1997; Morales and Soria, 1985;

Peláez-Campomanes et al., 2003), the MN6 of Manchones (Petter, 1976), Alhambra-Túneles (Peláez-Campomanes et al., 2003), Arroyo del Val (Fraile et al., 1997; Peigné et al., 2006) and La Barranca (Peigné et al., 2006), the MN8 of Can Mata 1 (Crusafont-Pairó and Villalta, 1951; Crusafont and Truyols, 1954; Villalta Comella and Crusafont-Pairó, 1943; cited as *P. marini* by Agustí et al., 1985, and also in part by Golpe-Posse, 1974), the MN7 + 8 of Hostalets Inferior indeterminate (Fraile et al., 1997; cited as *P. marini* by Crusafont and Truyols, 1954; Crusafont-Pairó and Villalta, 1951; Villalta Comella and Crusafont-Pairó, 1943), the MN8 or MN9 of Castell de Barberà (Petter, 1976), and the MN9 of Los Valles de Fuentidueña (Fraile et al., 1997; Ginsburg et al., 1981; identified as *P. turnauensis* by Crusafont-Pairó and Ginsburg, 1973, and as *Pseudaelurus* sp. by Golpe-Posse, 1974). Therefore, the presence of *P. quadridentatus* at the MN8 of the ACM fits well with the previously known range of this species in the Iberian Pensinsula (and elsewhere in Europe, e.g. Werdelin et al., 2010).

In contrast, only a few citations of *P. romieviensis* are available from the Iberian Peninsula, being recorded from the MN4 of Els Casots (Casanovas-Vilar et al., 2011b) and the MN5 of Chelas 1 (Antunes, 2000)—the remains from the MN4 of Buñol, attributed to *P. quadridentatus* (Belinchón and Morales, 1989; Fraile et al., 1997), might alternatively correspond to *P. romieviensis* on the basis of the small size of the m1—so this locality has not been incorporated in Fig. 5. The identification of *P. romieviensis* in the MN8 of ACM considerably extends the range of this taxon in Iberia (up to 11.6 Ma), approximately coinciding with the last appearance datum of this taxon elsewhere in Europe (Werdelin et al., 2010).

6. Summary and conclusions

New felid dentognathic remains from several localities of the local stratigraphic series of Abocador de Can Mata (MN7 and MN8, late Middle Miocene), in the area of els Hostalets de Pierola (Vallès-Penedès Basin, Catalonia, Spain), are described and attributed to three different species: *S. turnauensis*, *P. romieviensis*, and *P. quadridentatus* (Felidae: Felinae). The remains of *P. romieviensis* enable us to ascertain that, like *P. quadridentatus*, this species variably retained the p2, which cannot be therefore employed as a taxonomic criterion to distinguish these two species. The identification of *P. romieviensis* among the ACM material considerably extends the range of this species in the Iberian Peninsula, in agreement with the reported range for this species in the rest of Europe.

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References

Aguirre, E., Alberdi, M.T., Jiménez, E., Martín Escorza, C., Morales, J., Sesé, C., Soria, D., 1982. Torrijos: nueva fauna con *Hispanotherium* de la cuenca media del Tajo. Acta Geol. Hisp. 17, 39–61.

Agustí, J., Galobart, À., 1998. Noves localitats amb mamífers fòssils en el miocè de la Conca del Vallès-Penedès. Trib. Arqueol. 1996–1997, 9–23.

Agustí, J., Cabrera, L., Moyà-Solà, S., 1985. Sinopsis estratigráfica del Neógeno de la fosa del Vallés-Penedés. Paleontol. Evol. 18, 57–81.

Alba, D.M., Galindo, J., Casanovas-Vilar, I., Moyà-Solà, S., 2006a. La intervenció paleontològica a la Nova Fase del Dipòsit Controlat de Residus de Can Mata (Els Hostalets de Pierola, Anoia): Campanya novembre 2002–agost 2003. Trib. Arqueol. 2003–2004, 7–22.

Alba, D.M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Rotgers, C., Furió, M., Angelone, C., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Obradó, P., 2006b. Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l'Anoia, Cataluña), una sucesión de localidades del Aragoniense superior (MN6 y MN7 + 8) de la cuenca del Vallès-Penedès. Campañas 2002-2003, 2004 y 2005. Estudios Geol. 62, 295–312.

Alba, D.M., Galindo, J., Casanovas-Vilar, I., Robles, J.M., Moyà-Solà, S., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Rotgers, C., Furió, M., Angelone, C., 2007. La intervenció paleontològica a la nova fase del dipòsit controlat de Can Mata (Els Hostalets de Pierola, Anoia): campanyes 2002–2003, 2004 i 2005. Trib. Arqueol. 2006, 7–33.

Alba, D.M., Robles, J.M., Rotgers, C., Casanovas-Vilar, I., Galindo, J., Moyà-Solà, S., Garcés, M., Cabrera, L., Furió, M., Carmona, R., Bertó Mengual, J.V., 2009. Middle Miocene vertebrate localities from Abocador de Can Mata (els Hostalets de Pierola, Vallès-Penedès Basin, Catalonia, Spain): an update after the 2006–2008 field campaigns. Paleolusitana 1, 59–73.

Alba, D.M., Casanovas-Vilar, I., Robles, J.M., Moyà-Solà, S., 2011. Parada 3. El Aragoniense superior y la transición con el Vallesiense: Can Mata y la exposición paleontológica de els Hostalets de Pierola. Paleontol. Evol. Mem. Esp. 6, 95–109.

Alberdi, M.-T., Hoyos, M., Junco, F., López Martínez, N., Morales, J., Sesé, C., Soria, M.D., 1984. Biostratigraphy and sedimentary evolution of continental Neogene in the Madrid area. Paléobiol. Continent. 14, 47–68.

Alcalá, L., Cerdeno, E., Montoya, P., Morales, J., Pérez, B., Soria, D., 1990. Composición taxonómica y anatómica de los restos de macrovertebrados del Mioceno inferior continental de Loranca del Campo (Cuenca). Com. Reunión Tafonomía Fosilización. Madrid 1990, 7–12.

Álvarez Sierra, M.A., Calvo, J.P., Morales, J., Alonso-Zarza, A., Azanza, B., García Paredes, I., Hernández Fernández, M., van der Meulen, A.J., Peláez-Campomanes, P., Quiralte, V., Salesa, M.J., Sánchez, I.M., Soria, D., 2003. El tránsito Aragoniense-Vallesiense en el área de Daroca-Nombrevilla (Zaragoza, España). Col. Paleontol. Vol. Ext. 1, 25–33.

Antunes, M.T., 1959. Notes sur la Géologie et la Paléontologie du Miocène de Lisbonne. II. Carnassiers fissipèdes. Bol. Soc. Geol. Portugal 13, 269–292.

Antunes, M.T., 2000. Miocene mammals from Lisbon and geologic age. A showcase for marine-continental correlations. Ciênc. Terra (UNL) 14, 343–348.

Astibia, H., 1987. Los macromamíferos del Mioceno Medio de Tarazona de Aragón (Depresión del Ebro, provincia de Zaragoza). Paleontol. Evol. 21, 11–42.

Azanza, B., Alonso-Zarza, A.M., Álvarez-Sierra, M.A., Calvo, J.P., Fraile, S., García-Paredes, I., Gómez, E., Hernández-Fernández, M., Van der Meulen, A., De Miguel, D., Montoya, P., Morales, J., Murelaga, X., Peláez-Campomanes, P., Perez, B., Quiralte, V., Salesa, M.J., Sánchez, I.M., Sánchez-Marco, A., Soria, D., 2004. Los yacimientos de vertebrados continentales del Aragoniense superior (Mioceno medio) de Toril, Cuenca de Calatayud-Daroca. Geo-Temas 6, 271–274.

Bartrina, M.T., Cabrera, L., Jurado, M.J., Guimerà, J., Roca, E., 1992. Evolution of the central Catalan margin of the Valencia trough (western Mediterranean). Tectonophysics 203, 219–247.

de Beaumont, G., 1961. Recherches sur *Felis attica* Wagner du Pontien eurasiatique avec quelques observations sur les genres *Pseudaelurus* Gervais et *Proailurus* Filhol. Nouv. Arch. Mus. Hist. Nat. Lyon 6, 17–45.

de Beaumont, G., 1964. Remarques sur la classification des Felidae. Eclog. Geol. Helv. 57, 837–845.

de Beaumont, G., 1978. Notes complementaires sur quelques Félidés (Carnivores). Arch. Sci. Phys. Nat. Genève 31, 219–227.

Belinchón, M., Morales, J., 1989. Los carnívoros del Mioceno Inferior de Buñol (Valencia, España). Rev. Esp. Paleontol. 4, 3–8.

Blainville, H.M., 1843. Ostéographie, ou description iconographique comparée du squelette et du système dentaire des cinq classes d'animaux vertébrés récents et fossiles pour servir de base à la zoologie et à la géologie. Carnassiers des Felis. J.B. Baillière et Fils, Paris.

Bowdich, T.E., 1821. An Analysis of the Natural Classifications of Mammalia, for the Use of Students and Travelers. J. Smith, Paris.

Cabrera, L., Calvet, F., Guimerà, J., Permanyer, A., 1991. El registro sedimentario miocénico en los semigrabens del Vallès-Penedès y de El Camp: organización secuencial y relaciones tectónica-sedimentación. In: I Congreso Grupo Español del Terciario, Libro-Guía Excursión 4, Vic.132 p.

Cabrera, L., Roca, E., Garcés, M., de Porta, J., 2004. Estratigrafía y evolución tectonosedimentaria oligocena superior-neógena del sector central del margen catalán (Cadena Costero-Catalana). In: Vera, J.A. (Ed.), Geología de España, SGE-IGME, Madrid, pp. 569–573.

Casanovas-Vilar, I., Alba, D.M., Moyà-Solà, S., Galindo, J., Cabrera, L., Garcés, M., Furió, M., Robles, J.M., Köhler, M., Angelone, C., 2008. Biochronological, taphonomical and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae). J. Hum. Evol. 55, 589–603.

Casanovas-Vilar, I., Alba, D.M., Garcés, M., Robles, J.M., Moyà-Solà, S., 2011a. Updated chronology for the Miocene hominoid radiation in western Eurasia. Proc. Natl Acad. Sci. U S A 108, 5554–5559.

Casanovas-Vilar, I., Alba, D.M., Moyà-Solà, S., 2011b. Parada 1. Panorámica general de la cuenca y yacimiento de Els Casots (Subirats): una fauna de vertebrados del Aragoniense inferior. Paleontol. Evol. Mem. Esp. 6, 81–88.

Casanovas-Vilar, I., Alba, D.M., Robles, J.M., Moyà-Solà, S., 2011c. Registro paleontológico continental del Mioceno de la cuenca del Vallès-Penedès. Paleontol. Evol. Mem. Esp. 6, 55–80.

Crusafont-Pairó, M., 1952. La presencia del Félido *Pseudaelurus tournauensis* (Hoernes) en el Mioceno de Hostalets de Pierola y Sabadell (Vallés-Penedés). Not. Com. Inst. Geol. Min. Esp 28, 1–15.

Crusafont-Pairó, M., Ginsburg, L., 1973. Les Carnassiers fossiles de Los Vallès de Fuentiduena (Ségovie, Espagne). Bull. Mus. Natl Hist. Nat. 131, 29–45.

Crusafont-Pairó, M., Golpe-Posse, J.M., 1974. El nuevo yacimiento vallesiense de Ballestar (Lérida) (Nota preliminar). Bol. R. Soc. Esp. Hist. Nat. 72, 67–73.

Crusafont, M., Truyols, J., 1954. Catálogo paleomastológico del Mioceno del Vallés-Penedés y de Calatayud-Teruel. Segundo Cursillo Internacional de Paleontología, Museo de la Ciudad de Sabadell, Sabadell, 25 p.

Crusafont-Pairó, M., de Villalta, J.F., 1951. Los nuevos mamíferos del neogeno de España. Not. Com. Inst. Geol. Min. Esp. 22, 1–5.

Crusafont, M., de Villalta, J.F., Truyols, J., 1955. El Burdigaliense continental de la cuenca del Vallés-Penedés. Mem. Com. Inst. Geol. 12, 1–247.

de Gibert, J.M., Casanovas-Vilar, I., 2011. Contexto geológico del Mioceno de la cuenca del Vallès-Penedès. Paleontol. Evol. Mem. Esp. 6, 39–45.

Depéret, C., 1892. La faune de Mammifères miocènes de la Grive-Saint-Alban (Isère) et de quelques autres localités du bassin du Rhône. Arch. Mus. Hist. Nat. Lyon 5, 1–93.

Fischer von Waldheim, G., 1817. Adversaria zoologica. Mém. Soc. Imp. Nat. Moscou 5, 368–428.

Fortelius, M. (coordinator), 2012. New and Old Worlds Database of Fossil Mammals (NOW). University of Helsinki. http://www.helsinki.fi/science/now/ [accessed October 12, 2012].

Fraile, S., Pérez, B., De Miguel, I., Morales, J., 1997. Revisión de los carnívoros presentes en los yacimientos del Neógeno español. In: Calvo, J.P., Morales, J. (Eds.), Avances en el conocimiento del Terciario ibérico, pp. 77–80.

Gaillard, C., 1899. Mammifères miocènes de La Grive-Saint-Alban (Isère). Arch. Mus. Hist. Nat. Lyon 7, 1–41.

Gervais, P., 1848–1852. Zoologie et paléontologie françaises (animaux vertébrés) ou Nouvelles recherches sur les animaux vivants et fossiles de la France. Arthus Bertrand, Paris.

Ginsburg, L., 1961. La faune des carnivores miocènes de Sansan (Gers). Mem. Mus. Natl. Hist. Nat. Paris 9, 1–187.

Ginsburg, L., 1983. Sur les modalités d'évolution du genre néogène *Pseudaelurus* Gervais (Felidae, Carnivora, Mammalia). Coll. Int. CRNS 330, 131–136.

Ginsburg, L., 1999. Order Carnivora. In: Rössner, G.E., Heissig, K. (Eds.), The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, München, pp. 109–148.

Ginsburg, L., 2002. Les carnivores fossiles des sables de l'Orléanais. Ann. Paleontol. 88, 115–146.

Ginsburg, L., Morales, J., Soria, D., 1981. Nuevos datos sobre los carnívoros de Los Valles de Fuentidueña (Segovia). Estudios Geol. 37, 383–415.

Golpe-Posse, J.M., 1974. Faunas de yacimientos con suiformes en el Terciario español. Paleontol. Evol. 8, 1–87.

Golpe-Posse, J.M., 1981. Los mamíferos de las Cuencas de Cerdanya y Seu d'Urgell (depresiones pirenaicas) y sus yacimientos; Vallesiense Medio-Superior. Bol. Geol. Min. 92, 91–100.

Heizmann, E.P.J., 1973. Die Carnivoren des Steinheimer Beckens, B., Ursidae, Felidae, Viverridae sowie Ergänzungen und Nachträge zu den Mustelidae. Palaeontogr. Suppl. 8, 1–95.

Hernández Fernández, M., Cárdaba, J.A., Cuevas-González, J., Fesharaki, O., Salesa, M.J., Corrales, B., Domingo, L., Elez, J., López Guerrero, P., Sala-Burgos, N., Morales, J., López Martínez, N., 2006. Los yacimientos de vertebrados del Mioceno medio de Somosaguas (Pozuelo de Alarcón, Madrid): implicaciones paleoambientales y paleoclimáticas. Estudios Geol. 62, 263–294.

Hoernes, V.R., 1882. Säugetier-Reste aus der Braunkohle von Göriach bei Turnau in Steiermark. Jahrb. D. K. K. Geol. Reichsanstalt 32, 153–164.

Kretzoi, M., 1929. Feliden-Studien. A magyar Királyi Földtani Intézet Hazinyomdaja 24, 1–22.

Kretzoi, M., 1938. Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauna. Ann. Mus. Nat. Hung. 31, 88–157.

Kretzoi, N., 1945. Bemerkungen über das Raubtiersystem. Ann. Mus. Nat. Hung. 38, 59–83.

Koufos, G.D., 2008. Carnivores from the Early/Middle Miocene locality of Antonios (Chalkidiki, Macedonia, Greece). Geobios 41, 365–380.

Koufos, G.D., 2011. The Miocene assemblage carnivores from Greece. Estudios Geol. 67, 291–320.

Mazo, A.V., van der Made, J., Jordá, J.F., Herráez, E., Armenteros, I., 1998. Fauna y bioestratigrafía del yacimiento aragoniense de Montejo de la Vega de la Serrezuela (Segovia). Estudios Geol. 54, 231–248.

Mazo, A.V., Jordá, J.F., van der Made, J., Herráez, E., Armenteros, I., 1999. Montejo de la Vega de la Serrazuela (Segovia). Aportaciones a la bioestratigrafía del Aragoniense del sector SW de la Cuenca del Duero. Temas Geol. Min. ITGE 26, 274–275.

Mein, P., 1958. Les mammifères de la faune sidérolithique de Vieux-Collonges. Nouv. Arch. Mus. Nat. Lyon 5, 1–122.

Mein, P., Ginsburg, L., 2002. Sur l'âge relatif des différents dépôts karstiques miocènes de La Grive-Saint-Alban (Isère). Cah. Sci. 2/2002, 7–47.

Morales, J., Soria, D., 1985. Carnívoros y artiodáctilos de la provincia de Madrid. In: Alberdi, M.T. (Ed.), Geología y Paleontología del Terciario Continental de la Provincia de Madrid. CSIC, Madrid, pp. 81–97.

Morales, J., Alcalá, L., Hoyos, M., Montoya, P., Nieto, M., Pérez, B., Soria, D., 1993. El yacimiento del Aragoniense medio de La Retama (Depresión Intermedia, Provincia de Cuenca, España). Scripta Geol. 103, 23–39.

Moyà-Solà, S., Köhler, M., Alba, D.M., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Cabrera, L., Garcés, M., Almécija, S., Beamud, E., 2009a. First partial face and upper dentition of the Middle Miocene hominoid *Dryopithecus fontani* from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, NE Spain): taxonomic and phylogenetic implications. Am. J. Phys. Anthropol. 139, 126–145.

Peigné, S., Salesa, M.J., Antón, M., Morales, J., 2006. New data on carnivores from the Middle Miocene (Upper Aragonian, MN6) of Arroyo del Val area (Villafeliche, Zaragoza Province, Spain). Estudios Geol. 62, 359–371.

Peláez-Campomanes, P., Morales, J., Álvarez Sierra, M.A., Azanza, B., Fraile, S., García Paredes, I., Hernández Fernández, M., Herráez, E., Nieto, M., Pérez, B., Quiralte, V., Salesa, M.J., Sánchez, I.M., Soria, D., 2003. Updated biochronology of the Miocene mammal faunas from the Madrid basin (Spain). DEINSEA 10, 431–441.

Petter, G., 1976. Étude d'un nouvel ensemble de petits carnivores du Miocène d'Espagne. Géol. Méditerr. 3, 135–154.

Roca, E., Guimerà, J., 1992. The Neogene structure of the eastern Iberian margin: structural constraints on the crustal evolution of the Valencia Trough (Western Mediterranean). Tectonophysics 203, 203–218.

Roman, F., Viret, J., 1934. La faune de mammifères du Burdigalien de La Romieu (Gers). Mem. Soc. Geol. France 21, 1–67.

Rothwell, T., 2001. A partial skeleton of *Pseudaelurus* (Carnivora, Felidae) from the Nambé Member of the Tesuque Formation, Española Basin, New Mexico. Am. Mus. Nov. 3342, 1–31.

Rothwell, T., 2003. Phylogenetic systematics of North American *Pseudaelurus* (Carnivora, Felidae). Am. Mus. Nov. 3403, 1–64.

Salesa, M.J., Morales, J., 2000. La fauna de Carnívoros del yacimiento aragoniense de Somosaguas (Pozuelo de Alarcón, Madrid). Col. Paleontol. 51, 213–222.

Salesa, M.J., Antón, M., Morales, J., Peigné, S., 2011. Functional anatomy of the postcranial skeleton of *Styriofelis lorteti* (Carnivora, Felidae, Felinae) from the Middle Miocene (MN6) locality of Sansan (Gers, France). Estudios Geol. 67, 223–243.

Salesa, M.J., Antón, M., Morales, J., Peigné, S., 2012. Systematics and phylogeny of the small felines (Carnivora, Felidae) from the Late Miocene of Europe: a new species of Felinae from the Vallesian of Batallones (MN10, Madrid, Spain). J. Syst. Palaeontol. 10, 87–102.

Thenius, E., 1949. Die Carnivoren von Göriach (Steiermark). Beiträge sur Kenntnis der Säugetierreste des steirischen Tertiärs IV. Sitzungsber. Öster. Akad 158, 695–762.

Thomas, H., Sen, S., Khan, M., Battail, B., Ligabue, G., 1982. The Lower Miocene fauna of Al-Sarrar (eastern province, Saudi Arabia). J. Saudi Arabian Archaeol. 5, 109–136.

Turner, A., Antón, M., Salesa, M.J., Morales, J., 2011. Changing ideas about the evolution and functional morphology of Machairodontine felids. Estudios Geol. 67, 255–276.

de Villalta Comella, J.F., Crusafont-Pairó, M., 1943. Los vertebrados del Mioceno continental de la cuenca del Vallés-Panadés (provincia de Barcelona). I. Insectívoros. II. Carnívoros. Bol. Inst. Geol. Min. Esp. 56, 145–331.

Viranta, S., Werdelin, L., 2003. Carnivores. In: Fortelius, M., Kappelman, J., Sen, S., Bernor, R.L. (Eds.), Geology and Paleontology of the Miocene Sinap Formation, Turkey. Columbia University Press, New York, pp. 178–193.

Viret, J., 1951. Catalogue critique de la faune des mammifères miocènes de La Grive Saint-Alban (Isère). Nouv. Arch. Mus. Hist. Nat. Lyon 3, 1–103.

Wagner, A., 1857. Neue Beiträge zur Kenntniss der fossilen Säugthier-Ueberreste von Pikermi. Bayer. Akad. Wiss. Math.-Natur. Kl. Abh. 8, 111–158.

Werdelin, L., Peigné, S., 2010. Carnivora. In: Werdelin, L., Sanders, W.J. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 603–657.

Werdelin, L., Yamaguchi, N., Johnson, W.E., O'Brien, S.J., 2010. Phylogeny and evolution of cats (Felidae). In: Macdonald, D., Loveridge, A. (Eds.), The Biology and Conservation of Wild Felids. Oxford University Press, Oxford, pp. 59–82.

Chapter 8. The scimitar-toothed *Machairodus aphanistus* (Carnivora: Felidae) in the Vallès-Penedès Basin (NE Iberian Peninsula)

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The scimitar-toothed cat *Machairodus aphanistus* (Carnivora: Felidae) in the Vallès-Penedès Basin (NE Iberian Peninsula)

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Abstract

Here, we revise all the published and unpublished scimitar-toothed cat remains from the Vallès-Penedès Basin (NE Iberian Peninsula), in order to confirm their taxonomic attribution to *Machairodus aphanistus* as well as to provide more precise information about its chronological distribution in this basin. The studied material (including dentognathic as well as postcranial remains) comes from the following localities: Can Mata indeterminate (late MN7+8 or MN9), Creu Conill 22 (MN9), Can Poncic 1 (MN9), Can Llobateres 1 (MN9), Santiga (MN9), La Tarumba 1 (MN10), Viladecavalls (MN10), Ronda Oest Sabadell ROS-D3 (MN10), and Torrent de Febulines (MN10). Most of the studied material fits well with the morphologic and metrical features characteristic of the Vallesian species *M. aphanistus*, with the exception of the remains from Creu Conill 22 (an undescribed partial P4 formerly attributed to this taxon), which belongs in fact to a medium-sized hyaenid. From a biostratigraphic viewpoint, the removal of the Creu Conill material from the hypodigm of *M. aphanistus* has important implications, because this locality (11.1 Ma) was considered to record the first appearance datum of this taxon in the Vallès-Penedès Basin. However, the report of a previously unpublished talus from Can Mata (late MN7+8 or MN9) indicates that this taxon was present in this basin at least by the earliest Vallesian. Therefore, our results indicate that the first appearance datum of *Machairodus* in the Vallès-Penedès Basin might be somewhat younger than previously assumed, although dating uncertainties for the Can Mata remains preclude a more precise assessment. In contrast, the new mandibular remains from ROS-D3 (MN10) are likely coeval with those from La Tarumba 1, with the last appearance datum of *M. aphanistus* in the Vallès-Penedès Basin corresponding to Torrent de Febulines (ca. 9.1 Ma). The postcranial material described from various Vallès-Penedès localities further indicates that *M. aphanistus* displayed less cursorial adaptations than its purported descendant *Homotherium*.

Keywords: Fossil cats; Machairodontinae; Late Miocene; Vallesian; Catalonia.

Résumé

Nous révisons ici tous les restes, publiées et non publiées, de chats à dents de cimeterre du bassin de Vallès-Penedès (NE de la péninsula Ibérique), afin de confirmer leur attribution taxonomique à *Machairodus aphanistus*, ainsi que préciser en plus sa répartition chronologique dans ce bassin. Le matériel étudié (qui compris restes dentognathiques ainsi que postcrâniens) provient des localités suivantes: Can Mata indéterminé (tard MN7+8 ou MN9), Creu Conill 22 (MN9), Can Poncic 1 (MN9) , Can Llobateres 1 (MN9), Santiga (MN9), La Tarumba 1 (MN10) , Viladecavalls (MN10), Ronda Oest Sabadell ROS-D3 (MN10), et Torrent de Febulines (MN10). La plupart du matériel étudié correspond bien avec les caractéristiques morphologiques et métriques typiques de l'espèce vallésienne *Machairodus aphanistus*, à l'exception de les réstes de Creu Conill 22 (une P4 partielle non décrite auparavant attribué à ce taxon), qui appartient en fait à une Hyenidé de taille moyenne. Du point de vue biostratigraphique, l'élimination du matériel de Creu Conill de l'hypodigme de *M. aphanistus* a des importantes implications biochronologiques, parce que cette localité (11.1 Ma) a été considérée d'enregistrer la première donnée d'apparition de ce taxon dans le bassin de Vallès-Penedès. Toutefois, le rapport d'un astragale inédit de Can Mata (tard MN7+8 ou MN9) indique que ce taxon était présent dans ce bassin au moins près du début du Vallésien. Nos résultats donc indiquent que la première donnée de l'apparition de *Machairodus* dans le bassin de Vallès-Penedès pourrait être un peu plus jeune que présumé précédemment, bien que des incertitudes sur la datation pour les restes de Can Mata empêchent une évaluation plus précise. En revanche, la nouvelle reste mandibulaire de ROS-D3 (MN10) sont à peu près contemporains de ceux de La Tarumba 1, de sorte que la dernière donnée d'apparition de *M. aphanistus* dans le bassin de Vallès-Penedès correspondant à Torrent de Febulines (ca. 9.1 Ma). Le matériel postcrânien décrit

de diverses localités du Vallès-Penedès indique en outre que *M. aphanistus* affiché adaptations moins cursoriales que son descendant présumé *Homotherium*.

Mots clés: Félidés fossiles; Machairodontinae; Miocène Supérieur; Vallésien; Catalogne.

1. Introduction

1.1. The genus Machairodus

Machairodus Kaup, 1833 (Carnivora: Felidae: Machairodontinae) is an extinct genus of scimitar-toothed cats included in the tribe Machairodontini Gill, 1872 which also includes the genera *Amphimachairodus* Kretzoi, 1929 (formerly considered merely a subgenus of *Machairodus*), *Lokotunjailurus* Werdelin, 2003, *Xenosmilus* Martin et al., 1999 and *Homotherium* Fabrini, 1890. The earliest record of *Machairodus* apparently corresponds to *Machairodus robinsoni* Kurtén, 1976, from the Middle to Late Miocene of Bled Douarah in Tunisia (ca. 12.5–10 Ma; Kurtén, 1976; Geraads, 1989; Werdelin and Peigné, 2010), which is the only species of the genus currently recognized in Africa. The previously published (Geraads et al., 2002) African record of *Machairodus aphanistus* (Kaup, 1832), which is the type species of the genus, is currently uncertain (Werdelin and Peigné, 2010). In turn, *Amphimachairodus kabir* (Peigné et al. 2005), originally described as a species of *Machairodus*, was recently reassigned to *Amphimachairodus* by Werdelin and Peigné (2010). For further discussion of the genus allocation of some African machairodontine species, see also Werdelin (2003), Peigné et al. (2005), Werdelin and Sardella (2006) and Sardella and Werdelin (2007).

Outside Africa, *Machairodus* is also recorded from North America and Eurasia. In North America, two different species may be recognized, ranging from the Late Miocene to the Early Pliocene (Martin, 1998; Antón et al., 2013): *Machairodus catocopis* Cope, 1887 and *Machairodus tanneri* Martin and Schultz, 1975. *Amphimachairodus coloradensis* (Cook, 1922), formerly attributed to *Machairodus*, was recently reassigned to the genus *Amphimachairodus* by Antón et al. (2013). In Eurasia, only *M. aphanistus* is generally recognized, being mostly recorded in the Vallesian (MN9–MN10), whereas Turolian (MN11–MN12) and Ventian (MN13) specimens are generally referred to *Amphimachairodus giganteus* (Wagner, 1848) (Beaumont, 1975; Antón et al., 2004; Montoya et al. 2006), although with some exceptions (see below). Additional species of *Machairodus* are however recognized by some authors (Sotnikova, 1992; Peigné et al., 2005), including *Machairodus irtyschensis* Orlov, 1936 from the Early Pliocene of Pavlodar (Siberia; Orlov, 1936), *Machairodus kurteni* Sotnikova, 1992 from the Ventian (MN13) of Kalmakpai (Kazakhstan; Sotnikova, 1992), and *Machairodus horribilis* Schlosser, 1908 from China (Qiu et al., 2008). Based on their chronology, *M. kurteni* and *M. irtyschensis* might be alternatively attributable to *Amphimachairodus* and *Homotherium*, respectively. However, additional studies would be required to better ascertain their genus assignment, so we prefer to maintain tentatively the original attribution.

1.2. The European record of Machairodus aphanistus

European remains of *M. aphanistus* outside the Iberian Peninsula are generally scarce and fragmentary. This species is mainly recorded from MN9 to MN10 localities, although there are some records from MN11; they include: Eppelsheim (MN9, type locality;

Beaumont, 1975), Höwenegg (MN9; Bernor et al., 1988) and Dorn-Dürkheim 1 (MN11; Peigné et al., 2005) in Germany; Montredon and Soblay (MN10; Beaumont, 1975) in France; Charmoille (MN9; Beaumont, 1975) in Switzerland; Zillingdorf (MN9 or MN10; Beaumont, 1975; Peingé et al., 2005) in Austria; Csákvár (MN11; Morlo et al., 1997) in Hungary; Nessebar (MN9 or MN10; Spassov et al., 2006) in Bulgaria; and Kemiklitepe D (MN11; Bonis, 1994; Peigné et al., 2005; Spassov et al., 2006) and Mahmutgazi (MN11, Peigné et al., 2005) in Turkey.

In the Iberian Peninsula, *M. aphanistus* is recorded from several Spanish localities, including Los Valles de Fuentidueña (MN9, Duero Basin; Ginsburg et al., 1981), Batallones 1, 3 and 10 (MN10, Madrid Basin; Morales et al., 2008; Abella et al., 2011), and several Vallès-Penedès localities (Crusafont and Truyols, 1954; Crusafont Pairó, 1959, 1964; Crusafont-Pairó and Golpe-Posse, 1972; Crusafont Pairó and Kurtén, 1976; Golpe-Posse, 1974; Golpe-Posse et al., 1979; Beaumont and Crusafont-Pairó, 1982; Pons-Moyà, 1989; Fraile et al., 1997; Agustí et al., 1984, 1997; Alba et al., 2011). From older to younger, the previously known Vallès-Penedès localities are the following: Creu Conill 22, Can Poncic 1, Santiga and Can Llobateres 1, from MN9; and Torrent de Febulines and La Tarumba 1, from MN10. The remains from Los Valles de Fuentidueña were used to erect a distinct species, *Machairodus alberdiae* Ginsburg et al., 1981*,* which is currently considered a subjective junior synonym of *M. aphanistus* (Peigné et al., 2005). The most abundant and complete remains of the species have been recovered from Batallones (Antón et al., 2004; Salesa et al., 2005; Turner et al., 2011).

The Iberian record of *M. aphanistus* in the Vallès-Penedès Basin is thus more restricted than in Europe as a whole, where this species persists into MN11, being apparently replaced by its purported descendant, *A. giganteus*, from MN11 onward. Here, we describe several unpublished remains of *M. aphanistus* from different localities of the Vallès-Penedès Basin, namely Can Mata (late MN7+8–MN9), Can Llobateres 1 (MN9), Viladecavalls (MN10) and Ronda Oest Sabadell ROS-D3 (MN10), further providing new data on the remains from the previously known localities of Can Poncic 1, Santiga, Can Llobateres 1, La Tarumba 1 and Torrent de Febulines. Finally, we discuss the presence of *M. aphanistus* in Creu Conill 22, putatively considered the first record of the *Hippotherium–Machairodus* association in the Iberian Peninsula (Agustí et al., 1997; Casanovas-Vilar et al., 2006).

2. Age and geological background

The Vallès-Penedès Basin is a small and elongated half-graben, parallel to the Catalan coastline and bounded by the Catalan Coastal Ranges. It originated during the extensional processes that resulted in the opening of the Western Mediterranean in the latest Oligocene (Cabrera et al., 1991, 2004; Bartrina et al., 1992; Roca and Guimerà 1992; de Gibert and Casanovas-Vilar, 2011). The stratigraphic record of the basin covers most of the Miocene, starting at the Ramblian (MN3) and ending by the Turolian (MN12), and besides some marine and transitional deposits that mainly correspond to the Langhian (early Middle Miocene), the infilling consists of continental sediments deposited in a context of alluvial fans (Agustí et al., 1985; Casanovas-Vilar et al., 2011c). The main alluvial fan systems were sourced from the SE reliefs during the Early Miocene and from the NW ones during the Middle and Late Miocene (Cabrera et al., 1991, 2004; de Gibert and Casanovas-Vilar, 2011). The basin has been intensively sampled for more than 70 years, and the late Aragonian (late Middle Miocene, MN7+8) and Vallesian (Late Miocene, MN9–MN10) records are particularly well known. More than 200 mammal-bearing sites are known from this interval, being placed in a detailed bio- and magnetostratigraphic framework, so that their age is well constrained (Agustí et al., 1985, 1997; Casanovas-Vilar et al., 2011a,b).

The studied specimens mostly come from well-sampled Vallesian sites of the basin. Creu Conill 22 is the oldest Vallesian site from the area, and it has been correlated by means of magnetostratigraphy to chron C5r.1n, which implies an age of ca. 11.1 Ma for the base of the Vallesian (Garcés et al., 1996, 1997; Agustí et al., 1997). The age of Can Llobateres 1, la Tarumba 1 and Torrent de Febulines is also well constrained, thanks to combined bio- and magnetostratigraphic data. Can Llobateres 1 correlates with the latest part of the early Vallesian (MN9), yielding an age of 9.7 Ma (Garcés et al., 1996; Agustí et al., 1997). La Tarumba 1 would be slightly younger (ca. 9.6 Ma) and Torrent de Febulines would correspond to the last part of the Vallesian (ca. 9.1 Ma). The exact stratigraphic provenance of the Viladecavalls material is unknown, but the magnetostratigraphic data for the Viladecavalls section indicate that the series ranges from about 9.6 to 9.3 Ma (Garcés et al. 1996; Agustí et al., 1997). For Ronda Oest Sabadell (ROS), Santiga and Can Poncic 1, there are no magnetostratigraphic data, so their correlation is entirely based on biostratigraphy. Santiga and Can Poncic 1 have yielded abundant remains of the cricetid *Cricetulodon hartenbergeri*, characteristic of the *C. hartenbergeri* local range zone, which covers part of the early Vallesian and ranges from about 10.4 to 9.9 Ma (Casanovas-Vilar et al. 2011a).

The Ronda Oest Sabadell locality ROS-D3 is here reported for the first time. All ROS localities were discovered as a result of paleontological work motivated by the construction in 2009–2011 of a road near the city of Sabadell (Blaya-Martí et al., 2012). In the course of this work, several mammal-bearing sites were discovered and their stratigraphic position was accurately recorded. The preliminary study of the mammal succession (Blaya-Martí et al., 2012; I.C.V. unpublished data) indicates that ROS sites range in age from the late Vallesian to the early Turolian, i.e., from MN10 to MN11. Locality ROS-D3 is situated around meter 33 of the 97 m-thick series of ROS sector D, and placed 13 m below locality ROS-D6 within the same sector. Given that no significant faults or hiatuses were detected in this particular series, the age of both sites is assumed to be roughly similar. ROS-D3 did not deliver any small mammal remains that would allow a correlation to the Vallès-Penedès local zones. In contrast, the rich rodent assemblage from ROS-D6 includes the murids *Progonomys cathalai* and *Parapodemus* sp. nov., together with the cricetids *Kowalskia ambarrensis* and *Rotundomys* cf. *montisrotundi*, the latter being represented by just two molars. The presence of murids, coupled with that of the cricetids *Kowalskia* and *Rotundomys*, indicate a late Vallesian (MN10) age. However, the rodent assemblage is very different from all those known from other MN10 localities of the same area, such as Viladecavalls and Torrent de Febulines. The abundance of murids and the rarity of *Rotundomys* are particularly conspicuous. *Rotundomys montisrotundi* ranges from about 9.6 to 9.3 Ma in the Vallès-Penedès, whereas *P. cathalai* and *Parapodemus* sp. nov. are not known from any other site (I.C.V., unpublished data). In the densely-sampled Teruel Basin (east-central Spain), *P. cathalai* first occurs at around 9.3 Ma, the first murid species recorded being *P. hispanicus* at 9.7 Ma (Van Dam et al., 2001). In the same area, *Parapodemus* does not occur until the Turolian. A similar situation is seen in the French record, even though *P. cathalai* may occur in older sites (Mein, 1999). Accordingly, ROS-D6 may correlate to the second half of the late Vallesian, being close in age to Trinxera Nord Autopista (ca. 9.3 Ma) and Torrent de Febulines (ca. 9.1 Ma). In support of this interpretation, *K. ambarrensis* is represented by scarce remains in these sites, and absent from older late Vallesian localities of the same basin (such as Viladecavalls and la Tarumba 1).

Finally, the exact stratigraphic provenance of the Can Mata material is unknown. The fossiliferous area of Can Mata is located near the town of els Hostalets de Pierola, with its Miocene outcrops recording the Middle to Late Miocene boundary. Traditionally, several loosely defined localities and isolated finds from this area were grouped into Hostalets Inferior (MN7+8) and Hostalets Superior (MN9) (Golpe-Posse, 1974; Agustí et al., 1985). More recently, many strictly defined localities have been recognized in this area, corresponding to the synthetic stratigraphic series of Can Mata (including both Abocador de Can Mata and Ecoparc de Can Mata), which range in age at least from the early MN7+8 to MN9 (Alba et al., 2006, 2011b; Moyà-Solà et al., 2009; Casanovas-Vilar et al., 2011a). Most of the old finds from Can Mata would be probably situated around the locality of Can Mata 1, which is considered to be latest Aragonian (ca. 11.2 Ma; Casanovas-Vilar et al., 2011a; Alba et al., 2011b), thus being either late MN7+8 or early MN9 in age. Therefore, it is likely that this find represents the oldest Vallès-Penedès occurrence of *Machairodus*, which has not been thus far recovered from the late Aragonian (MN7+8) localities of the Abocador de Can Mata series (Alba et al., 2011b).

3. Material and methods

3.1 Abbreviations

Institutions and fossil collections: ICP, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona; IPS, collections from the ICP.

Fossil sites: CM: Can Mata; CNN: Creu Conill; CP: Can Poncic 1; SA: Santiga; CLL: Can Llobateres; LTR: La Tarumba; VC: Viladecavalls; TF: Torrent de Febulines; ROS: Ronda Oest Sabadell.

3.2 Studied material, comparative sample and measurements

The fossil remains described in this paper (Fig. 2) are housed at the ICP. The comparative sample includes fossil remains of *Machairodus aphanistus* from Los Valles de Fuentidueña housed at the ICP, as well as data from other Late Miocene European machairodontines based on data taken from the literature (Beaumont, 1975; Sotnikova, 1992; Antón et al., 2004; Peigné et al., 2005; Sardella and Werdelin, 2007; Salesa et al., 2012). Dental and mandibular measurements of the studied specimens were taken with a digital caliper to the nearest 0.1 mm.

4. Systematic Paleontology

Order: CARNIVORA Bowdich, 1821

Suborder: FELIFORMIA Kretzoi, 1945

Family: FELIDAE Fischer, 1817

Subfamily: MACHAIRODONTINAE Gill, 1872

Genus *Machairodus* Kaup, 1833

Machairodus aphanistus (Kaup, 1832)

(Figs. 2, 3, 5, 6)

4.1. Referred specimens

Can Mata: IPS30910, complete right talus.

Can Llobateres 1: IPS13169, complete left C1; IPS13178, crown fragment of right C1; IPS13166, complete left P3; IPS13164, complete left P4; IPS13170, right P4 lacking the protocone; IPS13168, right P4 lacking paracone and metacone; IPS15042, right P4 without parastyle and paracone; IPS15123, partial right P4; IPS13167, complete left p4; IPS13165, complete right m1; IPS15032, distal fragment of right m1; IPS15094, partial left scapula; IPS13176, complete right second metacarpal; IPS15045, proximal fragment of left second metacarpal; IPS15061, proximal fragment of right third metacarpal; IPS11381, left third metacarpal lacking the head; IPS13172, right fourth metacarpal; IPS15046, proximal fragment of left fifth metacarpal; IPS11020, right scapholunar; IPS11341, diaphysis of right femur; IPS13173, complete right third metatarsal; IPS15043, proximal fragment of right fourth metacarpal; IPS13174 and IPS13175, two complete right fifth metatarsals; IPS13171, right calcaneus; IPS15077, right navicular; IPS11183, left cuboid; IPS15021, IPS15022, IPS15015, and IPS15007, proximal phalanges; IPS15068, IPS15008, and IPS15017, middle phalanges.

Can Poncic 1: IPS15033, right premaxillary fragment with I2–I3; IPS13177, complete right p4.

Santiga: IPS13185, rostral fragment with left I1–M1 and right I1–M1.

Torrent de Febulines: IPS28929, two crown fragments of C1; IPS28932, left scapholunar; IPS28904, complete left fifth metatarsal.

Viladecavalls: IPS36058, proximal phalanx lacking the trochlea.

La Tarumba 1: IPS16286, right third metcarpal lacking the head.

Ronda Oest Sabadell ROS-D3: IPS62083, nearly complete left hemimandible with c1–m1 and associated complete right hemimandible with c1–m1.

4.2. Description and comparisons with unpublished material

Measurements: See Tables 1–3.

Upper teeth: The left P3 from CLL1 (IPS13166) displays a high protocone, slightly inclined lingually. The two accessory cusps are well developed, the distal cusp being mesiodistally longer than the mesial cusp. A marked cingulum runs from the distal portion of the P3 crown to the protruding distolingual expansion, as in *Amphimachairodus* and *Panthera leo* (Antón et al., 2004. Fig. 3D–F), thus resembling the condition displayed by IPS13185 from SA (Beaumont and Crusafont-Pairó, 1982). IPS13166 differs from *Amphimachairodus* and *Panthera leo* in the concave buccal profile and the presence of a weak cingulum on the distolingual corner of the crown (Antón et al. 2004).

Mandible: The mandible from ROS-D3 (IPS62083) is long, with relatively deep and robust corpora, a relatively slender and moderately verticalized symphysis that is higher than the corpus, and a postcanine diastema longer (42.2–43.3 mm) than in other specimens of *M. aphanistus*, thus closely resembling those of *A. giganteus* (Sotnikova, 1992; Antón et al., 2004; Sardella and Werdelin, 2007). In the right hemimandible, there are three mental foramina, two below the diastema and another one below the p3 and close to the inferior margin of the mandible; on the left side, the two former foramina are more closely packed and partially fused with one another (Fig. 2B,E). The mandibular flange is only weakly developed, as it is characteristic of *M. aphanistus*, whereas in contrast *A. giganteus* has a better-developed mandibular flange (Fig. 2B; Antón et al., 2004; Sardella and Werdelin, 2007). The corpus is thinner and shallower at the level of the distal portion of the diastema, and thickest and deepest at the level of the p4. The masseteric fossa is deep, reaching anteriorly the level of the m1 protoconid. The angular process is clearly individualized from the corpus and posterolingually projected. The coronoid process is rostrocaudally wide, posteriorly inclined and superiorly projecting well above the upper-most symphyseal level (Fig. 2A,D).

Lower teeth: Only the canines and cheek-teeth are preserved in the mandible from ROS-D3 (IPS62083). All these teeth are completely preserved, except for the missing tip of the right c1. The cheek teeth display a moderate degree of wear, with dentine exposure in both m1 and in the protoconid of the left p4 (Fig. 2B,E). c1 is high-crowned, proportionally larger than in *A. giganteus*, and implanted obliquely relative to the postcanine tooth row. The crown displays an oval (longer than broad) occlusal profile and is tilted distally (with its apex almost reaching the distalmost level of the crown base). The crown may be divided into a markedly convex buccal portion and a slightly concave distolingual portion. The latter is delimited by two (distal and mesiolingual) serrated crests that run from cervix to the apex. The mesiolingual crest is thicker than the distal one, and, unlike the latter, it ends shortly before reaching the crown apex; next to the former there is mesial shallow sulcus that runs from the cervix to about crown mid-height (Fig. 2A,B).

The premolars are tricuspid and somewhat broader distally than mesially. p3 displays a low and finely-serrated protoconid that is slightly tilted distalwards, well-developed mesial and distal accessory cuspids (the mesial one slightly smaller and more lingually situated than the distal one), and a distinct distal cingulid (Fig. 2C). p4 displays a similar morphology but is much larger than the preceding premolar. The protoconid has a similar occlusal morphology, although it is much higher, the mesial and distal accessory cuspids are comparatively better developed and similar in size to one another (being as high as the p3 protoconid), and the distal cingulid is even more conspicuous. As compared with the p4 from CLL1 (IPS13167) and CP (IPS13177), the p4 from ROS-D3 shows better developed and higher accessory cuspids and a stronger distal cingulid, thus more closely resembling the condition observed in *A. giganteus* than the previously-described specimens (Beaumont and Crusafont-Pairó, 1982; Geraads et al., 2004; Salesa et al., 2012).

The lower carnassial (m1) displays two main cuspids, the paraconid being lower and mesiodistally shorter than the protoconid, which is markedly asymmetrical (very tilted distally). The m1 further displays a short but distinct talonid with a distinct metaconid (Fig. 2C), which is relatively well developed as compared with other specimens of *M. aphanistus* (Antón et al., 2004). Another m1 is available from CLL1 (IPS13165). It displays a similar occlusal morphology as the carnassials from the ROS-D3 mandible (IPS62083), although that from CLL1 displays a less developed talonid that further lacks a distinct metaconid (Fig. 3A-C).

Scapula: A partial right scapula (distal fragment) from CLL1 (IPS15094; Fig. 6A–C) preserves the glenoid cavity, the neck and the supraglenoid tuberosity. The glenoid cavity displays a subcircular profile as in *Smilodon fatalis* and *Homotherium latidens* from Europe, thus differing from *Homotherium serum*, *Homotherium ischyrus* and extant large felids, which display a transversely wider cavity that is rather ovoid (Merriam and Stock, 1932; Rawn-Schatzinger, 1992; Ballesio, 1963; Martin et al., 2011). The supraglenoid tuberosity is mediolaterally wider than in *Homotherium*, thus resembling the condition observed in extant *Panthera leo*.

Carpus: One scapholunar from CLL1 (IPS11020; Fig. 6H,I) shares several characters with *Homotherium*. The radial facet is clearly convex and narrower than in extant large felids and *Smilodon*, thus more similar to the condition seen in *Homotherium*. The proximal process is palmomedially situated, whereas in extant large felids and *Homotherium* this process is more palmarly projected, and in *Smilodon* it is clearly projected medially. The facet for the radial sesamoid is large and rounded, as in *Homotherium* (Merriam and Stock, 1932; Rawn-Schatzinger, 1992; Ballesio, 1963; Hearst et al., 2011; Martin et al., 2011). The scapholunar has a distal rectangular outline, with the facet for the radial sesamoid oriented along the dorsoplantar plane. The facet for the trapezoid, situated on the dorsomedial corner of the bone, is triangular and slightly convex, being separated from the facet for the trapezium by a narrow dorsopalmar ridge. The facet for the trapezium extends towards the palmar margin, as in *Homotherium* and *Panthera leo*, but unlike in *Smilodon* (Merriam and Stock, 1932; Rawn-Schatzinger, 1992; Ballesio, 1963; Hearst et al., 2011). The facet for the magnum facet is very concave, running from the palmar to the dorsal side. The facet for the unciform is rectangular and narrower than in extant large felids and *Homotherium*, thus being similar to the condition displayed by *Smilodon* (Merriam and Stock, 1932; Rawn-Schatzinger, 1992; Ballesio, 1963; Hearst et al., 2011). The scapholunar from CLL1 (IPS11020) displays the same morphological features as that previously published from TF (IPS28932; Fig. 6F,G; Pons-Moyà, 1990), although the latter is somewhat larger in size (Table 3).

Metacarpus: There are two second metacarpals available from CLL1: IPS13176 (Fig. 5 P–T), which is complete; and IPS15045, which only preserves the proximal portion. IPS13176 is stouter (proximodistally shorter and mediolaterally wider) than in *Homotherium*, *Smilodon* and *Panthera leo*, thus more closely resembling the condition of *Xenosmilus* (Fig. 8). The diaphysis is slightly curved palmarly, as in *Panthera atrox* but unlike in the other taxa mentioned above (Merriam and Stock, 1932; Ballesio, 1963; Rawn-

Schatzinger, 1992; Martin et al., 2011). The base displays a triangular proximal profile, as in *Homotherium*, *Smilodon* and extant large felids (Merriam and Stock, 1932; Rawn-Schatzinger, 1992; Christiansen and Adolfssen, 2007). The articular facet for the trapezoid is markedly concave, as in extant large felids, *Megantereon* and *Smilodon*, thus differing from the flat facet displayed by *Homotherium* (Merriam and Stock, 1932; Ballesio, 1963; Rawn-Schatzinger, 1992; Christiansen and Adolfssen, 2007). The facet for the trapezium is triangular and relatively small, as in *Homotherium*, whereas in *Xenosmilus* it is more circular and in *Smilodon* larger and more elongated (Merriam and Stock, 1932; Ballesio, 1963; Rawn-Schatzinger, 1992; Martin et al., 2011). The articular facets for the magnum, present on the lateral side of the metacarpal base, are poorly preserved in the two available specimens. The articular facet for the third metacarpal is very conspicuous and distally projected, similar to the morphology displayed by extant large felids and *Homotherium*.

The third metacarpal is represented by three specimens: IPS11381 from CLL1 (Fig. 5U–Y) is complete, whereas IPS15061 from CLL1 and IPS16286 from LTR (Fig. 5K–O) only preserve the proximal portion. The base is poorly preserved in all the available specimens, although it can be discerned that the facet for the magnum is concave, as in *Xenosmilus*, *Megantereon* and *Smilodon*, whereas in contrast the facet for the magnum is convex, as in *Homotherium* and *Panthera* (Rawn-Schatzinger, 1992; Christiansen and Adolfssen, 2007; Martin et al., 2011). The proximolateral facet for the unciform is posteriorly elongated and less triangular than in *Panthera leo*, thus resembling the morphology displayed by *Homotherium*, *Meganteron* and *Xenosmilus* (Rawn-Schatzinger, 1992; Christiansen and Adolfssen, 2007; Martin et al., 2011). The dorsalmedial facet for the second metacarpal is dorsodistally elongated compared to *Homotherium*, *Megantereon* and *Xenosmilus*, thus resembling the condition displayed by *Panthera leo* (Rawn-Schatzinger, 1992; Ballesio, 1963; Christiansen and Adolfssen, 2007; Martin et al., 2011). The diaphysis is slender (mediolaterally narrow relative to length) and subtriangular in cross-section.

A proximal fragment of a fifth metacarpal from CLL1 (IPS15046; Fig. 5E‟–I‟) shows that the facet for the unciform is rectangular and very convex, thus being similar in shape but less posteromedially inclined than in *Homotherium*, and more clearly differing from the triangular morphology displayed by *Smilodon, Panthera atrox* and extant *Panthera leo* (Merriam and Stock, 1932; Rawn-Schatzinger, 1992; Ballesio, 1963). The medial articular tubercle for the fourth metacarpal is less developed than in extant large felids and *Panthera atrox*, thus resembling the condition seen in *Smilodon* and *Homotherium* (Merriam and Stock, 1932; Rawn-Schatzinger, 1992). The proximolateral tuberosity is flattened or depressed, as in *Smilodon* and *Homotherium*, whereas in extant large cats and *Panthera atrox* it is generally convex (Merriam and Stock, 1932; Rawn-Schatzinger, 1992).

Tarsus: The right talus from CM (IPS30901; Fig. 6D,E) is complete and well preserved. The trochlea is grooved and shallower than in extant large felids, thus resembling the condition observed in *Homotherium*, *Amphimachairodus* and *Smilodon*. In contrast, the neck is relatively longer than in *Homotherium*, *Amphimachairodus*, *Smilodon* and *Panthera leo* (Merriam and Stock, 1932; Ballesio, 1963; Berta, 1987; Salesa et al., 2012). On the plantar side, the astragalar foramen can be discerned, although it is poorly preserved. The sustentacular and navicular facets are also poorly preserved, being separated by a deep and wide groove from the rectangular (mediolaterally wide) and strongly convex astragalocalcanear facet, resembling the morphology of the various species of *Homotherium* (Merriam and Stock, 1932; Ballesio, 1963; Berta, 1987).

A right navicular from CLL1 (IPS15077; Fig. 6J–K) shows that the astragalar facet is rounded and slightly concave, as in other Machairodontini. The ectocuneifrom facet is slightly larger than the mesocuneiform facet, further being merely separated from one another dorsally by a ridge as in *Smilodon* and *Homotherium*. The cuboid and calcaneal facets are contiguous but separated by a weak ridge, as in *Smilodon* and *Homotherium* (Merriam and Stock, 1932; Ballesio, 1963; Berta, 1987; Martin et al., 2011). The morphology of the described specimen fits perfectly with that previously reported for the same element from Los Valles de Fuentidueña (IPS12664; Crusafont-Pairó and Ginsburg, 1973).

The left cuboid from CLL1 (IPS11183; Fig. 6L–Q) similarly shows the same morphology displayed by the specimen from Los Valles de Fuentidueña (IPS12661) reported by Crusafont-Pairó and Ginsburg (1973). The calcaneal proximal facet is quadrangular and slightly convex, thus differing from the more rectangular and flat morphology displayed by *Homotherium*. IPS11183 is proximodistally higher than in *Homotherium* and *Smilodon*, more closely approaching the condition observed in extant large felids (Merriam and Stock, 1932; Rawn-Schatzinger, 1992; Martin et al., 2011). The ectocuneiform facet is dorsoventrally high and located more dorsally than in *Homotherium*. The small and triangular navicular facet is located on the dorsodistal corner of the bone, like in *Homotherium*. In lateral view, the oblique, deep and wide groove for the insertion of the m. peroneus longus is more marked and deeper than in the specimen from Los Valles de Fuentidueña (Crusafont-Pairó and Ginsburg, 1973), thus more closely approaching the condition of *Homotherium* (Martin et al., 2011). The facets for the fourth and fifth metatarsals are visible on the distal portion of the bone, although poorly preserved.

Metatarsus: A proximal fragment of fourth metatarsal from CLL1 (IPS15043, Fig. 5Z–D‘’) shows that the proximal facet for the cuboid is rectangular and slightly convex, further being mediolaterally broader on its plantar than on its dorsal portion, as in other

Machairodontini, but unlike in pantherines (Rawn-Schatzinger, 1992; Martin et al., 2011). There is only a single, deep and distally-projected facet for the fifth metatarsal, whereas in *Homotherium*, *Smilodon*, *Amphimachairodus* and pantherines there are two deep but less distally-projected facets (Merriam and Stock, 1932; Ballesio, 1963; Berta, 1967; Rawn-Schatzinger, 1992; Salesa et al., 2012). The fourth metatarsal displays two medial facets for the third metatarsal: a subcircular one, situated dorsoproximally; and a more rectangular and inclined one, situated more palmarly. The circular dorsal facet is generally situated more proximally in *Homotherium*, *Smilodon* and *Panthera leo* than in the studied specimen, whereas the posterior facet in the latter resembles that observed in *Panthera leo* (Merriam and Stock, 1932; Ballesio, 1963; Berta, 1967; Rawn-Schatzinger, 1992).

Three fifth metatarsals are available: one from CLL1 (IPS13175) published by Beaumont and Crusafont-Pairó (1982), another from TF (IPS28904, Fig. 5F–J) published by Golpe-Posse et al. (1979) and Pons-Moyà (1990), and a third one CLL1 (IPS13174, Fig. 5A-E) that remained unpublished. All these specimens display the morphology already described by Beaumont and Crusafont-Pairó (1982) and Pons-Moyà (1990), although that from TF is comparatively stouter and further displays a very deep ligamental groove on its proximoplantar portion that is not observed in the specimens from CLL1 (Fig. 8).

Phalanges: Four complete proximal phalanges from CLL1 (IPS15015, IPS15007, IPS15022 and IPS15021; Fig. 6R–Y) and a proximal fragment from VC (IPS36058) are available. Their comparison with extant *Panthera leo* and the extinct *Homotherium latidens* specimens do not enable their attribution to either the manus or the pes, or to any specific ray. These specimens display the same morphology as that previously described from Los Valles de Fuentidueña (IPS12667; Crusafont-Pairó and Ginsburg, 1973), being characterized by a mediolaterally robust diaphysis, a vertically oriented proximal articular surface and a deep ligamental groove on its proximal portion, and thus resembling the morphology displayed by *Amphimachairodus*, *Homotherium* and *Smilodon* (Gaudry, 1862; Merriam and Stock, 1932; Ballesio, 1963; Berta, 1967; Salesa et al., 2012).

The comparison of three middle phalanges from CLL1 (IPS15068, IPS15008 and IPS15017; Fig. 6A“–H“) with those of pantherines and *H. latidens* do not allow us to provide with an anatomical attribution to either manual or pedal phalanges. IPS15068 (Fig. 6E“–H“) and IPS15008 (Fig. 6A“–D“) have slender and longer shafts than in IPS15017. In general terms, the reported middle phalanges seem slightly stouter than those of *Panthera leo*. The same elements of *Homotherium* and *Smilodon* seem generally slenderer and proximodistally shorter (Merriam and Stock, 1932; Ballesio, 1963; Berta, 1987).

5. Discussion

5.1. Taxonomic attribution

Creu Conill: Agustí et al. (1997) reported the presence of *Machairodus aphanistus* from CCN22 (MN9; 11.1 Ma) on the basis of an undescribed left P4 (IPS28746; Fig. 4A–C). In fact, the morphology of this P4, which does not preserve the protocone, is quite different from those of *M. aphanistus*. The parastyle in IPS28746 lacks the well-developed buccal cingulum that is characteristic of *M. aphanistus*, and which can be observed in the P4 of this taxon available from the Vallès-Penedès Basin from CLL1 (IPS13170; Fig. 3G–I) and SA (IPS13185). Moreover, IPS28746 from CCN22 displays a slightly marked lingual cingulum running from the distal aspect of the metacone to the mesial portion of the paracone (Fig. 4B), which cannot be observed in the Vallès-Penedès material of *M.*

aphanistus, but which is displayed by medium-sized Late Miocene hyaenids from this basin, such as *Thalassictis*. We therefore remove IPS28746 from the hypodigm of *M. aphanistus* and attributed it to Hyaenidae indet. (see a discussion of the biostratigraphic implications below).

Can Mata: The talus from the classical collections of CM (IPS30901) shares several characters with those of *Panthera leo* (such as a moderately large neck, and a deep and mediolaterally compressed trochlea). In these features, this taxon differs from *Homotherium* and *Amphimachairodus*, which usually display a relatively shorter talar neck, together with a narrow and mediolaterally wide trochlea (Merriam and Stock, 1932; Ballesio, 1963; Berta, 1967; Salesa et al., 2012). The characters displayed by the studied talus therefore agree with the purported less derived morphology of *M. aphanistus* compared with both *Amphimachairodus* and *Homotherium.*

Can Poncic, Can Llobateres and Santiga: The remains of *Machairodus* from CP1, CLL1 and SA were published by Beaumont and Crusafont-Pairó (1982), who attributed them to *Machairodus* cf. *aphanistus*. Here we describe previously unpublished material from CLL1, mostly consisting in postcranial remains. The latter closely resemble in morphology the postcranial material of *M. aphanistus* from Los Valles de Fuentidueña (Crusafont-Pairó and Ginsbug, 1973), although the metacarpal shafts and the phalanges are stouter than in other machairodontins (more similar to the stoutly built metacarpals and phalanges of *Panthera leo*).

La Tarumba and Viladecavalls: The felid material from LTR, in the area of Viladecavalls, was originally described and published by Villalta Comella and Crusafont Pairó (1943, 1948), who attributed it to *Felis antediluviana* and *Felis* sp. Villalta Comella and Crusafont Pairó (1943), in particular, reported from this locality a corpus fragment with p4–m1, whereas Villalta Comella and Crusafont Pairó (1948) reported a few postcranials (a second, third and fourth metacarpals, and a proximal phalanx) that they considered might belong to the same taxon recorded by the dentognathic fragment. The morphology of the right third metacarpal (IPS16286) is clearly that of a felid, and the proportions and morphology of the base allows us to include it in the hypodigm of *M. aphanistus* (Table 3), together with other postcranial specimens from the same locality. In contrast, the other metacarpals and the proximal phalanx described by Villalta Comella and Crusafont Pairó (1948) are mediolaterally wider and proximodistally shorter, which together with the morphology of the articular facets indicates an alternative attribution to an ursid, probably *Indarctos vireti*. In contrast, the mandibular fragment (IPS35093) described by Villalta Comella and Crusafont Pairó (1943) is attributable to *Paramachaerodus* sp., on the basis of its shallow mandibular corpus, the presence of a well-developed accessory cuspids and a distinct buccal cingulid in the p4, and an m1 protoconid clearly longer mediodistally than the paraconid (J.M.-M. and J.M.R., unpublished data). Here we also report a previously undescribed proximal phalanx (IPS36058) coming from an undeterminate stratigraphic horizon from the area of Viladecavalls. This specimen can be attributed to *M. aphanistus* based on similarities (robust shaft and deep ligamental groove) with the previously published material from Los Valles de Fuentidueña (Crusafont-Pairó and Ginsburg, 1973).

Ronda Oest Sabadell: The mandible from ROS-D3 is ascribed to *M. aphanistus* based on several characters displayed by material of this taxon from other Eurasian localities, such as Batallones-1 (Antón et al., 2004; Salesa et al., 2005; Turner et al., 2011), CLL1 (Beaumont and Crusafont-Pairó, 1982; this study), and Eppelsheim and Charmoille (Beaumont, 1975). According to the emended diagnosis of this species provided by Antón et al. (2004), these features include: large lower canines of oval cross-section; large lower premolars with a complete set of accessory cuspids; well-developed metaconid-talonid complex in m1; thick and high mandibular ramus; high and posteriorly inclined coronoid process; and undeveloped mandibular flange. The ROS specimen can be thus distinguished from *A. giganteus* by the possession of larger c1, the relatively broader p4, the non-reduced talonid-metaconid complex in the lower carnassial, and the poorly-developed flange. The specimen from ROS thus merely shows a few slight differences compared to the remains from other Eurasian localities, namely: relatively longer postcanine diastema; shorter p3 relative to p4 (Figs. 2E); better-developed premolar accessory cuspids (especially in p4); and better developed m1 metaconid. *Amphimachairodus* displays several derived dental features relative to *Machairodus* (Geraads et al., 2004), which support the purported phyletic lineage constituted by the Vallesian *M. aphanistus*, the Turolian-Ventian *A. giganteus*, and the Plio-Pleistocene *Homotherium* (Kurtén and Anderson, 1980; Sotnikova, 1992). Dental evolution throughout this lineage would reflect the progressive acquisition of several traits already displayed to some degree by the Turolian-Ventian species (Geraads et al., 2004), including the reduced c1, shorter p3 (usually absent in *Homotherium*), larger p4 with a well-developed mesial accessory cuspid, and loss of the m1 talonid.

In the above-mentioned regards, the ROS specimen displays some derived traits compared to typical *M. aphanistus*, including the somewhat reduced p3 (Fig. 2A) and the longer postcanine diastema. Given that the ROS specimen fits with the known chronostratigraphic range of *M. aphanistus* from the Vallès-Penedès Basin and elsewhere in Eurasia, these slight differences support the view that the characters employed to distinguish Vallesian from Turolian-Ventian machairodontins are more variable than customarily recognized (Beaumont, 1975; Sotnikova, 1992), further including symphyseal height, development of the mandibular flange, length of the postcanine diastema, and relative size between the premolars. We therefore conclude that the above-mentioned slight dentognathic differences merely reflect the intraspecific variability of *M. aphanistus*. This is also supported by the fact that the ROS mandible still retains a well-developed p4 mesial accessory cuspulid as well as a distinct m1 talonid with a large metaconid (even larger than in typical *M. aphanistus*), which according to Geraads et al. (2004) should be interpreted as primitive features. Only a few complete mandibles of *M. aphanistus* are known from Eurasia, except from the large collection from Batallones, which in the future will hopefully enable a more complete assessment of intraspecific variability in this species.

Torrent de Febulines: The felid remains from TF were originally published by Golpe-Posse et al. (1979), who attributed the following remains to *M. aphanistus*: two C1 crown fragments (IPS28932), one scapholunar (IPS28932), a fifth metacarpal (IPS28904), a first metacarpal and an acetabulum fragment. The two latter specimens were not found among the ICP collections by the authors, and subsequently Pons-Moyà (1990), who restudied the *Machairodus* remains from TF, only described the remains that are reported here. According to Pons-Moyà (1990), these fossils should be attributed to *Amphimachairodus giganteus*, based on the buccolingual compression and crenulated morphology of the two canine fragments, as well as the morphological similarities of the fifth metatarsal with the material of this taxon from Concud (Pons-Moyà, 1990). Our assessment of the material indicates that the TF specimens display the same morphology as those from CLL1 and SA, merely differing from the latter by the slightly larger dimensions (and hence stouter appearance) of the former (Table 3). The scarce available material from TF thus lacks clear resemblances with *Amphimachairodus*, leading us to conclude that the above-mentioned differences in size compared to specimens of *M. aphanistus* from SA and CLL1 are merely attributable to the large degrees of interspecific variability and sexual dimorphism characteristic of medium to large-sized felids.

5.2. Locomotor inferences

Machairodus aphanistus is mainly known on the basis of craniodental material, including several mandibles from various European sites and even complete skulls from Batallones-1 (Antón et al., 2004). In contrast, the postcranial anatomy of this early scimitar-toothed cat is practically unknown. Only scarce postcranial material was published by Crusafont-Pairó and Ginsburg (1973), Beaumont and Crusafont-Pairó (1982) and Pons-Moyà (1990), who nevertheless did not provide any inferences on the locomotor behavior of this species. The newly described postcranial remains of *M. aphanistus* (basically, carpals, metacarpals, tarsals, metatarsals and phalanges) allow us to provide important new data for better understanding the locomotor and predatory behaviour of this taxon. The metacarpals and metatarsals are clearly stouter (mediolaterally wider) than in *Homotherium*, thus more closely resembling those of *Panthera leo* (Fig. 8; Ballesio, 1963; Rawn-Schatzinger, 1992). The proximodistally-elongated calcaneus, and the relatively long neck as well as deep and mediolaterally compressed trochlea of the talus are also more similar to those of *Panthera leo* than to those of *Homotherium* (Ballesio, 1963; Rawn-Schatzinger, 1992). In contrast, the cuboid articular facets for the calcaneus and metatarsals are parallel, as in *Acinonyx* and *Homotherium*, instead of diverging as in *P. leo* (Ballesio, 1963; Rawn-Schatzinger, 1992; Hearst et al., 2011). The middle phalanges are proximodistally long, as in *P. leo*, rather than short as in *Homotherium*, but like those of the latter they display a lesser degree of mediolateral asymmetry than in *P. leo* (Ballesio, 1963; Rawn-Schatzinger, 1992; Hearst et al., 2011).

The long calcaneus and the morphology of talus (with a moderately long neck and a mediolaterally compressed and deep trochlea), similar to those of *P. leo*, indicate a digitigrade locomotion for *M. aphanistus* (Ballesio, 1963; Rawn-Schatzinger, 1992). In contrast, *Homotherium* displays a proximodistally short calcaneum and a bear-like talus with a proportionally short neck, these features being rather associated with a semiplantigrade stance with the ability to place the foot nearly flat on the ground (Ballesio, 1963; Rawn-Schatzinger, 1992).

The morphology of the studied cuboid and the lesser degree of asymmetry in the middle phalanges (which implies a smaller degree of claw retraction; Gonyea, 1976) resemble the condition seen in *Homotherium serum* and *H. latidens* (Ballesio, 1963; Rawn-Schatzinger, 1992; Hearst et al., 2011). A smaller degree of claw retraction is usually related to the condition seen in *Acinonyx jubatus* and canids, which have non-retractile claws so as to combine high speed with catching ability (Rawn-Schatzinger, 1992). In the case of *Homotherium* and probably *M. aphanistus* the lesser degree of asymmetry in the middle phalanges may be associated with a high degree of traction during hunting at high speeds (Ewer, 1973; Eaton, 1974; Rawn-Schatzinger, 1992).

Several authors have previously suggested long-distance travel capabilities in open habitats for *Homotherium* (Ballesio, 1963; Rawn-Schatzinger, 1992; Hearst et al., 2011). The detailed study of the postcranial remains of *Homotherium* shows that clearly cursorial features (the proportions of the hindlimbs and the non-retractile claws) are associated with more generalized terrestrial features (such as the morphology of the talus and calcaneum). This evidence suggests moderate cursorial abilities and a body plan adapted for running in

Homotherium (Rawn-Schatzinger, 1992). In contrast, *M. aphanistus* appears as a more stoutly-built species that generally more closely resembles *P. leo*, including the morphology of the tarsal bones. This is evidenced, among other features, by the stoutness of the metapodials of *M. aphanistus*, which are mediolaterally much wider than in the more lightly-built *Homotherium*. The morphology of the middle phalanges, proximodistally long (as in *P. leo*) and with a low degree of asymmetry (resembling *Homotherium*), implies a moderate capacity of traction during hunting at high speeds, and foreshows to some degree the more derived traits displayed in this regard by *Homotherium* (Rawn-Schatzinger, 1992) Overall, thus, *M. aphanistus* displays several postcranial features more primitive than in *Homotherium*, with the former being apparently less adapted for long-distance travel and high-speed hunting than its putative descendant.

5.8. Biostratigraphy

Before this study, the earliest record of the genus *Machairodus* in the Vallès-Penedès Basin was thought to be in the early MN9 locality of CCN22, being slightly younger than the locality of CCN20, which records the first appearance datum of the equid *Hippotherium* in this basin, with an estimated age of 11.1 Ma (Agustí et al., 1997. Garcés et al., 1997). In fact, Agustí et al. (1997) considered that the putative joint dispersal of *Hippotherium* and *Machairodus* might be a major dispersal event of eastern immigrants, marking the beginning of „MN9a" (*Megacricetodon ibericus*+*Hippotherium* biozone). Agustí and Galobart (1998) reported the presence of *Machairodus* sp. from CCN20, although an inspection of the ICP collections showed that only a single carnivoran remain superficially resembling this taxon was available from locality CCN22, as reported by Agustí et al.

(1997) and Casanovas-Vilar et al. (2006). Here we show that this specimen belongs in fact to a hyaenid, indicating that the first appearance datum of *M. apahanistus* in the Vallès-Penedès might be younger than previously assumed.

On the other hand, the previously undescribed talus from CM described here probably represents the oldest Vallès-Penedès record of this genus. This specimen comes from the historical collections amassed decades ago by Miquel Crusafont and co-workers around Can Mata de la Garriga in els Hostalets de Pierola. This area records the Aragonian/Vallesian transition at 11.1 Ma (Alba et al., 2006, 2011b; Moyà-Solà et al., 2009; Casanovas-Vilar et al., 2011a), so that uncertainties concerning the precise stratigraphic horizon of provenance precludes determining with certainty whether the described talus is MN7+8 or MN9 in age. However, this specimen indicates at least that *M. aphanistus* was already recorded in this basin by the earliest Vallesian. All the remaining Vallès-Penedès material of this taxon comes from younger localities, the oldest ones being CP1 and SA, with an estimated age comprised between 9.9 and 10.4 Ma (MN9). The new material from ROS-D3 (9.7–8.7 Ma, MN10), in contrast, is dated to the late Vallesian, being probably coeval or slightly younger than that from LTR (ca. 9.6 Ma, MN10). However, the certain last occurrence datum of *M. aphanistus* in the Vallès-Penedès Basin corresponds to the site of TF (ca. 9.1 Ma, MN10). Overall, the chronostratigraphic range of *M. aphanistus* in the Vallès-Penedès Basin agrees with its known chronological distribution in the rest of Europe, where it is mainly recorded in MN9–MN10, with doubtful and scarce records in the early Turolian (MN11) that might be alternatively attributable to *A. giganteus* (Antón et al., 2004).

6. Summary and conclusions

All the available craniodental and postcranial remains of the Late Miocene scimitar-toothed cat *Machairodus aphanistus* from the Vallès-Penedès Basin are reviewed here, including previously unpublished material. The studied material comes from the following localities: Can Mata indeterminate (late MN7+MN8 or MN9), Creu Conill 22 (MN9), Can Poncic 1 (MN9), Can Llobateres 1 (MN9), Santiga (MN9), La Tarumba 1 (MN10), Viladecavalls (MN10), Ronda Oest Sabadell ROS-D3 (MN10), and Torrent de Febulines (MN10). We show that the previously assumed oldest record of *M. aphanistus* in the Vallès-Penedès Basin, coming from Creu Conill 22 (11.1 Ma), corresponds in fact to a hyaenid, although based on the whole available sample the species is recorded from both MN9 and MN10. The postcranial remains described in this paper suggest that *M. aphanistus* is a stoutly-built species, more closely resembling the extant *Panthera leo* instead of the more slender homotheriin *Homotherium,* which is customarily considered to have displayed a digitigrade locomotion with abilities for long-distance travel in open habitats. The more primitive postcranial morphology displayed by *M. aphanistus* suggests that this taxon was less adaptated for traveling long distances than its purported descendant *Homotherium*.

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8. References

Abella, J., Domingo, M.S., Valenciano, A., Montoya, P., Morales, J., 2011. La asociación de carnívoros de Batallones 3, Mioceno superior del Cerro de los Batallones, Cuenca de Madrid. Paleontol. Evol. memòria especial núm. 5, 21–24.

Agustí, J., Moyà-Solà, A., Gibert, J., 1984. Mammal distribution dynamics in the eastern margin of the Iberian Peninsula during the Miocene. Paléobiol. Contin. 14, 33–46.

Agustí, J., Cabrera, L., Moyà-Solà, S., 1985. Sinopsis estratigráfica del Neógeno de la fosa del Vallès-Penedès. Paleontol. Evol. 18, 57–81.

Agustí, J., Cabrera, Ll., Garcés, M., Parés, J.M., 1997. The Vallesian mammal succession in the Vallès-Penedès basin (northeast Spain): Paleomagnetic calibration and correlation with global events. Palaeogeogr. Palaeoclim. Palaeoecol. 133, 149–180.

Alba, D.M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Rotgers, C., Furió, M., Angelone, C., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Obradó, P. 2006. Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l'Anoia, Cataluña), una sucesión de localidades del Aragoniense superior (MN6 y MN7+8) de la cuenca del Vallès-Penedès. Campañas 2002-2003, 2004 y 2005. Estudios Geológicos 62, 295–312.

Alba, D. M., Casanovas-Vilar, I., Moyà-Solà, S., Robles, J. M., 2011a. Parada 4. El Vallesiense inferior y su transición con el Vallesiense superior: Can Llobateres. Paleontol. Evol. memòria especial núm. 6, 111–123.

Alba, D. M., Casanovas-Vilar, I., Robles, J.M., Moyà-Solà, S., 2011b. Parada 3. El Aragoniense superior y la transición con el Vallesiense: Can Mata y la exposición paleontological de els Hostalets de Pierola. Paleontol. Evol. Memòria especial núm. 6, 95–109.

Antón, M., Salesa, M.J., Morales, J., Turner, A., 2004. First known complete skulls of the scimitar-toothed cat *Machairodus aphanistus* (Felidae, Carnivora) from the Spanish Late Miocene site of Cerro Batallones-1. J. Vert. Paleontol. 24, 957–969.

Antón, M., Salesa, M.J., Siliceo, G., 2013. Machairodont adaptations and affinities of the Holarctic late Miocene homotherin *Machairodus* (Mammalia, Carnivora, Felidae): The case of *Machairodus catocopis* Cope, 1887. J. Vert. Paleontol. 33, 1202–1213.

Ballesio, R., 1963. Monographie d‟un *Machairodus* du gisement villafranchien de Senèze : *Homotherium crenatidens* Fabrini. Trav. Lab. Géol. Fac. Sci. Lyon 9, 1–127.

Bartrina, M.T., Cabrera, L., Jurado, M.J., Guimerà, J., Roca, E., 1992. Evolution of the central Catalan margin of the Valencia trough (western Mediterranean). Tectonophysics 203, 219–247.

Beaumont, G., 1975. Recherches sur les Félidés (Mammifères, Carnivores) du Pliocène inférieur des sables à *Dinotherium* des environs d'Eppelsheim. Arch. Sci. 28**,** 369–405.

Beaumont, G., Crusafont-Pairó, M., 1982. Les Félidés (Mammifères, Carnivores) du Vallésien du Vallès, Catalogne, Espagne. Arch. Sci. 35, 41–64.

Bernor, R.L., Kovar-Eder, J., Lipscomb, D., Rögl, F., Sen, S., Tobien, H., 1988. Systematic, stratigraphic and palaeoenvironmental contexts of first-appearing *Hipparion* in the Vienna basin, Austria. J. Vert. Paleontol. 8, 427–452.

Berta, A., 1987. The sabercat *Smilodon gracilis* from Florida and a discussion of its relationships (Mammalia, Felidae, Smilodontine). Bull. Fla. Mus. Nat. Hist. Biol. Sci. 31, 1–63.

Blaya Martí, E., Obradó, P., Robles, J.M., Sala, J., Alba, D.M., 2012. Memòria de la intervenció paleontològica preventiva a les obres de prolongació de la Ronda Oest Sabadell, tram comprès entre la carretera N-150 i la BV-1248 (Sabadell, el Vallès Occidental): 2008-2011. FOSSILIA Serveis Paleontològics i Geològics SL, unpublished report.

Bonis, L. de, 1994. Les gisements de Mammifères du Miocène supérieur de Kemiklitepe, Turquie. 2: Carnivores. Bull. Mus. Natl. Hist. Nat, 16,19–39.

Cabrera, L., Calvet, F., Guimerà, J., Permanyer, A., 1991. El registro sedimentario miocénico en los semigrabens del Vallès-Penedès y de El Camp: organización secuencial y relaciones tectónican-sedimentación. In: I Congreso Grupo Español del Terciario, Libro-Guía Excursión 4, 132 pp. Vic.

Cabrera, L., Roca, E., Garcés, M., de Porta, J., 2004. Estratigrafía y evolución tectonosedimentaria oligocena superior-neógena del sector central del margen catalán (Cadena Costero-Catalana). In: Vera, J.A. (Ed.), Geología de España. SGE-IGME, Madrid, pp. 569–573.

Casanovas-Vilar, I., Agustí, A., 2007. Ecogeographical stability and climate forcing in the late Miocene (Vallesian) rodent record of Spain. Palaeogeogr. Palaeoclim. Palaeoecol 248, 169–189.

Casanovas-Vilar, I., Furió, M., Agustí, J., 2006. Rodents, insectivores and paleoenvironment associated to the first-appearing hipparionine horses in the Vallès-Penedès Basin (Northeastern Spain). Beitr. Paläont. 30, 89–107.

Casanovas-Vilar, I., Alba, D.M., Garcés, M., Robles, J.M., Moyà-Solà, S., 2011a. Updated chronology for the Miocene hominoid radiation in Western Eurasia. Proc. Natl. Acad. Sci. USA 108, 5554–5559.

Casanovas-Vilar, I., Alba, D.M., Robles, J.M., Moyà-Solà, S., 2011b. Registro paleontológico continental del Mioceno de la cuenca del Vallès-Penedès. Paleontol. Evol. memòria especial 6, 55–80.

Crusafont, M., Truyols, J., 1954. Catálogo paleomastológico del Mioceno del Vallés-Penedés y de Calatayud-Teruel. Segundo Cursillo Internacional de Paleontología. Museu de la Ciudad de Sabadell, Sabadell.

Crusafont Pairó, M., 1959. Primer hallazgo en España del género *Ursavus* (Carnivora, Ursidae). Not. Com. Inst. Geol. Min. Esp. 55, 137–144.

Crusafont Pairó, M., 1964. La biota de Can Llobateres (Sabadell) y su significación biológica. Curs. Conf. Inst. “ ucas Mallada” 9, 177–179.

Crusafont-Pairó, M., Golpe-Posse, J.M., 1972. New Pongids from the Miocene of the Vallès Penedes Basin (Catalonia, Spain). J. Hum. Evol. 2, 17–23.

Crusafont-Pairó, M., Ginsburg, L., 1973. Les Carnassiers fossiles de Los Vallès de Fuentidueña (Ségovie, Espagne). Bull. Mus. Natl. Hist. Nat. 131, 29–45.

Crusafont Pairó, M., Kurtén, B., 1976. Bears and bear-dogs from the Vallesian of the Vallès-Penedès Basin, Spain. Acta Zool. Fenn. 144, 1–29.

Christiansen, P., Adolfssen, J.S., 2007. Osteology and ecology of *Megantereon cultridens* SE311 (Mammalia; Felidae; Machairodontinae), a sabrecat from the Late Pliocenedearly Pleistocene of Senéze, France. Zool. J. Linn. Soc. Lond. 151, 833–883.

de Gibert, J.M., Casanovas-Vilar, I., 2011. Contexto geológico del Mioceno de la cuenca del Vallès-Penedès. Paleontol. Evol. memòria especial 6, 39–45.

Eaton, R.L., 1974. The Cheetah: the biology, ecology and behaviour of an endangered species. Van Nostrand Reinhold Co., New York, 178 p.

Ewer, R.F., 1973. The carnivores. Cornell University Press, New York, 494 p.

Fraile, S., Pérez, B., De Miguel, I., Morales, J., 1997. Revisión de los carnívoros presentes en los yacimientos del Neógeno español. In: Calvo, J.P. and Morales, J. (Eds.) Avances en el conocimiento del Terciario ibérico, pp. 77–80.

Garcés, M., Agustí, J., Cabrera, L., Parés, JM. 1996. Magnetostratigraphy of the Vallesian (late Miocene) in the Vallès-Penedès Basin (northeast Spain). Earth and Planetary Science Letters 142, 381-396.

Garcés, M., Cabrera, L., Agustí, J., Parés, J.M., 1997. Old World first appearance datum of "*Hipparion*" horses: Late Miocene large-mammal dispersal and global events. Geology 25, 19–22.

Gaudry A., 1 6 -1 6 . Animaux fossiles et géologie de l‟Attique. F. Savy, Paris, 475p.

Geraads, D., 1989. Vertébrés fossiles du Miocène supérieur du Djebel Krechem el Artsouma (Tunisie Centrale). Comparaisons biostratigraphiques. Geobios 22, 777–801.

Geraads, D., Alemseged, Z., Bellon, H., 2002. The late Miocene mammalian fauna of Chorora, Awash basin, Ethiopia: systematics, biochronology and the ^{40}K-^{40}Ar ages of the associated volcanics. Tertiar. Res. 21, 113–122.

Geraads, D., Kaya, T., Tuna, V., 2004. A skull of *Machairodus giganteus* (Felidae, Mammalia) from the Late Miocene of Turkey. N. Jb. Geol. Paläont. Mon. 2, 95–110.

Ginsburg, L., Morales, J., Soria, D., 1981. Nuevos datos sobre los carnívoros de los Valles de Fuentidueña (Segovia). Estudios Geol. 37, 383–415.

Golpe-Posse, J.M., 1974. Faunas y yacimientos con suiformes del Terciario español. Paleontol. Evol. 8, 1–87.

Golpe Posse, J.M., Santafe, L., Lopis, J.V., Casanovas, C., 1979. Datos sobre el Vallesiense medio-superior de los alrededores de Terrassa. Acta Geol. Hisp. 14, 356–361.

Gonyea, W.J., 1976. Behavioral implications of saber-toothed felid morphology. Paleobiol. 2, 332–342.

Hearst, J.M., Martin, L.D., Babiarz, J.P., Naples, V.L., 2011. Osteology and myology of *Homotherium ischyrus* from Idaho. In: Naples, V.L., Martin, L.D., Babiarz, J.P.(Eds.), The Other Saber-tooths: Scimitar-tooth Cats of the Western Hemisphere. The John Hopkins University Press, Baltimore, pp. 123–183.

Kurtén, B., 1976. Fossil Carnivora from the Late Tertiary of Bled Douarah and Cherichira, Tunisia. Not. Serv. Geol. Tunisie 42, 177–214.

Kurtén, B., Anderson, E., 1980. Pleistocene Mammals of North America. Columbia University Press, New York.

Martin, L.D., 1998. Felidae. In: Janis, C.J., Scott, K.M., Jacobs, L.L. (Eds.), Evolution of Tertiary Mammals of North America, Vol. 1: Terrestrial Carnivores, Ungulates and Ungulate like Mammals, Cambridge University Press, Cambridge, pp. 144–151.

Martin, L.D., Naples, V.L., Babiarz, J.P., 2011. Revision of the new World Homotheriini. In: Naples, V.L., Martin, L.D., Babiarz, J.P. (Eds.), The Other Saber-tooths: Scimitar-tooth Cats of the Western Hemisphere. The John Hopkins University Press, Baltimore, pp. 185–194.

Mein, P. 1999. The Late Miocene small mammal succession from France, with emphasis on the Rhône Valley localities. In: Agustí, J., Rook, L. & Andrews, P. (Eds.), Hominoid Evolution and Climatic Change in Europe. Volume 1: The Evolution of Neogene Terrestrial Ecosystems in Europe. Cambridge University Press, Cambridge, pp. 140–164.

Merriam JC, Stock C., 1932. The Felidae of Rancho la Brea. No. 422. Carnegie Institution of Washington, Washington.

Montoya, P., Morales, J., Robles, F., Abella, J., Benavent, J.V., Marín, M.D., Ruiz Sánchez, F.J., 2006. Las nuevas excavaciones (1995-2006) en el yacimiento del Mioceno final de Venta del Moro, Valencia. Estudios Geológicos 62, 316–326.

Morales, J., Pozo, M., Silva, P.G., Domingo, M.S., López-Antoñanzas, R., Álvarez Sierra, M.A., Antón, M., Martín Escorza, C., Quiralte, V., Salesa, M.J., Sánchez, I.M., Azanza, B., Calvo, J.P., Carrasco, P., García-Paredes, I., Knoll, F., Hernández Fernández, M., van den Hoek Ostende, L., Merino, L., van der Meulen, A., Montoya, P., Peigné, S., Peláez-Campomanes, P., Sánchez Marco, A., Turner, A., Abella, J., Alcalde, G.M., Andrés, M., DeMiguel, D., Cantalapiedra, J.L., Fraile, S., García Yelo, B.A., Gómez Cano, A.R., López Guerrero, P., Oliver Pérez, A., Siliceo, G., 2008. El sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid: estado actual y perspectivas. Palaeontol Nova Publ. Sem. Paleontol. Zaragoza. 8, 41–117.

Morlo, M., 1997. Die Raubtiere (Mammalia, Carnivora) aus dem Turolium von Dorn-

Dürkheim 1 (Rheinhessen). Teil 1: Mustelida, Hyaenidae, Percrocutidae, Felidae. Cour. Forsch.-Inst. Senckenberg 197, 11–47.

Moyà-Solà, S., Köhler, M., Alba, D.M., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Cabrera, L., Garcés, M., Almécija, S., Beamud, E., 2009. First partial face and upper dentition of the Middle Miocene hominoid *Dryopithecus fontani* from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, NE Spain): taxonomic and phylogenetic implications. Am. J. Phys. Anthropol. 139, 126–145.

Orlov, Yu. A., 1936. Tertiäre Raubtiere des Westlichen Sibiriens. I. Machairodontinae. Trav. Inst. Paleozool. Acad. Sci. URSS 5, 111–152.

Peigné, S., Bonis, L. de, Likius, A., Mackaye, H. T., Vignaud, P., Brunet, M., 2005. A new Machairodontine (Carnivora, Felidae) from the Late Miocene hominid locality of TM66, Toros-Menalla, Chad. C. R. Palevol 4, 243–253.

Pons-Moyà, J., 1990. Presencia de carnívoros turolienses en el Vallesiense terminal (MN 10) de Terrassa (Catalunya). Paleontol. Evol. 23, 199–203.

Qiu, Z.-X., Shi, Q.-Q., Liu, J.-Y., 2008. Description of skull material of *Machairodus horribilis* Schlosser, 1903. Vert. PalAsiat. 46, 265–283.

Roca, E., Guimerà, J., 1992. The Neogene structure of the eastern Iberian margin: structural constraints on the crustal evolution of the Valencia Trough (Western Mediterranean). Tectonophysics 203, 203–218.

Rawn-Schatzinger, V., 1992. The scimitar cat *Homotherium serum*, Cope. ISM Rep. Invest. 47, 1–80.

Sardella, R., Werdelin, L., 2007. *Amphimachairodus* (Felidae, Mammalia) from Sahabi (Latest Miocene–Earliest Pliocene, Libya), with a review of African Miocene Machairodontinae. Riv. Ital. Paleontol. Stratigr. 113, 67–77.

Salesa, M.J., Antón, M., Morales, J., 2005. Inferred behaviour and ecology of the primitive sabre-toothed cat *Paramachairodus ogygia* (Felidae, Machairodontinae) from the Late Miocene of Spain. J. Zool. 268, 243–254.

Salesa, M.J., Pesquero, M.D., Siliceo, G., Antón, M., Alcalá, L., Morales, J., 2012. A rich community of Felidae (Mammalia, Carnivora) from the Late Miocene (Turolian, MN13) site of Las Casiones (Villalba Baja, Teruel, Spain). J. Vert. Paleontol. 32, 658–676.

Sotnikova, M.V., 1992. A new species of *Machairodus* from the late Miocene Kalmakpai locality in eastern Kazakhstan (USSR). Ann. Zool. Fennici 28, 361–369.

Spassov, N., Tzankov, Tz., Geraads, D., 2006. Late Neogene stratigraphy, biochronology, faunal diversity and environments of south-western Bulgaria. Geodiversitas 28, 477–498.

Turner, A., Antón, M., Salesa, M. J., Morales, J., 2011. Changing ideas about the evolution and functional morphology of Machairodontine felids. Estudios Geol. 67, 255–276.

Van Dam, J.A., Alcalá, L., Alonso-Zarza, A., Calvo, J.P., Garcés, M., Krijgsman, W., 2001. The upper Miocene mammal record from the Teruel-Alfambra region (Spain). The MN system and continental stage/age concepts discussed. J. Vert. Paleontol. 21, 367–385.

Villalta Comella, J.F. de and Crusafont Pairó, M., 1943. Los vertebrados del Mioceno continental de la cuenca del Vallés-Panadés (provincia de Barcelona). I. Insectívoros. II. Carnívoros. Bol. Inst. Geol. Min. Esp. 56, 145–331.

Werdelin, L., 2003. Mio-Pliocene Carnivora from Lothagam, Kenya. In: Leakey, M.G., Harris, J.M. (Eds.), Lothagam: the Dawn of Humanity in Eastern Africa, Columbia University Press, New York, pp. 261–328.

Werdelin L. and Sardella R., 2006. The "*Homotherium*" from Langebaanweg, South Africa, and the origin of *Homotherium*. Palaeontogr. Abt. A. 277, 123–130.

Werdelin, L. and Peigné, S., 2010. Carnivora. In: Werdelin, L., Sanders, W.J. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 603–657.

Figures legends

Fig. 1. Geographic map showing the location of the Vallès-Penedès Basin within the Iberian Peninsula (top left), and the schematic geologic map of this basin, showing the main geologic units and the paleontological sites with fossil remains of *Machairodus aphanistus*. Abbreviations: **CM**, Can Mata indeterminate; **CCN,** Creu Conill 22; **CLL**, Can Llobateres 1; **CP,** Can Poncic 1; **SA**, Santiga; **LTR**, La Tarumba 1; **ROS-D3**, Ronda Oest de Sabadell; **TF**, Torrent de Febulines.

Fig. 2. Carte géographique montrant la situation du bassin de Vallès-Penedès dans la péninsule Ibérique (en haut à gauche), et carte géologique schématique de ce bassin, montrant les principales unités géologiques ainsi que les sites paléontologiques avec des restes fossiles de *Machairodus aphanistus*. Abréviations: **CM**, Can Mata indeterminate; **CCN,** Creu Conill 22; **CLL**, Can Llobateres 1; **CP,** Can Poncic 1; **SA**, Santiga; **LTR**, La Tarumba 1; **ROS-D3**, Ronda Oest de Sabadell; **TF**, Torrent de Febulines.

Fig. 2. Mandibular remains of *Machairodus aphanistus* from ROS-D3: **A–C**: right hemimandible with c1–m1 IPS62083 in **A**: lingual; **B**: buccal; **C**: occlusal views. **D–F**: left partial hemimandible with c1–m1 IPS62083 in **D**: lingual; **E**: buccal; **F**: occlusal views.

Fig. 2. Restes mandibulaires de *Machairodus aphanistus* de ROS-D3: **A–C**: hemimandibule droite avec c1–m1 IPS62083 en vues **A**: linguale; **B**: buccale; **C**: occlusale. **D–F**: hemimandibule gauche partielle avec c1–m1 IPS62083 en vues **D**: linguale; **E**: buccale; **F**: occlusale.

Fig. 3. Isolated dental remains of *Machairodus aphanistus* from the Vallès-Penedès Basin. **A–C**, right m1 IPS13165 from CLL1 in **A**, buccal; **B**, lingual; **C**, occlusal views. **D–F**, right P3 IPS13166 from Can Llobateres 1 in **D**, buccal; **E**, lingual; **F**, occlusal views. **G–H**, right P4 IPS 13170 from Can Llobateres 1 in **G**, buccal; **H**, lingual; **I**, occlusal views.

Fig. 3. Restes dentaires isolées de *Machairodus aphanistus* de bassin de Vallès-Penedès. **A–C**, m1 droite IPS13165 de CLL1 en vues **A**, buccale; **B**, linguale; **C**, occlusale. **D–F**, P3 droite IPS13166 de CLL1 en vues **D**, buccale; **E**, linguale; **F**, occlusale. **G–H**, P4 droite IPS 13170 de CLL1 en vues **G**, buccale; **H**, linguale; **I**, occlusale.

Fig. 4. Isolated left P4 IPS28746 of Hyaenidae indet. from CCN22 previously attributed to *Machairodus aphanistus*. **A**, buccal; **B**, lingual; **C**, occlusal views.

Fig.4. P4 gauche isolée de Hyaenidae indet. de CCN22 précédemment attribué à *Machairodus aphanistus*. Vues **A**, buccale; **B**, linguale; **C**, occlusale.

Fig. 5. Postcranial remains of *Machairodus aphanistus* from the Vallès-Penedès Basin. **A–E**, right metatarsal V IPS13174 from CLL1 in **A**, dorsal; **B**, medial; **C**, plantar; **D**, lateral; **E**, proximal views. **F–J**, left metatarsal V IPS28904 from TF in **F**, dorsal; **G**, lateral; **H**, plantar; **I**, medial; **J**, proximal views. **K–O**, right metacarpal III IPS16286 from LTR in **K**, dorsal; **L**, medial; **M**, palmar; **N**, lateral; **O**, proximal views. **P–T**, right metacarpal II

IPS13176 from CLL1 in **P**, dorsal; **Q**, medial; **R**, palmar; **S**, lateral; **T**, proximal views. **U–Y**, left metacarpal III IPS11381 from CLL1 in **U**, dorsal; **V**, lateral; **W**, palmar; **X**, medial; **Y**, proximal views. **Z–D'**, partial right metatarsal IV IPS15043 from CLL1 in **Z**, dorsal; **A'**, medial; **B'**, plantar; **C'**, lateral, **D“**, proximal views. **E'–I'**, proximal fragment of left fifth metacarpal IPS15046 from CLL1 in **E'**, dorsal, **F'**, medial, **G'**, palmar, **H'**, lateral, **I'**, proximal views.

Fig. 5. Restes postcrâniens de *Machairodus aphanistus* du bassin de Vallès-Penedès. **A–E**, métatarsien V droit IPS13174 de CLL1 en vues **A**, dorsale; **B**, médiale; **C**, plantaire; **D**, latérale; **E**, proximale. **F–J**, métatarsien V gauche IPS28904 de TF en vues **F**, dorsale; **G**, latérale; **H**, plantaire; **I**, médiale; **J**, proximale. **K–O**, métacarpien III droit IPS16286 de LTR en vues **K**, dorsale; **L**, médiale; **M**, palmaire; **N**, latérale; **O**, proximale. **P–T**, métacarpien II droit IPS13176 de CLL1 en vues **P**, dorsale; **Q**, médiale; **R**, palmaire; **S**, latérale; **T**, proximale. **U–Y**, métacarpien III gauche IPS11381 de CLL1 en vues **U**, dorsale; **V**, latérale; **W**, palmaire; **X**, médiale; **Y**, proximale. **Z–D'**, métatarsien IV droit IPS15043 de CLL1 en vues **Z**, dorsale; **A'**, médiale; **B'**, plantaire; **C'**, latérale; **D“**, proximale. **E'–I'**, métacarpien IV gauche IPS15046 de CLL1 en vues **E'**, dorsale, **F'**, médiale, **G'**, palmaire, **H'**, latérale, **I'**, proximale.

Fig. 6. Postcranial remains of *Machairodus aphanistus* from the Vallès-Penedès Basin. **A–C**, partial left scapula IPS15094 from CLL1 in **A**, lateral; **B**, medial; **C**, distal views. **D–E**, right talus IPS30901 from CM in **D**, dorsal; **E**, plantar views. **F–G**, left scapholunar IPS28932 from TF in **F**, proximal; **G**, distal views. **H–I**, right scapholunar IPS11020 from CLL1 in **H**, proximal; **I**, distal views. **J–K**, right navicular IPS15077 from CLL1 in **J**,

dorsal; **K**, plantar views. **L–Q**, left cuboid IPS11183 from CLL1 in **L**, lateral; **M**, medial; **N**, proximal; **O**, plantar, **P**, distal; **Q**, dorsal views. **R–U**, proximal phalanx IPS15007 from CLL1 in **R**, dorsal; **S**,**U,** lateral/medial; **T**, volar views. **V–Y**, proximal phalanx IPS15015 from CLL1 in **V**, dorsal; **W, Y**, lateral/medial; **X**, volar views. **Z–C'**, middle phalanx IPS15008 from CLL1 in **Z**, dorsal; **A', C'**, lateral/medial; **B'**, volar views. **D'–G'**, middle phalanx IPS15068 from CLL1 in **D'**, dorsal; **E',G'**, lateral/medial; **F'**, volar views.

Fig. 6. Restes postcrâniens de *Machairodus aphanistus* du bassin de Vallès-Penedès Basin. **A–C**, scapula gauche partielle IPS15094 de CLL1 en vues **A**, latérale; **B**, médiale; **C**, distale. **D–E**, astragale droit IPS30901 de CM en vues **D**, dorsale; **E**, plantaire. **F–G**, scapholunaire gauche IPS28932 de TF en vues **F**, proximale; **G**, distale. **H–I**, scapholunaire droit IPS11020 de CLL1 en vues **H**, proximale; **I**, distale. **J–K**, naviculaire droit IPS15077 de CLL1 en vues **J**, dorsale; **K**, plantaire. **L–Q**, cuboïde gauche IPS11183 de CLL1 en vues **L**, latérale; **M**, médiale; **N**, proximale; **O**, plantaire, **P**, distale; **Q**, dorsale. **R–U**, phalange proximale IPS15007 de CLL1 en vues **R**, dorsale; **S**,**U,** latérale/médiale; **T**, volaire. **V–Y**, phalange proximale IPS15015 de CLL1 en vues **V**, dorsale; **W, Y**, latérale/médiale; **X**, volaire. **Z–C'**, phalange moyenne IPS15008 de CLL1 en vues **Z**, dorsale; **A', C'**, latéral/médiale; **B'**, volaire. **D'–G'**, phalange moyenne IPS15068 de CLL1 en vues **D'**, dorsale; **E',G'**, latérale/médiale; **F'**, volaire.

Fig. 7. Dental proportions of the lower cheek teeth in *Machairodus aphanistus* from ROS compared with other Late Miocene machairodontines. All points represent individual data, except for Batallones-1, where only the mean and the minimum-maximum ranges were available. **A**, p3; **B**, p4; **C**, m1.

Fig. 7. Proportions dentaires des premolaries et molaires inférieures de *Machairodus aphanistus* de ROS comparées avec ceux d‟autres machairodontins du Miocène Supérieur. Tous les points représentent les données individuelles, à l‟exception de Batallones-1, où seule la moyenne et les intervalles minimum-maximum étaient disponibles. **A**, p3; **B**, p4; **C**, m1.

Fig. 8. Proportions of the metacarpals and metatarsals of *Machairodus aphanistus* from CLL and TF compared with those of other machairodontines and pantherines. **A**, Mtc II; **B**, Mtc IV; **C**, Mtt III ; **D**, Mtt V.

Fig. 8. Proportions des métacarpiens et métatarsiens de *Machairodus aphanistus* de CLL et TF par rapport à ceux d‟autres machairodontines et pantherines. **A**, Mtc II; **B**, Mtc IV; **C**, Mtt III; **D**, MttV.

Figure 1

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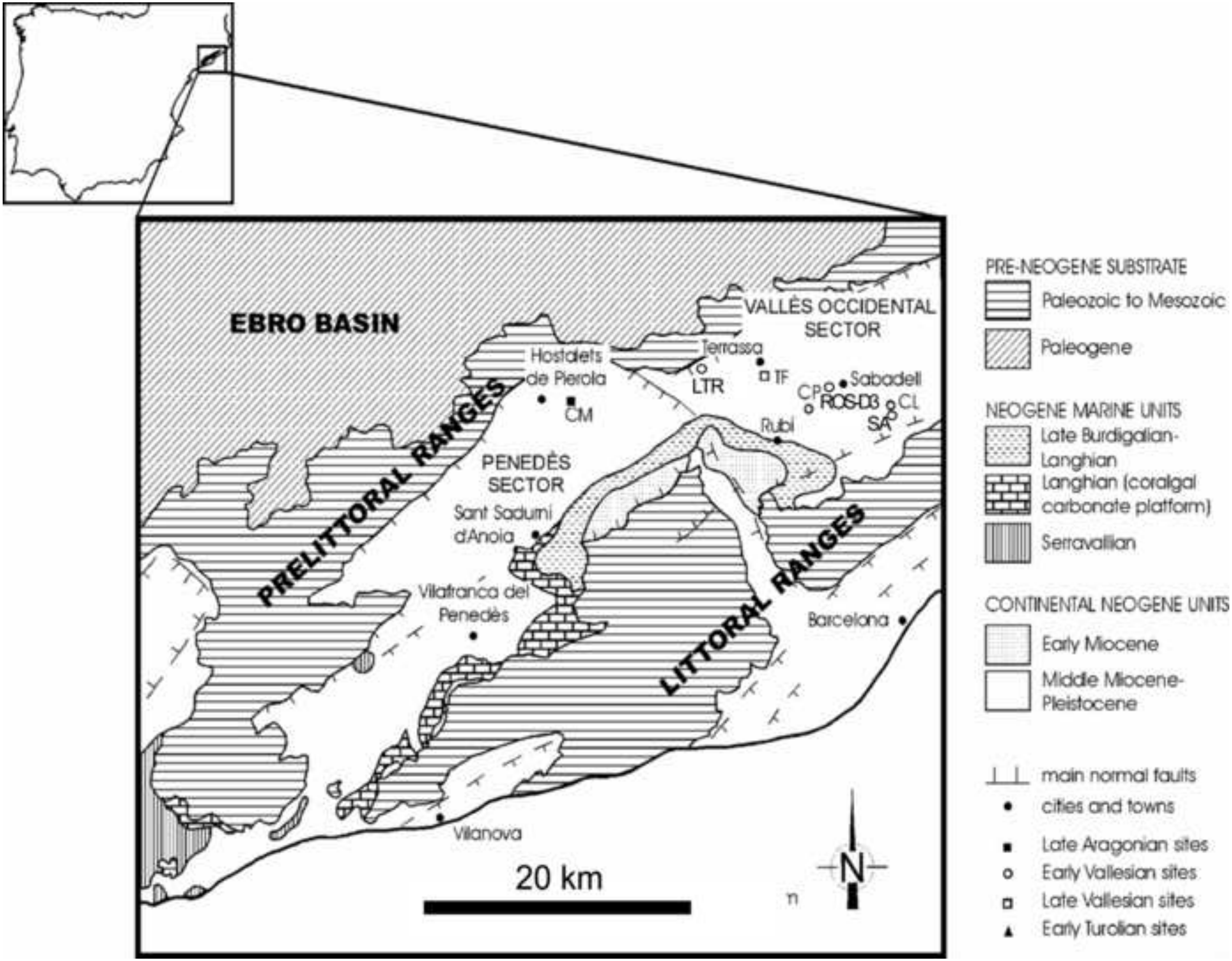

Figure 2

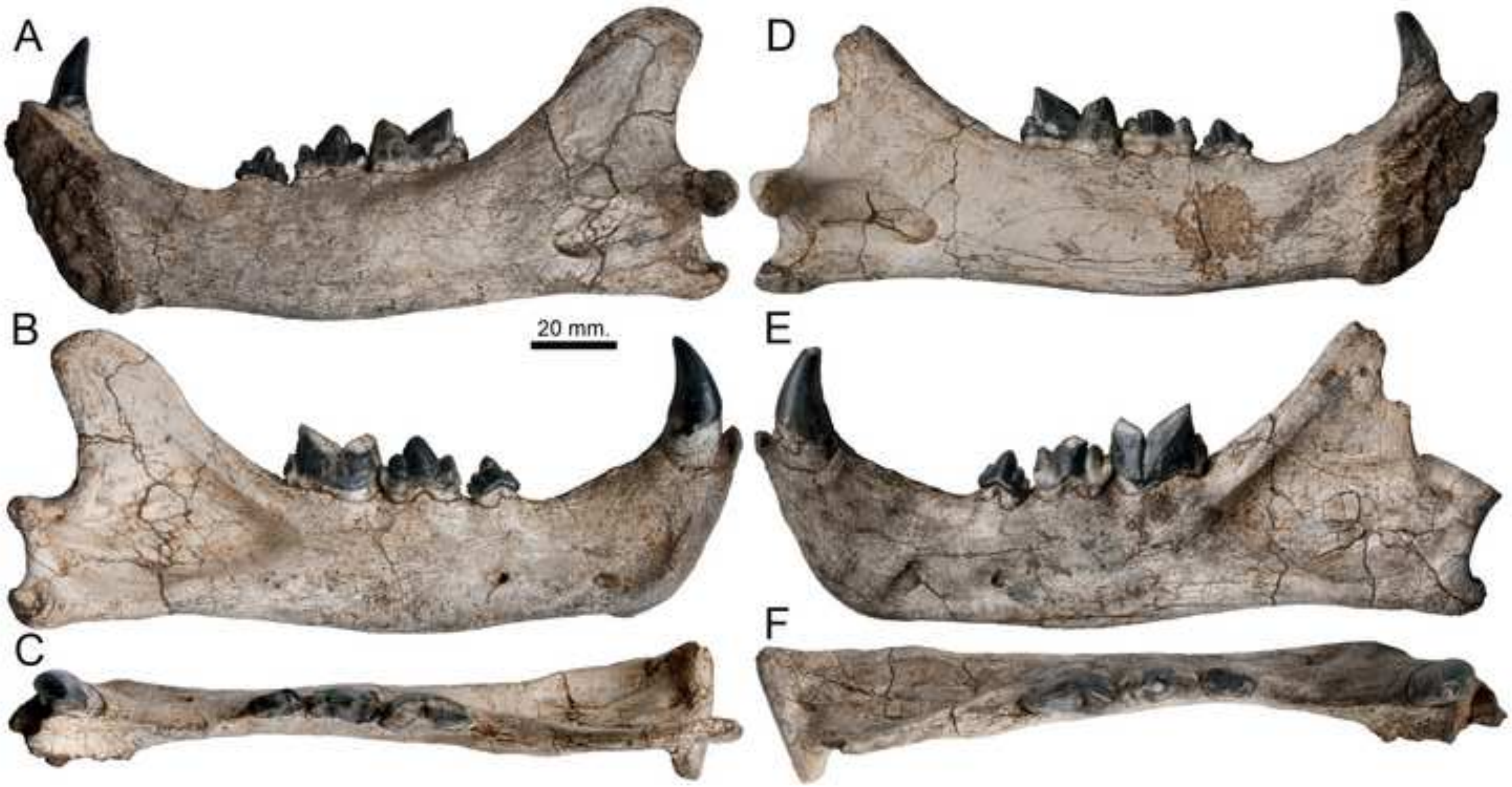

Figure 3

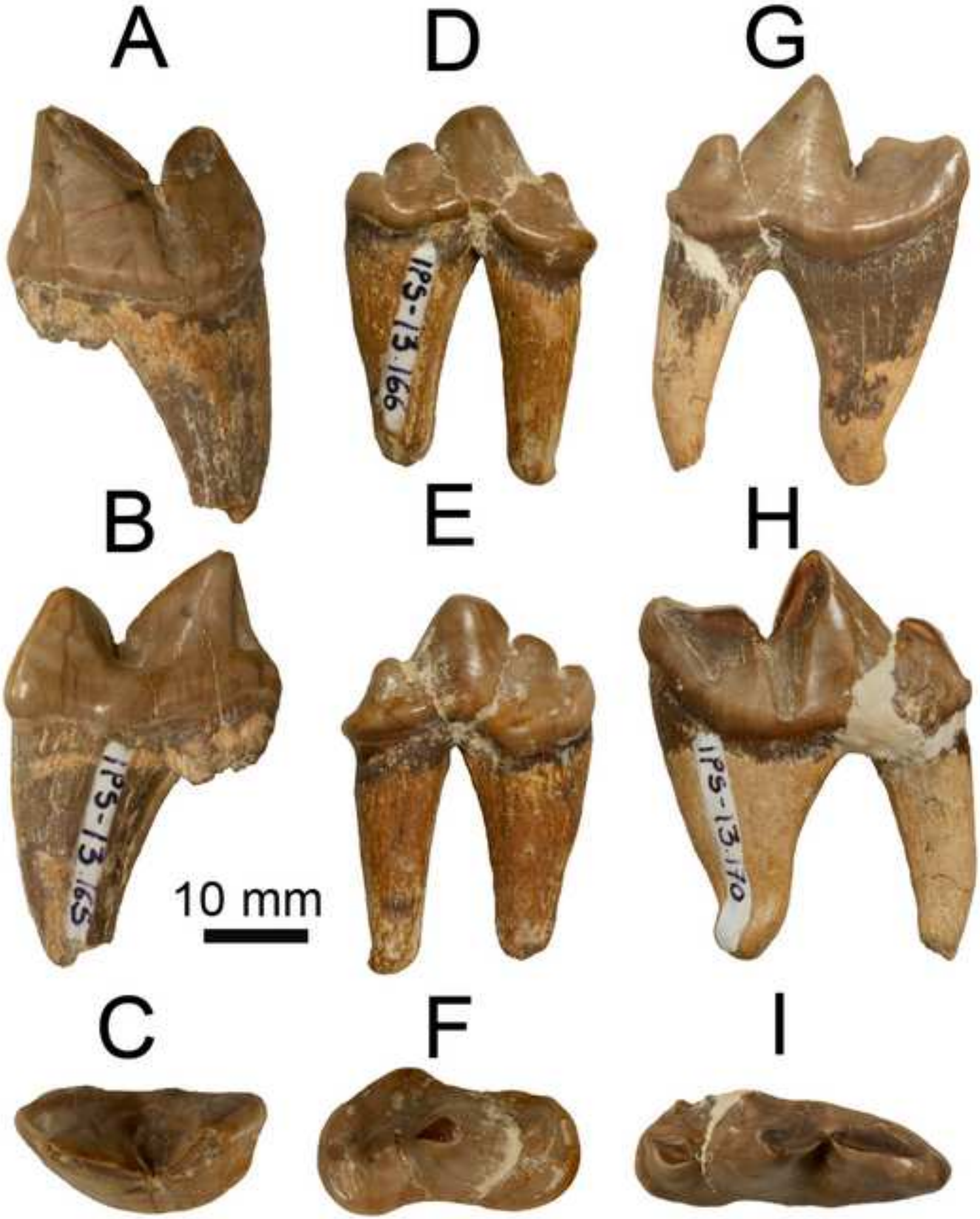

Figure 4

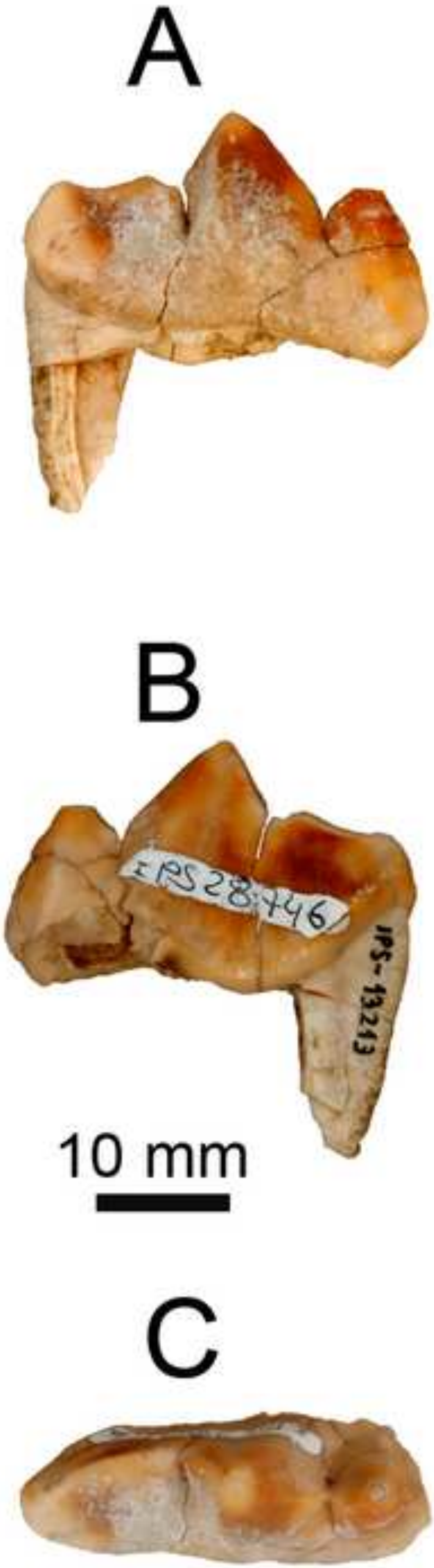

Figure 5

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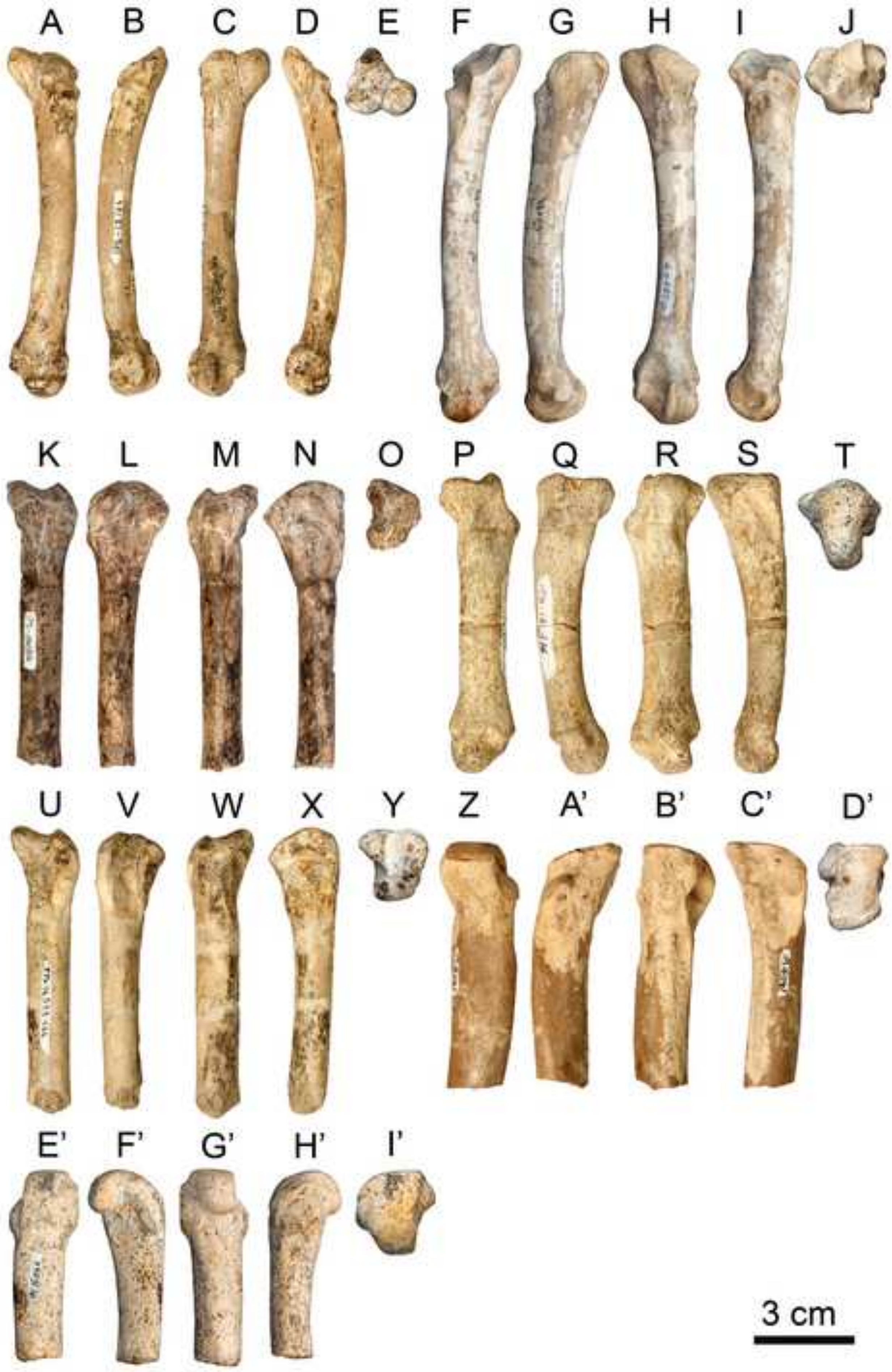


Figure 6

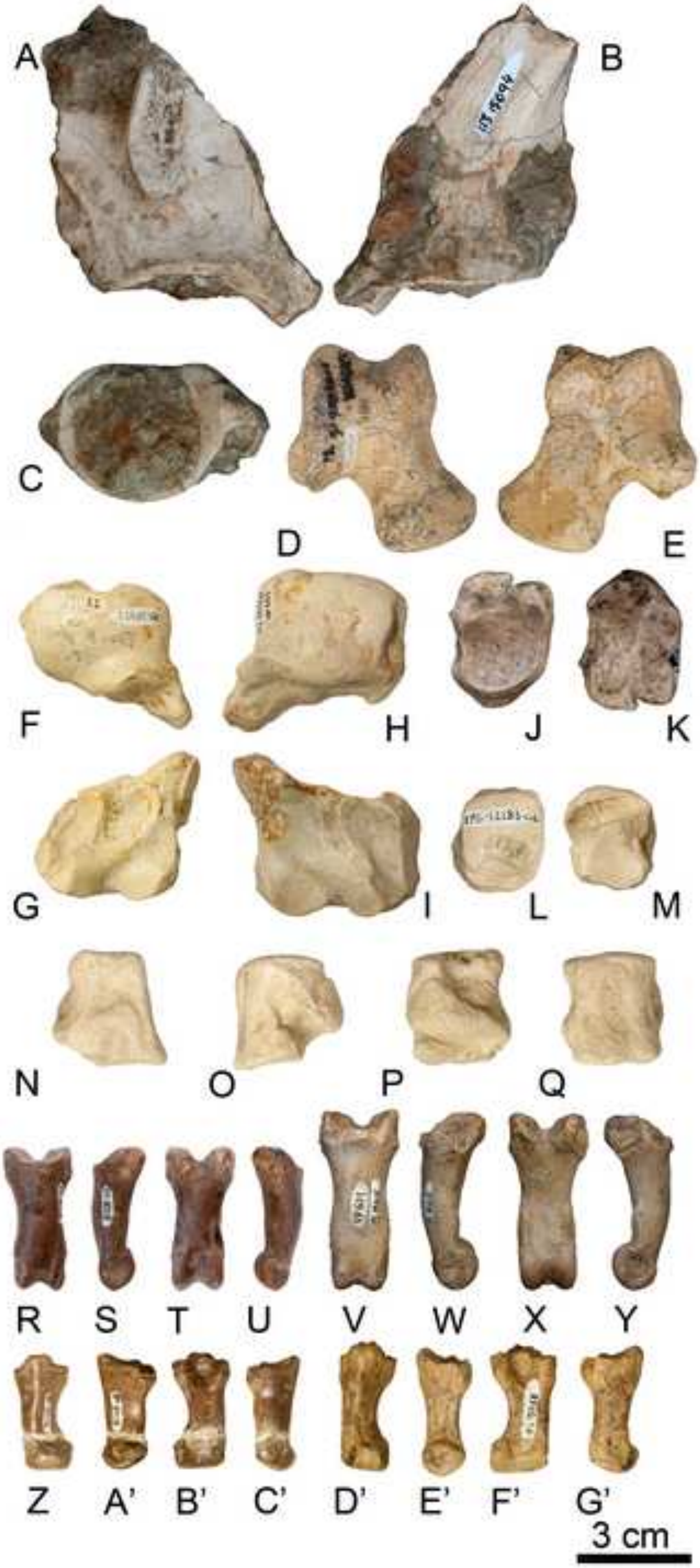
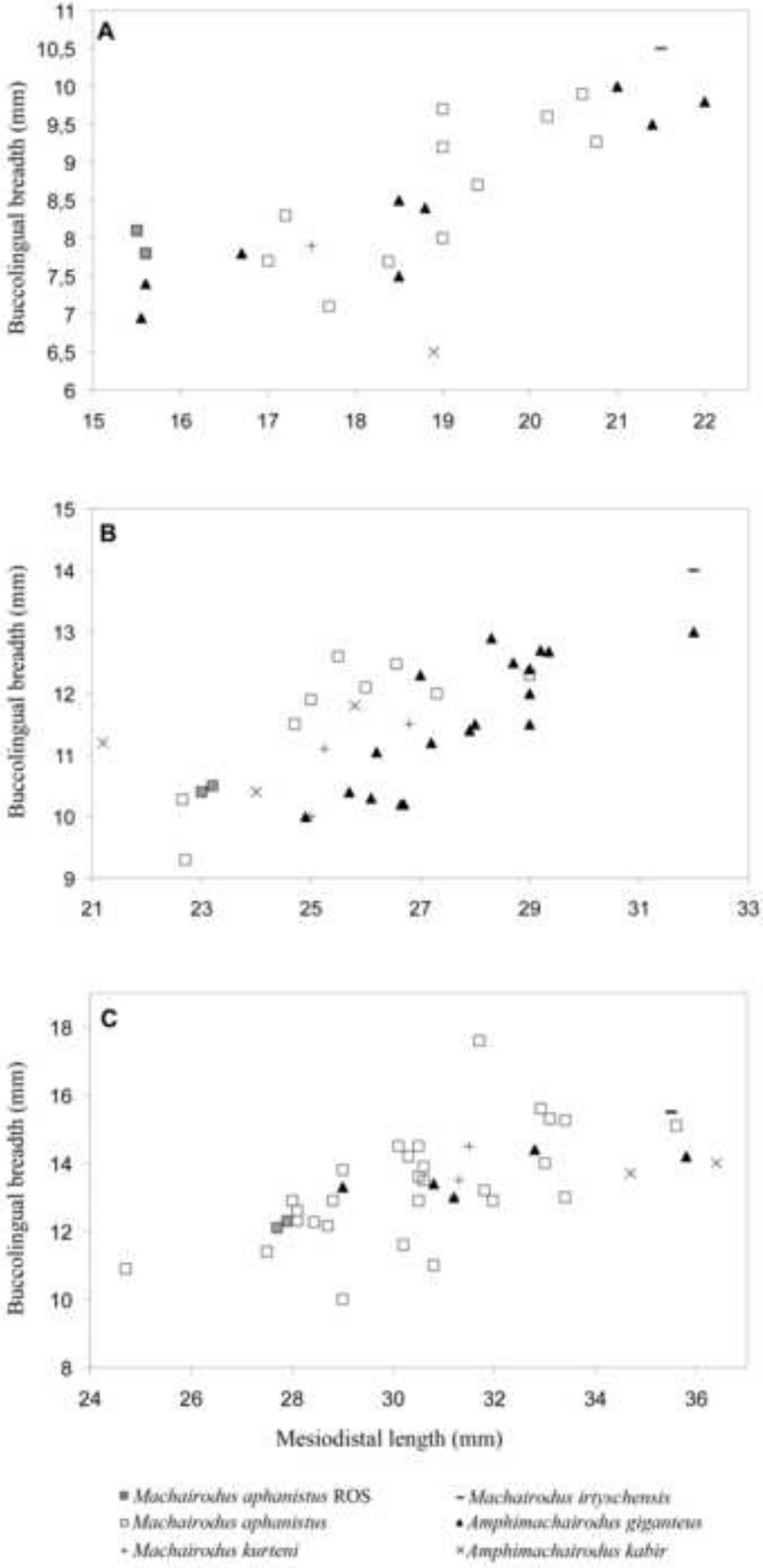


Figure 7


A
Buccolingual breadth (mm)
11
10,5
10
9,5
9
8,5
8
7,5
7
6,5
6
15
16
17
18
19
20
21
22
B
Buccolingual breadth (mm)
15
14
13
12
11
10
9
21
23
25
27
29
31
33
C
Buccolingual breadth (mm)
18
16
14
12
10
8
24
26
28
30
32
34
36
Mesiodistal length (mm)
■ Machairodus aphanistus ROS
□ Machairodus aphanistus
+ Machairodus kurteni
- Machairodus irtyschensis
▲ Amphimachairodus giganteus
× Amphimachairodus kabir

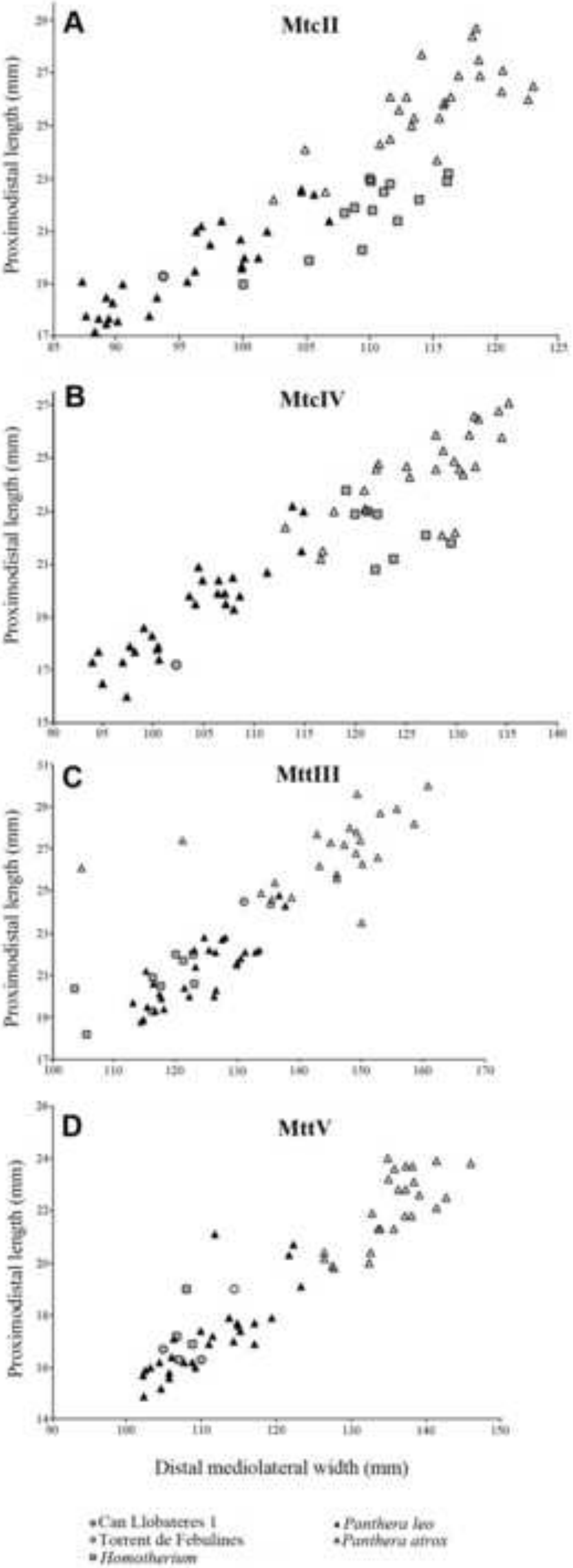

A
MtcII
Proximodistal length (mm)
17
19
21
23
25
27
29
85
90
95
100
105
110
115
120
125
B
MtcIV
Proximodistal length (mm)
90
95
100
105
110
115
120
125
130
135
140
C
MttIII
Proximodistal length (mm)
17
19
21
23
25
27
29
31
100
110
120
130
140
150
160
170
D
MttV
Proximodistal length (mm)
14
16
18
20
22
24
26
90
100
110
120
130
140
150
Distal mediolateral width (mm)
Can Llobateres 1
Torrent de Febulines
Homotherium
Panthera leo
Panthera atrox

Table / Tableau 1

Table 1. Measurements (in mm) of the upper dentition of *Machairodus aphanistus* from the Vallès-Penedès Basin.

		C1			**P3**		**P4**					**M1**	
Catalog No.	**Site**	**L**	**W**	**H**	**L**	**W**	**L**	**W**	**Lps**	**Lpa**	**Lme**	**L**	**W**
IPS13185	SA	24.2	14.1	62.0	23.1	12.9	36.9	18.2	11.4	13.9	14.3	7.0	11.3
IPS13185	SA	24.3	14.7	65.6	21.6	13.9	36.8	21.3	10.3	13.5	14.1	7.9	15.1
IPS13169	CLL1	23.1	12.2	50.0									
IPS13178	CLL1	26.8	13.9										
IPS13166	CLL1				22.2	11.8							
IPS13170	CLL1						33.2		9.1	12.6	11.9		
IPS13164	CLL1						32.9	15.3	8.3	13.2	12.8		
IPS13168	CLL1							15.1	8.2				
IPS15123	CLL1										12.1		
IPS15042	CLL1									12.1	14.1		
IPS28929	TF	30.2	13.7										

Abbreviations: L, mesiodistal length; W, labiolingual breadth; H, crown height; Lps, mesiodistal length of P4 parastyle; Lpa, mesiodistal length of P4 paracone; Lme, mesiodistal length of P4 metastyle. See Materials and Methods for locality abbreviations.

Table / Tableau 2

Table 2. Measurements (in mm) of the lower dentition and mandible of *Machairodus aphanistus* from the Vallès-Penedès Basin.

			c1			**p3**		**p4**		**m1**				
Catalog No.	**Laterality**	**Locality**	**L**	**W**	**H**	**L**	**W**	**L**	**W**	**L**	**W**	**Lpa**	**Lpr**	**Lt**
IPS62083	Left	ROS-D3	17.8	11.1	25.5	15.6	7.8	23.2	10.5	27.7	12.1	13.9	14.4	5.2
IPS62083	Right	ROS-D3	16.8	11.2	27.4	15.5	8.1	23.0	10.4	27.9	12.3	14.7	13.4	4.8
IPS13167	Left	CLL1						21.5	9.9					
IPS13177	Right	CP1						22.3	10.4					
IPS13165	Right	CLL1								26.5	12.5	13.3	12.9	3.2
IPS15032	Right	CLL1									12.5			
Catalog No.		**Locality**	**Ld**	**Lm**	**LSD**	**Hp4**	**Hm1**	**Hd**	**Hr**	**Hs**				
IPS62083	Left	ROS-D3	43.3	211.8	66.4	41.6	41.4	35.0		65.3				
IPS62083	Right	ROS-D3	42.2	208.5	66.3	40.1	41.1	35.4	84.6	64.3				

Abbreviations: L, mesiodistal length; W, labiolingual breadth; H, crown height; Lpa, mesiodistal length of m1 paraconid; Lpr, mesiodistal length of m1 protoconid; Lt, mesiodistal length of m1 talonid; Ld, mesiodistal length of the diastema; Lm, maximum mandibular length; LSD, mesiodistal length of the postcanine tooth row; Hp4, mandibular corpus height at p4; Hm1, mandibular corpus height at m1; Hd, mandibular corpus height at the diastema; Hr, maximum mandibular ramus height; Hs, maximum symphysis height. See Materials and Methods for locality abbreviations.

Table / Tableau 3

Table 3. Measurements (in mm) of the postcranial remains of *Machairodus aphanistus* from the Vallès-Penedès Basin.

Catalog No.	Element	Locality	L	PMLD	MMLD	DMLD	PDPD	MDPD	DDPD	APG	MLG	MLD	MLDp	MLDd	Hm	Hl	DPD	PDD
IPS15094	Scapula	CLL1								44.7	34.6							
IPS11020	Scapholunar	CLL1										43.8					36.9	26.1
IPS28932	Scapholunar	TF										49.1					39.4	27.6
IPS13176	Metacarpal II	CLL1	93.7	23.1	14.4	19.3	24.3	13.7	15.2									
IPS15045	Metacarpal II	CLL1		21.2			23.7											
IPS11381	Metacarpal III	CLL1		20.2	13.1		20.5	11.5										
IPS15061	Metacarpal III	CLL1		19.6			20.8											
IPS16286	Metacarpal III	LTR		22.8	13.1		25.5	11.3										
IPS13172	Metacarpal IV	CLL1	102.3	16.9	12.3	17.2	19.3	11.8	17.6									
IPS15046	Metacarpal V	CLL1		19.9	13.4		21.2	12.0										
IPS11341	Femur	CLL1			29.4			25.8										
IPS30901	Talus	CM											51.2		53.8	39.2		
IPS13171	Calcaneus	CLL1											24.4	30.5	95	87.9		
IPS15077	Navicular	CLL1										25.1					34.7	17.0
IPS11183	Cuboid	CLL1										25.6					31.3	28.8

IPS13173	Metatarsal III	CLL1	131	25.7	17.9	24.5		15.6	23.4
IPS15043	Metatarsal IV	CLL1		18.0	13.2		21.7	13.1	
IPS13175	Metatarsal V	CLL1	110.0	18.7	10.3	16.3	14.8	11.0	16.6
IPS13174	Metatarsal V	CLL1	104.9	20.4	9.6	16.7	16.8	10.6	16.2
IPS28904	Metatarsal V	TF	114.4	23.11	11.0	19	22.3	12.9	19.5
IPS36058	Proximal phalanx	VC		18.7	14.7		16.4	10.2	
IPS15007	Proximal phalanx	CLL1	39.2	19.2	12.8	14.4	14.4	10.7	10.6
IPS15015	Proximal phalanx	CLL1	47.3	20.6	13.9	15.1	17.7	10.9	12.1
IPS15021	Proximal phalanx	CLL1	46.8	20.4	13.9	15.3	16.1	10.8	11.8
IPS15022	Proximal phalanx	CLL1	39.7	17.8	12.9	15.5	15.5	11.3	10.5
IPS15068	Middle phalanx	CLL1	33.3	16.5		14.3	14.1		11.2
IPS15017	Middle phalanx	CLL1	30.7	17.2		14.9	14.2		10.1
IPS15008	Middle phalanx	CLL1	35.4	16.6		15.0	14.3		11.4

Abbreviations: L, proximodistal length; PMLD, proximal mediolateral width; MMLD, mediolateral width at midshaft; DMLD, distal mediolateral width; PDPD, proximal dorsopalmar height; MDPD, dorsopalmar width at midshaft; DDPD, distal dorsopalmar height; APG, anteroposterior diameter of the glenoid cavity; MLG, mediolaterial diameter of the glenoid cavity; MLD, maximum mediolateral diameter;

MLDp, proximal maximum mediolateral diameter; MLDd, distal maximum mediolateral diameter; Hm, medial height; Hl, lateral height; DPD, maximum dorsopalmar height; PDD, maximum proximodistal length.

DISCUSSION AND CONCLUSIONS

Chapter 9. Discussion

This dissertation provides with an updated review of fossil carnivorans from the Miocene of the Vallès-Penedès Basin, based not only on the study of the available fossil material, but also on an extensive review of the previously-published relevant literature. Particular taxa have been studied in greater depth in Chapters 5 to 8 and Appendix 1, mostly from a taxonomic and phylogenetic viewpoint, although chronostratigraphic and paleobiogeographic implications are further discussed. Given that each chapter bears its own discussion and conclusions, these will not be restated but merely summarized here. This chapter is therefore more focused on the overall taxonomic revision of Miocene carnivorans from the Vallès-Penedès Basin as a whole (see Appendix 2 for further details). This revision (Tables 9.1 and 9.2) represents a considerable update compared to the synthesis provided by Pons-Moyà (1990). The latter represents the most recent publication specifically devoted to the carnivoran record from the Miocene of the Vallès-Penedès Basin, although other subsequent publications further reported carnivoran records in the form of faunals lists (Moyà Solà & Rius Font 1993; Agustí et al. 1997; Agustí & Galobart 1997; Garcés et al. 1997; Gómez-Alba 1997; Checa Soler & Rius Font 2000; Alba et al. 2006, 2007, 2009, 2010a,b, 2011a,b,c; Casanovas-Vilar et al. 2006, 2008, 2011a,b,c,d; Casanovas-Vilar 2007; Carmona et al. 2011; see also Chapters 5 to 8 and Appendix 1).

The most representative sites with carnivorans from the Vallès-Penedès Basin are contextualized from a biostratigraphic viewpoint in Chapter 4, which is focused on hominoid-bearing localities from Western Eurasia. The main stratigraphic sections of the Middle to Late Miocene of the Vallès-Penedès Basin are thus correlated with those from the rest of Europe, since this is a critical time span for the evolutionary radiation of hominoid primates in Western Europe. The information provided in the remaining Chapters 5 to 8 and Appendix 1 is summarized and integrated with data from other taxa in Table 9.1, which lists all the families, genera and species of carnivorans considered to be present in the Miocene of the Vallès-Penedès Basin. Their updated taxonomic attribution, together with previously-published ones assignments (e.g., synonyms) are specified, further indicating their locality of provenance, their approximate chronostratigraphic range, as well as the various published sources as superscripts (including Chapters 5 to 8 and Appendix 1). For practical reasons, localities within some local stratigraphic series (such as ACM, B40OV and ROS) are not detailed. In part, changes in the taxonomic attribution stem from revisions in the taxonomy of many of the reported taxa, but to a large extent they also correspond to corrections of previous taxonomic assignments.

In Table 9.2, the information provided in Table 9.1 is summarized, by providing the citations per locality of each of the various carnivoran taxa from the Miocene of the Vallès-Penedès Basin. During the Early Miocene, i.e., the Ramblian (MN3) and the early Aragonian (MN4), only a few carnivoran families are recorded in the Vallès-Penedès Basin (they are not recorded before, because no older deposits are available in the basin; Casanovas-Vilar et al. 2011a,c). In the MN3, only scarce carnivoran remains (commonly not attributable to genus and species, corresponding to families Felidae, Viverridae, Amphicyonidae and Mustelidae) are recorded in this basin (mainly from Molí Calopa). The record of these families during the MN3 in the Vallès-Penedès thereby contrasts with their much richer record during the MN4, in which the carnivoran guild is dominated by Amphicyonidae of subfamily Amphicyoninae (genera *Amphicyon*), Felidae of subfamily Felinae (genera *Styriofelis* and *Pseudaelurus*) and small Mustelidae of subfamilies Mustelinae (*Martes*) and Gulolinae (*Iberictis*). There are also some remains attributed to the Viverridae and Hyaenidae of subfamily Ictitheriinae (*Protictitherium*). All these families are well represented in Els Casots, and to a lesser extent in Can Canals.

The extreme scarcity of carnivoran records in the Vallès-Penedès Basin during the middle Aragonian (MN5–MN6) is due to the virtual lack of continental deposits, as a result of several marine transgressions that occurred during this time span (Casanovas-Vilar et al. 2011a). Nevertheless, a few carnivoran remains have been recovered from Ca n'Almirall (MN5?-MN6). Subsequently, in the late Middle Miocene (late Aragonian, MN7+8), carnivoran paleobiodiversity becomes higher than before (including the MN4), with new species, genera and even subfamilies of felids and, especially, viverrids and mustelids, being first recorded. Moroever, by this time ursids and barbourofelids make their first appearance in the basin, and hyaenids show a particularly high diversity. Some of the carnivorans recorded in the late Aragonian and/or early Vallesian are endemic of the Vallès-Penedès Basin, such as the viverrids *Semigenetta grandis* and *Semigenetta ripolli*, the hyaenid *Thalassictis montadai*, and the mustelids *Limnonyx sinerizi* and *Palaeomeles pachecoi*. In contrast, the diversity of amphicyonids during this time interval decreases compared to the Early Miocene, whereas hemicyonids progressively become less abundant during the Middle Miocene, until they become extinct in the basin during the early Vallesian. The great diversity of Vallès-Penedès carnivorans during the Middle Miocene is best reflected in more than a hundred localitites from the stratigraphic series of ACM (and some classical localities from els Hostalets de Pierola, such as Can Mata 1), and to a lesser extent in other localities from the areas of Sant Quirze.

The early Vallesian (MN9) has long been considered a hotspot of mammalian paleobiodiversity in the Vallès-Penedès Basin, and available data for carnivorans confirm that there is an increase in diversity from the late Aragonian to the early Vallesian. Given that the number of carnivoran-bearing localities from these time intervals is similar (12 in the MN7+8 and 11 in the MN9), this is likely to reflect an actual peak in carnivoran diversity. All the carnivoran families previously present during the Early Miocene in the Vallès-Penedès Basin are still recorded in the early Vallesian. Ailurids are first recorded in the Vallès-Penedès Basin by this time. The highest number of carnivoran taxa is recorded at Can Llobateres 1 and, to a lesser extent Castell de Barberà (formerly attributed to the MN7+8, but here referred to the MN9) and Can Poncic 1. Can Llobateres 1 shows faunal similarities in the carnivoran taxa with coeval localities from other Iberian basins, such as Los Valles de Fuentidueña (MN9) in the Duero Basin (Segovia) (Alberdi Alonso 1981; Ginsburg et al. 1981; Fraile et al. 1997). Can Llobateres 1, in particular, records 9 families, 15 genera and 16 species of carnivorans, whereas Los Valles de Fuentidueña records 5 families, 11 genera and 11 species. This indicates a somewhat higher diversity in Can Llobateres 1 (due to the presence of some endemic taxa, especially mustelids), but further suggests that the peak in carnivoran paleobiodiversity during the early Vallesian is not restricted to the Vallès-Penedès Basin.

The high mammalian paleobiodiversity recorded during the early Vallesian (MN9) is followed by a drastic decrease in the late Vallesian (MN10), with carnivorans being best represented at La Tarumba 1 (Viladecavalls) and, to a lesser extent, Torrent de Febulines (Terrassa). This purported faunal turnover, occurred during the Vallesian (termed the 'Vallesian crisis'; Agustí & Moyà-Solà 1990; Casanovas-Vilar et al. 2010) and, among macrommals, affecting mainly medium-sized taxa (such as hominoid primates, small suoids, cervids and mustelid carnivorans), has been considered to reflect an actual biodiversity crisis that might be related to the progressive climatic cooling (and associated paleoenvironmental changes) accentuated by this time (Agustí & Moyà-Solà 1990; Fortelius et al. 1996; Agustí et al. 1997, 1999, 2003, 2013; Fortelius & Hokkanen 2001; Domingo et al. 2014). However, sampling artifacts should be taken into account so as to be more certain about the timing and extent of this purported faunal turnover. For example, studies based on micromammals (rodents and insectivores) have shown that the abrupt diversity decrease between the MN9 and MN10 is largely a sampling effect, suggesting that the faunal turnover was more progressive and extended in time (Casanovas-Vilar et al. 2014). Therefore, additional analyses would be required to confirm that the peak in carnivoran diversity during the MN9, and the subsequent drastic diversity drop in the MN10, are not largely an artifact of the record caused by a sampling bias. The latter possibility is not supported by the number of carnivoran-bearing localities known from these intervals (11 in the MN9 and 15 in the MN10), but it still remains a valid possibility in the light of the extraordinary sampling effort devoted for many decades to some MN9 sites (especially Can Llobateres 1; Begun et al. 1990; Alba et al. 2011b,c; Galobart et al. 2011). In any case, some faunal turnover surely took place during the Vallesian, since in the MN10 various carnivoran families (Viverridae, Barbourofelidae, Herpestidae, Amphicyonidae, Hemicyonidae, Ursidae, Ailuridae and Mephitidae) are no longer recorded at the Vallès-Penedès Basin. The most important drop in diversity, however, concerns the mustelids, recorded by 9 genera and 12 species until the end of the MN9, but only by 1 genera and 1 species during the MN10. Moreover, the diversity of carnivorans as a whole during the MN10 in the Vallès-Penedès Basin is low compared to that in other Iberian basins (such as Madrid and Teruel), in which hyaenids and felids are also the best represented families. For example, La Tarumba 1 records 2 families, 4 genera and 4 species of carnivorans (Table 9.2), whereas at Cerro de los Batallones there are 6 families, 13 genera and 9 species recorded (Morales et al. 2008; Abella et al. 2011; Valenciano et al. 2013).

This trend of decreasing mammalian paleobiodiversity is further accentuated in the Turolian (MN12), in which carnivorans also reach their lowest paleobiodiversity in the Vallès-Penedès Basin. Thus, carnivorans are not recorded in any MN11 Vallès-Penedès locality, and they are only recorded in 3 localities from the MN12. By this time, carnivorans are merely represented by Hyaenidae and Felidae, which are best represented in Torrentet de Traginers (Piera; classically attributed to the MN11, but here reassigned to the MN12, following a recent restudy of the rodent assemblage; Casanovas-Vilar, pers. com.). Unlike in the MN9/MN10 transition, the drastic decrease diversity in carnivoran diversity from the MN10 to the MN12 is paralleled by a decrease in the number of carnivoran-bearing localities in the basin (from 15 to only 3), suggesting that diversity counts might be distorted to some extent by a sampling bias. Carnivoran diversity in the Vallès-Penedès during the Turolian is somewhat lower, at the species and genus level, than that from other Iberian basins, with 3 genera and 3 species being recorded at Torrentet de Traginers, compared to 5 genera and 4 species at Puente Minero (MN11, Teruel Basin; Alcalá et al. 1991) and 5 genera and 6 species at Crevillente 2 (MN12; Alcalá et al. 1991). The two latter localities are also clearly more diverse at the family level, by further including ursids and mustelids, whereas only felids and hyaenids are recorded at Torrentet de Traginers.

Overall, during the whole Miocene of the Vallès-Penedès Basin (MN3 to MN12), 11 carnivoran families are recorded (Amphicyonidae, Hemicyonidae, Mustelidae, Felidae, Viverridae, Hyaenidae, Ursidae, Ailuridae, Mephitidae, Herpestidae and Barbourofelidae). The Canidae were formerly recognized in the MN9 localities of Can Poncic 1 and Can Llobateres 1 based on postcranial material (Crusafont-Pairó & Golpe-Posse 1973b; Crusafont Pairó & Kurtén 1976, respectively), but following the revision of the material provided in this dissertation, these remains are reassigned to the Ursidae. A summary of the record of each one of the five above-mentioned carnivoran families in the Vallès-Penedès Basin is provided below.

Viverridae. In the Vallès-Penedès Basin, viverrids (genets and related taxa) are first recorded in the early Aragonian (MN3), extending their range until the late Vallesian (MN10). The earliest remains are attributed only to family. Later on, the Viverrinae, which are represented by genus *Semigenetta*, is recorded in late Aragonian (MN7+8) localities, such as those from the Abocador de Can Mata series and the area of els Hostalets de Pierola. This subfamily attains its highest diversity during the early Vallesian (MN9), being last recorded in the late Vallesian (MN10) locality of Torrent de Febulines.

Barbourofelidae. The members of this family ('false sabertooths') were traditionally included into the Nimravidae, but currently they are distinguished as a distinct family, which evolved a saber-toothed morphotype independently from both nimravids and machairodontines. In the Vallès-Penedès Basin, barbourofelids are recorded by a single genus and species, *Albanosmilus jourdani*, which is recorded during the late Aragonian (MN7+8) and the early Vallesian (MN9), thereby overlapping with true saber-toothed cats (machairodontines) by the earliest Miocene. In Chapter 6, this taxon is revised based on all the remains available from the Vallès-Penedès Basin, including previously-unpublished remains from Abocador de Can Mata, which show previously unknown morphological details of this taxon. On this basis, an emended diagnosis of this species is provided, and the genus *Albanosmilus* is resurrected, given the extent of the cranial differences with the type species of genus *Sansanosmilus*, in which it was formerly included. Based on the newly-reported remains, a cladistic analysis of the family is also performed in Chapter 6. This analysis supports the monophyly of tribe Barbourofelini (genera *Sansanosmilus*, *Albanosmilus* and *Barbourofelis*), which contrasts with the paraphyletic status of the more primitive tribe Afrosmilini. Among barbourofelins, *Albanosmilus* is more derived than the

Eurasian *Sansanosmilus*, but more primitive than most of the North American *Barbourofelis* spp. However, the North American species *"Barbourofelis" whitfordi* does not show significant differences from *A. jourdani*, being thus reallocated in genus *Albanosmilus*, and suggesting that the *Barbourofelis* clade originated from an *Albanosmilus*-like ancestor that dispersed from Eurasia into North America sometime during the late Aragonian or early Vallesian.

Felidae. Together with mustelids, felids (true cats) are extensively recorded from the Ramblian (MN3) to the Turolian (MN12) in the Vallès-Penedès Basin. Two subfamilies are recorded, felines and machairodontines. Felines (conical-toothed cats) are the first felids in the basin, raging from the MN3 to the MN9. Two different genera with four species are recorded in the Vallès-Penedès Basin: *Styriofelis turnauensis*, *Styriofelis lorteti*, *Pseudaelurus romieviensis* and *Pseudaelurus quadridentatus*. In Chapter 7, new remains of these genera from various localities from Abocador de Can Mata (MN7+8) are described, and the chronostratigraphic range of the various included species in the Vallès-Penedès is revised. This study further shows that some features, previously considered diagnostic among *Pseudalurus* spp., are no longer valid from a taxonomic viewpoint, although the two species recorded in the Vallès-Penedès can be distinguished based on both size and other occlusal details. The description of these feline remains also considerably extend the previously-known range of *P. romieviensis* in the Vallès-Penedès Basin. The last feline recorded in the Vallès-Penedès Basin is *P. quadridentatus*, which in the MN9 overlaps with members of subfamily Machairodontinae (saber-toothed cats). Although *P. quadridentatus* has been frequently considered as the origin of the machairodontine radiation, the former still lacks the more markedly-compressed upper canines and associated saber-like morphology typical of the Machairodontinae. In the Vallès-Penedès Basin, machairodontines are recorded from the early Vallesian (MN9) to the middle Turolian (MN12), being represented by members of various tribes: the Machairodontini (genus *Machairodus*) in the MN9 and MN10; the Smilodontini (cf. *Promegantereon*) in the MN10; and the Metailurini (genus *Stenailurus*) in the MN12. Accordingly, only the machairodontine tribe Homotheriini would not be recorded in the Vallès-Penedès Basin. In Chapter 8, new remains of *Machairodus aphanistus* from this basin are described, including that from some new localities of Ronda Oest Sabadell and els Hostalets de Pierola. Furthermore, carnivoran remains from Creu Conill are removed from the hypodigm of this taxon, which has some relevant consequences for the age of first local apparance of this taxon in the Vallès-Penedès Basin. The postcranial remains described in this study enable to make some locomotor inferences for *Machairodus*, according to which it would be less cursorial (less adapted for long-distance travel and high-speed hunting) than its putative descendant, the homotheriin *Homotherium.*

Hyaenidae. Like felids, hyaenids (hyenas) show an extensive record in the Vallès-Penedès Basin, ranging from the early Aragonian (MN4) to the middle Turolian (MN12). However, unlike the former, hyaenids display a high diversity, with more genera and species recorded in this basin than any of the remaining carnivoran families. In particular, hyaenids are recorded by 6 genera from two subfamilies in the Vallès-Penedès Basin: the Hyaeninae (genera *Hyaenictis* and *Adcrocuta*) from the MN10 to the MN12 and the Ictitheriinae (genera *Thalassictis*, *Hyaenictitherium*, *Plioviverrops* and *Protictitherium*) from the MN4 to the MN12. The largest hyaenid diversity in the basin is attained during the late Aragonian (MN7+8) and the early Vallesian (MN9), when many small to medium-sized ictitheriine taxa are recorded. Hyaenines are larger and less diverse, being represented only by two species that are restricted from the late Vallesian (MN10) to the middle Turolian (MN12).

Herpestidae. Herpestids are represented by a single genus (*Leptoplesictis*) with 2 species from the early Aragonian (MN4) until the arly Vallesian (MN9). The earliest herpestid in the basin is *Leptoplesictis aurelianensis*, recorded in localities such as Els Casots, Costablanca and El Canyet. In the late Aragonian (MN7+8) and early Vallesian (MN9), this genus is represented by *Leptoplesictis filholi* from the area of els Hostalets de Pierola. The low diversity of this family contrasts with its wide range in the Vallès-Penedès Basin across the whole Miocene.

Amphicyonidae. Amphicyonids ('bear-dogs') are the most widely represented carnivorans in the Early Miocene of the Vallès-Penedès Basin, being recorded during the MN3 in Molí Calopa and in multiple MN4 localities (such as Les Cases de la Valenciana and Els Casots) by scarce isolated dental remains mostly attributable to either the medium-sized genus *Amphicyon* or the small-sized genus *Ictiocyon*. The range of this family further extends until the early Vallesian (MN9), in which the largest genus of this family (*Magericyon*) and the rarer *Thaumastocyon* are both recorded at Can Llobateres 1. Unlike in other Iberian basins, in the Vallès-Penedès amphicyonids are no longer recorded from the MN9-MN10 onwards (thus being one of the taxa that presumably became locally extinct as a result of the Vallesian Crisis).

Hemycionidae. Formerly, this family ('dog-bears') had been merely recognized as an ursid subfamily, although currently they are distinguished as a separate family, given their hypercarnivorous adaptations. In the Vallès-Penedès, hemicyonids are recorded from the

MN4 (*Plithocyon conquense* from Els Casots) to the MN7+8 (*Hemicyon goeriachensis* from HP), in agreement with their record from elsewhere in Iberia (from the MN2 to the MN9). Hemicionids decrease in diversity during the Middle Miocene, becoming extinct during the Late Miocene of the Vallès-Penedès Basin.

Ursidae. True bears are recorded in the Vallès-Penedès Basin from the late Aragonian (MN7+8) to the late Vallesian (MN10), including members of the genus *Ursavus* (subfamily incertae sedis) from the MN9; and the subfamily Ailuropodinae (genera *Kretzoiarctos* and *Indarctos*) from the MN7+8 to the MN10. In the Vallès-Penedès Basin, *Ursavus* is only poorly known, and additional studies will be required to further clarify its taxonomic identity and phylogenetic relationships. The last recorded ursid in this basin corresponds to the ailuropodid genus *Indarctos*, recorded both in the early and late Vallesian (MN9 and MN10). In contrast, the earliest record of this family in the Vallès-Penedès corresponds to genus *Kretzoiarctos*, which is described in Appendix 1, based on new ACM remains (MN7+8) for the species previously referred to as *Agriarctos beatrix*. Also, a new tribe (Indarctini) is erected in Appendix 1 for the genus *Indarctos*. A cladistic analysis of extant and extinct ursid genera performed in Appendix 1 confirms that *Kretzoiarctos* is (like other extinct genera, namely *Agriarctos* and *Ailurarctos*) more closely related to extant giant pandas (tribe Ailuropodini) than to indactins, the former further representing the oldest recorded member of the giant panda lineage.

Ailuridae. In the Vallès-Penedès Basin, ailurids (relatives of the extant lesser panda) display a similar temporal range to ursids, i.e., from the early Vallesian (MN9) to the late Vallesian (MN10), but a mcuh lower diversity. Thus, ailurids are only represented in this basin by one genus with a single species (*Simocyon batalleri*), besides some remains from Can Llobateres 1 merely attributed to Ailuridae indet. The finds of *Simocyon* are isolated and lack a clear stratigraphic provenance, so that the stratigraphic range of this family in the Vallès-Penedès Basin is restricted but unclear.

Mephitidae. In the Vallès-Penedès Basin, mephitids (skunks and related taxa) are recorded by three species (*Plesiomeles cajali*, *Mesomephitis medius* and *Promephitis pristinidens*), whose fossil remains are scarce but relatively well-represented in various localities from late Aragonian (MN7+8) to the late Miocene (MN10). The genera *Plesiomeles* and *Mesomephitis*, described on the basis of dental remains, are restricted to the Vallès-Penedès Basin. Due to the fragmentary nature of the available remains, their phylogenetic relationships with other mephitids remain currently unclear, and a revision in greater depth of the family is required in the future to confirm some of the taxonomic attributions.

Mustelidae. Mustelids (including otters, badgers, weasels, martens, and other related taxa) are the most widely recorded carnivoran family in the Vallès-Penedès Basin. They are first recorded in the Ramblian (MN3) and early Aragonian (MN4), mainly by subfamilies Mustelinae (*Martes*) and Gulolinae (*Iberictis* and *Ischyrictis*). The genus *Martes*, in fact, is the best represented genus of the whole family (5 species), with its chronostratigraphic range extending until the MN10. Melines are also represented in the Vallès-Penedès, with 2 genera and 2 species restricted to the MN7+8 and MN9. The taxonomic knowledge on this subfamily is however too provisional, and a revision in greater depth is required in the future to confirm some of the taxonomic attributions presented here, as well as to further decipher their phylogenetic relationships. Finally, the subfamilies Lutrinae and Leptarctinae are recorded during the late Aragonian (MN7+8) and early Vallesian (MN9), being represented by a single genus and species each: *Lymnonyx sinerizi* (Lutrinae) and *Trocharion albanense* (Leptarctinae). The latter taxon has been reviewed in Chapter 5 of this dissertation, based on previously-unpublished remains from Abocador de Can Mata. The new material enables to better describe the dental, mandibular and cranial morphology of this taxon, including features of the skull that were previously unknown (such as the double rhomboid morphology of the temporal crests). A phylogenetic analysis including other leptarctines and basal mustelids, and further incorporating the newly reported features for *Trocharion*, indicate that this taxon is the basal-most member of this subfamily, as shown among others by the retention of first upper and lower premolars. Interestingly, like basal mustelids, *Trocharion* retains a carnassial notch (an indentation in the upper carnassial or P4), which apparently was independently lost is other leptarctines as well as in other more derived mustelids. In the Vallès-Penedès Basin, mustelids attain their highest diversity in the early Vallesian (MN9), being represented by a plethora of genera and species, many of them restricted to the Vallès-Pendès Basin or even a single locality (such as *Marcetia santigae* and *Hoplictis petteri* from Can Llobateres 1). This contrasts with the much reduced number of mustelids recorded during the late Vallesian (MN10), with *Martes melibulla* and *Martes* sp. being the last mustelids recorded in this basin, and this family being no longer recorded from the Turolian of the Vallès-Penedès.

Table 9.1. Updated taxonomy of Miocene carnivorans from the Vallès-Basin Basin, indicating the revised taxonomic attributions as well as the previous taxonomic allocations for the material from each locality.

Family	Current attribution	Previous citations	Localities	Range
Carnivora	Carnivora indet.	Carnivora indet.[3, 4, 48, 80]	CAL[3, 4, 48, 80]	MN5?-MN6
Viverridae	Viverridae indet. [3, 13, 24, 26, 27, 43, 80]	Viverridae indet. (mida petita) [48]	ACM [80] CC [48] ECM[13] LCV [24, 48] MC [3, 24, 26, 27, 43]	MN3–MN9
		Herpestes cf. *dissimilis* [48]		
	Semigenetta sansaniensis [3, 4, 23, 24, 48, 50, 51, 75]	*Plesictis* sp. (?) [16, 24, 69, 70, 75]	CM1 [23, 38, 43, 48, 50, 51, 70] HP [3, 4, 16, 24, 50, 69, 70, 73, 75]	MN7+8–MN9
		Viverra sansaniensis [16, 43, 50, 69, 70]		
		(?) *Plesictis mutatus* [43, 48, 50, 51, 73, 75]		
		Semigenetta mutata [24, 48]		
	Semigenetta cf. *sansaniensis* [80]	cf. *Semigenetta* sp. [8]	ACM [8, 80] TF [8]	MN7+8-MN10
	Semigenetta ripolli [12, 50, 51, 57]	*Semigenetta mutata* [30, 32, 38, 40, 43, 48]	CLL1 [12, 30, 32, 38, 40, 43, 48, 50, 51, 57]	MN9
	Semigenetta grandis [43, 50, 51]	Viverridae indet. [37, 48]	CB [37, 43, 48, 50, 51]	MN9
Barbourofelidae	*Albanosmilus jourdani* [23, 42, 62, 70, 71, 75, 76]	*Machairodus ogygius* [15]	ACM [7, 8, 9, 11, 17, 18, 62] CB [45, 48, 62] CCN20 [5, 62] CLL1 [6, 12, 32, 40, 45, 62] CM1 [4, 23, 38, 48, 62, 70] CMS [4, 62] CP1 [6, 24, 38, 42, 45, 48, 62] HPI [3, 6, 24, 25, 61, 62, 75, 79] SA [44, 62] SQ [3, 15, 23, 24, 48, 62, 68, 70, 71,	MN7+8–MN9
		Felidae indet. [45]		
		Machairodus andresi [69]		
		Albanosmilus jourdani var. *andresi* [70]		
		Grivasmilus jourdani[24, 25, 38, 40, 48, 79]		
		Machairodus sp. [24, 32]		
		Sansanosmilus jourdani vallesiensis [45]		
		Sansanosmilus jourdani [3, 4, 5, 6, 7, 8, 9, 11, 12, 17, 18, 61]		

			[76, 79]	
Felidae	Felidae indet.[80]	Felidae indet.	ACM[80], CB[80], CLL1[80], CP1[80]	MN7+8-MN9
	‘*Felis vireti*‘ (nomen dubium)	*Felis vireti* [3, 24, 27, 31, 48]	CJ [4, 24, 27, 31, 48] LTR1 [3, 48] MC [3, 4, 24, 27, 31, 48]	MN3–MN10
		Viverridae indet [3, 4, 48]		
	Pseudaelurus quadridentatus [8, 16, 23, 24, 38, 48, 57, 63, 69, 70, 75]	Felidae indet. [68]	ACM [8, 63] CB [57] CCN20 [80] CM1 [4, 23, 38, 48, 70] CP1 [38] HP [70] HPI [16, 24, 69, 75] SQ [80]	MN7+8–MN9
		Pseudaelurus marini [4, 23, 24, 48, 70, 75, 80]		
	Pseudaelurus romieviensis [63]	*Pseudaelurus* sp. [7, 9, 11, 17]	ACM [7, 9, 11, 17, 20, 63] CS [20] SM [20]	MN4–MN7+8
		Prosansanosmilus sp. [20]		
	Styriofelis sp.	Carnivora indet. (small size) [33, 48]	CBL [20, 33, 46, 48] CC [20, 25, 29] EC [20, 48]	MN4
		Pseudaelurus turnauensis [25, 29, 48]		
		?*Pseudaelurus* sp. (small size) [46]		
		Pseudaelurus sp. [20]		
	Styriofelis turnauensis [63]	*Pseudaelurus transitorius* [16, 48, 69, 70, 75]	ACM [8, 18, 63] CB [57] CC [48] CV [22, 48] HPI [3, 16, 24, 63, 69, 70, 75] SB [5, 18, 20] SC [22, 24] VV [24, 27, 48]	MN3–MN9
		Pseudaelurus turnauensis [5, 7, 18, 22, 24, 27, 28, 48, 57]		
		Pseudaelurus spp. [3, 20]		
	Styriofelis lorteti	*Pseudaelurus lorteti* [3, 24, 25, 48]	SM [3, 24, 25, 27, 48]	MN4
		Pseudaelurus (*Schizailurus*) *lorteti* [27]		

	Machairodus aphanistus[6, 12, 28, 30, 32, 38, 40, 45, 48, 49, 53, 64]	*Amphimachairodus giganteus*[58]	CLL1[6, 12, 28, 30, 32, 38, 40, 42, 45, 48, 53] CM[53, 64] CP1[6, 24, 30, 38, 40, 45, 48, 53] CPE[16, 24, 53, 58] LTR1[3, 6, 48, 53, 64, 77,] ROS[53, 64] SA[45, 53] TF[49]	MN7+8/MN9–MN10
		Pseudaelurus sp.[24]		
		Machairodus cf. *aphanistus*[45]		
		Paramachairodus aphanistus[42, 49]		
		Felis sp.[16, 77]		
		Machairodus sp.[3, 24, 30, 48]		
	cf. *Promegantereon ogygia*	*Felis antediluviana*[3, 24, 30, 48, 70, 74]	CPE[58] LTR1[24, 30, 48] TNA[49] VL[3, 70, 74]	MN10
		Paramachaerodus sp.[49]		
		Paramachaerodus orientalis[58]		
	Stenailurus teilhardi[4, 18, 35, 48]	*Machairodus* sp.[24]	TT[4, 16, 18, 23, 24, 35, 48, 74]	MN12
		Felis sp.[16]		
		?*Metailurus* sp.[23, 24]		
		?*Paramachairodus orientalis*[74]		
Hyaenidae	Hyaenidae indet.[80]	*Machairodus aphanistus*[5]	ACM[80] CCN22[5, 6] CM1[80] CP1[80]	MN7+8
		Machairodus sp.[6]		
	cf. *Hyaenictis* sp.[80]	cf. *Hyaenictis* sp.[80]	ROS[80]	MN10
	Hyaenictis almerai[3, 24, 26, 30, 48, 76, 77]	*Hyaenictis graeca*[15, 16, 69, 70]	SMT[3, 15, 16, 24, 26, 30, 48, 69, 70, 76, 77]	MN10
	Adcrocuta eximia[3, 4, 6, 18]	*Crocuta eximia*[23, 24, 25, 26, 30, 74, 77]	CPL[3, 4, 24, 25, 26, 30, 48, 74, 77] TRR[23] TT[4, 6, 18, 23, 24, 25, 26, 30, 48, 74, 77]	MN10-MN12
		Percrocuta eximia[48]		
	Thalassictis sp.	*Hyaena eximia*[15]	BG[24, 47] HPI[16, 70, 75] SQ[3, 15, 24, 48]	MN7+8–MN9
		Ictitherium sp.[16, 24, 48, 70, 75]		
		Hyaenidae indet.[3, 24, 48]		

	Thalassictis robusta[10]	*Ictitherium robustum*[3, 23, 24, 30, 48, 69, 70, 74]	B40OV[10] SMT[24, 30, 48, 69, 70] TRR[23] VL[3, 74]	MN10
	Thalassictis montadai[7, 8, 9, 11, 12, 17, 18]	*Ictitherium montadai*[16, 23, 24, 25, 30, 69, 70, 75]	ACM[7, 8, 9, 11, 12, 18] CBR[34, 48] CM1[4, 23, 24, 38, 39, 48, 70] CP1[40, 48] BCV1[17] HPI[3, 16, 25, 30, 34, 69, 75] MB[24]	MN7+8-MN9
		Progenetta montadai[4, 34, 38, 40]		
		Ictitherium montadai vallesiensis[30, 31]		
		Progenetta montadai vallesiensis[34, 48]		
		Progenetta montadai montadai[39, 48]		
		Progenetta montadai urgellensis[39]		
		Miohyaena montadai[3]		
	Hyaenictitherium wongii	*Ictitherium hipparionum*[24, 30, 70, 74]	HPS[24, 30, 74] PI[70]	MN9-MN12
	Plioviverrops orbignyi	*Ictitherium orbignyi*[24, 25, 30, 48, 69, 70, 74]	SBL[24, 25, 30, 48, 69, 70, 74]	MN9
	Plioviverrops guerini[4, 48]	*Herpestes crassus*[16]	HP[16, 70, 75] TGM[48] TT[4, 23, 69, 70, 74, 77]	MN7+8-MN12
		Herpestes cf. *crassus*[69, 70, 75]		
		Herpestes guerini[23, 74, 77]		
	Protictitherium crassum[5, 7, 9, 11, 12, 17, 18]	*Progenetta crassa* form A[34]	ACM[7, 8, 9, 11, 17, 18] CLL1[6, 12, 30, 32, 34, 38, 40, 48] CLL2[24, 34]	MN7+8–MN10
		Progenetta crassa form B[34]		
		Progenetta cf. *crassa*[30, 32, 38]		
		Progenetta crassa[24, 30, 40, 48]		
		Ictitheriinae indet.[8]		
	Protictitherium gaillardi[12, 48, 49, 57]	*Progenetta gaillardi*[38, 45]	ACM[7, 8, 11, 17] CB[57] CLL1[12, 32, 40, 57] CM1[24, 38, 70] CP1[6, 34, 38, 45] CS[19] HPI[24, 25, 34, 75] SA[45] TNA[49]	MN4–MN10
		Herpestes cf. *dissimilis*[24, 25, 70, 75]		
		Progenetta crassa[24, 25, 32, 45]		
		Progenetta gaillardi form A[34, 40]		
		Progenetta gaillardi form B[34, 40]		
		Protictitherium crassum[6]		
		cf. *Protictitherium* sp.[7, 9, 11, 12, 17]		
		Protictitherium sp.[19]		

		cf. *Ictitherium* sp.[8]	TSA[49]	
		Progenetta sp.[38]		
	?*Protictitherium llopis*i	*Progenetta crassa llopisi*[34]	CBA[34]	MN11–MN12
Herpestidae	*Leptoplesictis aurelianensis*	*Palaeogale minuta*[47, 80]	CBL[80] CC[48] CS[80] EC[48]	MN4
	Leptoplesictis filholi[65, 66]	*Herpestes aurelianense*[16, 24, 69, 70, 75]	BCV1[7, 9, 11, 17] CM1[16, 24, 65, 66, 69, 70, 75] HP[57]	MN7+8-MN9
		cf. *Leptoplesictis* sp.[7]		
		Leptoplesictis cfr. *aurelianense*[7, 9, 11, 12, 17]		
		Herpestes (*Leptoplesictis*) sp.[57]		
Amphicyonidae	*Amphicyon* sp.[19, 20, 48]	*Amphicyon* cf. *helbingi*[24, 27, 68]	CBL[48] CJ[4, 20] CS[19] EC[20] LCV[20, 24, 27, 31, 68, 80] MC[3, 4, 20, 24, 27, 48]	MN3-MN4
		Cynelos cf. h*elbingi*[48]		
		Amphicyon steinheimensis[3, 27, 48]		
		cf. *Amphicyon* steinheimensis[4, 22, 31, 80]		
		cf. *Amphicyon* sp.[4]		
	Amphicyon major[6, 38, 40, 48]	*Amphicyon major*[6, 38, 40, 48]	CB[48] CP1[6, 38, 40]	MN9
	Amphicyon olisiponensis[19, 80]	*Amphicyon olisiponensis*[19, 80]	CS[19, 80]	MN4
	Ictiocyon socialis	*Amphicyon* (*Ictiocyon*) *dehmi*[27, 46, 48]	EC[26, 27, 46, 48]	MN4
		Ictiocyon sp.[26]		
	Magericyon castellanus[80]	*Magericyon castellanus*[80]	CLL1[80]	MN9
	Thaumastocyon dirus	*Agnotherium antiquus*[12]	CLL1[6, 12, 26, 28, 30, 32, 38, 40, 48]	MN9
		Amphicyon sp.[6, 12, 28, 30, 32, 48]		
		Amphicyon cf. *major*[40]		
		Amphicyon major[12, 38, 48]		

		Hyaenidae indet. sp. 1 [38]		
		Pseudarctos sp. [12]		
		Agriotherium sp. [26]		
Hemicyonidae	*Hemicyon goeriachensis* [2, 47]	*Pseudocyon sansaniensis* [23, 24, 73, 76]	CMA (=CPA, HP and HPI) [2, 23, 24, 47, 48, 73, 76]	MN7+8
		Hemicyon sansaniensis [48]		
		Plithocyon armagnacensis [2]		
	Plithocyon conquense	*Hemicyon stehlini* [19]	CS [19, 20, 80]	MN4
		Hemicyon sp. [20, 80]		
Ursidae	*Ursavus brevirhinus* [12, 30, 32, 40, 48, 80]	*Ursavus primaevus* [12, 28, 30, 32, 38, 40, 48, 80]	CCN20 [6, 80] CLL1 [12, 28, 30, 32, 38, 40, 48, 80]	MN9
		Ursavus sp. [6]		
		Canidae indet. [38, 40]		
	Ailuropodinae indet.	*Ursavus brevirhinus*[38]	CP1 [38, 40]	MN9
		Ursavus primaevus[40]		
	Kretzoiarctos beatrix [1]	Amphicyonidae indet. [8]	ACM [1, 8]	MN7+8
	Indarctos punjabiensis	*Indarctos atticus* [6, 58, 80]	LTR1 [6, 77, 80] TF [58]	MN10
		Felis sp. [77]		
	Indarctos vireti [3, 6, 12, 24, 25, 26, 30, 32, 38, 40, 48, 72, 74, 77, 78]	*Indarctos vireti* [3, 6, 12, 24, 25, 26, 30, 32, 38, 40, 48, 72, 74, 77, 78]	CLL1 [6, 12, 30, 32, 38, 40, 48] CP1 [6, 38, 40, 48, 78] CPL [24, 25, 26, 48, 72, 74, 77, 78] VL [3, 6]	MN9-MN10
		Agriotherium (*Hyaenarctos*) sp. [74, 77]		
		Agriotherium insignis var. *pontiensis* [24]		
Ailuridae	*Protursus simpsoni* [38, 40, 48, 54]	*Metarctos batalleri* [38, 40]	CLL1 [12, 38, 40, 48, 54, 67]	MN9
		Simocyon simpsoni [12, 67]		
	Simocyon batalleri [54]	*Metarctos batalleri* [24, 30, 48, 68, 69, 73, 76, 79]	BS [24, 30, 54, 76, 79] SS [48, 68, 69, 73]	MN9–MN10
Mephitidae	?*Plesiomeles* sp.	Melinae indet. sp. 1 [57]	CP1 [52, 57] CB [52, 57]	MN9
		Melinae indet. sp. 2 [57]		
		?*Plesiomeles* sp.[52]		

		?*Plesiomeles pusilla*[52]		
	Plesiomeles cajali[24, 26, 30, 52, 78]	*Plesiomeles cajali*[24, 26, 30, 52, 78]	CT[24, 26, 30, 52, 78]	MN10
	Plesiomeles aff. *cajali*	*Melinae sp.* 3[52, 57]	CP1[52, 57]	MN9
	Promephitis pristinidens[3, 12, 38, 40, 48, 55]	*Promephitis* sp.[24, 30, 74]	CLL1[12, 38, 40, 48] CP1[38] CPL[3, 24, 30, 48, 55, 74]	MN9–MN10
	Mesomephitis medius[12, 38, 40, 48, 56, 57, 80]	*Martes pusilla*[24]	ACM[80] CCN20[80] CLL1[12, 38, 40, 48, 56, 80] CP1[38, 56, 57, 80] HP[23, 24, 56] SA[80]	MN7+8–MN9
		Proputorius medius[56]		
		Proputorius sp. nov.[23]		
		?*Martes pusillus*[57]		
		Melinae indet.[80]		
Mustelidae	Mustelidae indet.[4, 13, 48, 79]	Mustelidae indet.[4, 13, 48, 79]	ACM[79] CJ[4, 48] ECM[13]	MN4–MN9
	Mustelinae indet.	Mustelinae indet.[57, 79]	CC[79], SA[57]	MN4–MN9
	Martes sp.	*Martes* sp.[7, 10, 19, 80]	ACM[7] B40/OV[10] CB[80] CS[80]	MN4–MN10
	Martes delphinensis[3, 16, 24, 48, 69, 70, 75, 80]	*Martes delphinensis*[3, 16, 24, 47, 68, 69, 74, 79]	BG[24, 47] (=HPI[3, 16, 24, 68, 69, 74, 79])	MN7+8
	Martes munki[3, 7, 9, 17, 23, 24, 46, 48, 55, 69, 70, 76]	*Martes* cf. *munki*[47, 53]	ACM[7, 9, 17] EC[46, 47, 53] SM[3, 4, 47, 75] SQ[3, 4, 23, 24, 47, 68, 69, 72, 75]	MN4–MN7+8
		Martes laevidens[3, 4, 47]		
		Martes or “*Mustela*” *larteti*[3, 23, 24, 47, 72, 75]		
	Martes cf. *andersoni*[40, 48, 56]	*Martes* cf. *andersoni*[40, 48, 56]	CP1[40, 48, 56]	MN9
	Martes melibulla[12, 38, 40, 48, 52, 55]	*Martes* sp.[38, 48, 55]	CLL1[12, 28, 30, 32, 38, 40, 48, 52, 55] TNA[48, 55]	MN9–MN10
		Martes munki[12, 30, 32, 40, 48]		
		Martes delphinensis[12, 28, 30, 32, 48]		

		Martes cf. *melibulla* [58]		
	Martes basilii	*Martes* cf. *basilii* [57]	CP1 [57]	MN9
	Stromeriella franconica [3, 4, 24, 27, 31, 48]	*Stromeriella franconica* [3, 4, 24, 27, 31, 48]	MC [3, 4, 24, 27, 31, 48]	MN3
	Circamustela dechaseauxi [12, 38, 40, 48, 56]	*Martes* sp. [55]	CLL1 [12, 38, 40, 48, 55, 56, 57]	MN9
		(?) *Circamustela dechaseauxi* [57]		
	Marcetia santigae [12, 38, 40, 48, 56]	*Paralutra* sp. [12, 30, 32, 38, 40, 48]	CLL1 [12, 30, 32, 38, 40, 48, 56]	MN9
	Ischyrictis mustelinus [7, 9, 11, 12, 17, 41, 55]	*Laphyctis mustelinus* [16, 23, 69, 70, 73, 75, 76]	ACM [7, 8, 9, 11, 12, 17] CM1 [4, 23, 25, 38, 41, 48, 55, 70] HP [3, 16, 69] HPI [75] SQ [3, 25, 48, 69, 70, 73, 75, 76]	MN7+8
		Laphictis sp. [31]		
		Laphictis mustelinus [25, 38]		
		Ischyrictis cf. *mustelinus* [8]		
		Ischyrictis (*Laphyctis*) *mustelinus* [3, 4, 48]		
	Ischyrictis cf. *bezianensis*	*Ischyrictis zibethoides* [24, 27, 31, 46]	TV [24, 27, 31, 46]	MN4
	Trochictis narcisoi [12, 47, 52, 57]	*Taxodon* cf. *sansaniensis* [38, 40, 48, 55]	CLL1 [12, 26, 38, 40, 48, 52, 55, 57]	MN9
		Taxodon sansaniensis [12, 26]		
	Hoplictis helbingi [36]	*Hoplictis helbingi* [36]	CB [36]	MN9
	Hoplictis petteri [12]	*Ischyritcis* (*Ischyrictis*) *petteri* [36, 40, 48]	CLL1 [12, 30, 32, 36, 38, 40, 48, 55, 56]	MN9
		Ischyrictis sp. [38, 55, 56]		
		Plesiogulo sp./*Plesiogulo* sp. nov. [12, 30, 32, 40, 48]		
	Iberictis buloti [19]	*Iberictis buloti* [19]	CS [19]	MN4
	Palaeomeles pachecoi [3, 4, 23, 24, 26, 38, 44, 48, 52, 70, 73, 75, 80]	Lutrinae nov. indet. [16]	ACM [80] CB [44, 52] CM1 [4, 23, 24, 26, 38, 48, 70] CV [24, 48] HP [3, 16, 52, 69, 73, 75, 80]	MN7+8-MN9
		Melidae indet. [69]		
	Sabadellictis crusafonti [12, 38, 40, 48, 52, 55]	*Sabadellictis crusafonti* [12, 38, 40, 48, 52, 55]	CLL1 [12, 38, 40, 48, 52, 55]	MN9
	Limnonyx sinerizi [21, 24, 26, 30, 38, 40, 48]	*Limnonyx sinerizi* [21, 24, 26, 30, 38, 40, 48]	CP1 [21, 24, 26, 30, 38, 40, 48]	MN9

	Trocharion albanense [3, 7, 8, 9, 11, 12, 17, 18, 23, 24, 38, 40, 48, 56, 57, 59, 60, 73, 76]	*Trocharion albanense* [3, 7, 8, 9, 11, 12, 17, 18, 23, 24, 38, 40, 48, 56, 57, 59, 60, 73, 76]	ACM [7, 8, 9, 11, 17, 18] BDA [59, 60] CB [48, 56, 60] CLL1 [12, 38, 40, 48, 56, 60] SQ [3, 23, 24, 48, 60, 73, 76]	MN7+8–MN9

Locality abbreviations: **ACM**, local stratigraphic series of Abocador de Can Mata; **B40OV**, Autovia Orbital de Barcelona, stretch Olesa de Montserrat–Viladecavalls; **BCV1**, Barranc de Can Vila 1; **BDA**, Decanting Pond of Rainwater (ACM sector); **BG**, Barranc Gran; **BS**, Bòvila Sagués; **CAL**, Ca n'Almirall; **CBA**, Can Baiona; **CB**, Castell de Barberà; **CBL**, Costablanca; **CBR**, Can Barra (Sant Quirze); **CC**, Can Canals; **CCN20**, Creu Conill 20; **CCN22**, Creu Conill 22; **CJ**, Can Julià; **CLL1**, Can Llobateres 1; **CLL2**, Can Llobateres 2; **CM**; Can Mata; **CMA**, Can Marcet; **CM1**, Can Mata 1 (=Bretxa de Can Mata); **CMS**, Can Missert (=Cerámicas Terras S.A.); **CPA**, Can Parellada; **CPE**, Can Perallada; **CPL**, Can Purull; **CP1**, Can Poncic 1; **CS**, Els Casots; **CT**, Can Trullàs; **CV**, Can Vila; **EC**, El Canyet; **ECM**, local stratigraphic series of Ecoparc de Can Mata; **HP**, Hostalets de Pierola indeterminate; **HPI** Hostalets de Pierola Inferior; **HPS**, Hostalets de Pierola Superior; **LCV**, Les Cases de la Valenciana; **LTR1**, La Tarumba 1; **MB**, Mas Bernich, **MC**, Molí Calopa; **PI**, Piera; **ROS**, local stratigraphic series of Ronda Oest de Sabadell; **SA**, Santiga; **SB**, Sant Andreu de la Barca; **SBL**, Sabadell; **SC**, Serra d'en Camero; **SM**, Sant Mamet; **SMT**, Sant Miquel del Toudell; **SQ**, Sant Quirze del Vallès; **TF**, Torrent de Febulines; **TGM**, Torrent del Gall Mullat; **TNA**, Trinxera Nord de l'Autopista; **TSA**, Trinxera Sud de l'Autopista; **TRR**, Terrassa, **TT**, Torrentet de Traginers; **TV**, Torrent de Vilaroc; **VL**, Viladecavalls; **VV**, Vinya Vella.

1, Abella et al. (2012); **2**, Abella et al. (2014); **3,** Agustí et al. (1984); **4**, Agustí et al. (1985); **5**, Agustí & Galobart (1997); **6**, Agustí et al. (1997); **7**, Alba et al. (2006); **8**, Alba et al. (2007); **9**, Alba et al. (2009); **10**, Alba et al. (2010); **11**, Alba et al. (2011a); **12**, Alba et al. (2011b); **13**, Alba et al. (2012); **14**, Bataller (1921); **15**, Bataller (1924); **16**, Bataller (1941); **17**, Casanovas-Vilar et al. (2008); **18**, Casanovas-Vilar et al. (2011a); **19**, Casanovas-Vilar et al. (2011b); **20**, Casanovas-Vilar et al. (2011c), **21**, Crusafont Pairó (1950); **22**, Crusafont Pairó (1952); **23**, Crusafont-Pairó (1953); **24**, Crusafont & Truyols (1954); **25**, Crusafont Pairó & Truyols Santoja (1954); **26**, Crusafont-Pairó (1955); **27**, Crusafont et al. (1955); **28**, Crusafont Pairó (1959a); **29**, Crusafont Pairó (1959b); **30**, Crusafont Pairó and Truyols Santoja (1960); **31**, Crusafont-Pairó (1962); **32**, Crusafont Pairó (1964); **33**, Crusafont Pairó et al. (1968); **34**, Crusafont Pairó & Petter (1969); **35**, Crusafont-Pairó & Aguirre (1972); **36**, Crusafont-Pairó (1972); **37**, Crusafont-Pairó & Golpe-Posse (1972); **38**, Crusafont-Pairó & Golpe-Posse (1973a); **39**, Crusafont Pairó & Golpe-Posse (1973b); **40**, Crusafont Pairó & Kurtén (1976); **41**, Crusafont-Pairó (1979a); **42**, Crusafont-Pairó (1979b); **43,** Crusafont-Pairó & Golpe-Posse (1981); **44**, Crusafont Pairó & Golpe-Posse (1982); **45**, de Beaumont & Crusafont-Pairó (1982); **46**, Galindo (2000); **47**, Ginsburg and Morales (1998); **48,** Golpe-Posse (1974); **49**, Golpe-Posse et al. (1979); **50**, Golpe-Posse (1981a); **51**, Golpe-Posse (1981b); **52**, Golpe-Posse (1984); **53**, Madurell et al. (IN PRESS); **54**, Peigné et al (2005); **55**, Petter (1963); **56**, Petter (1967); **57**, Petter (1976); **58**, Pons-Moyà (1990); **59**, Robles et al. (2009); **60**, Robles et al. (2010a); **61**, Robles et al. (2010b); **62**, Robles et al. (2013a); **63**, Robles et al. (2013b); **64**, Robles et al. (2013c); **65**, Roth (1987); **66**, Roth (1988); **67**, Thenius 1977; **68,** Vicente i Castells (1987); **69**, Villalta Comella & Crusafont Pairó (1941); **70**, Villalta Comella & Crusafont Pairó (1943a); **71**, Villalta Comella & Crusafont Pairó (1943b); **72**, Villalta Comella & Crusafont Pairó (1943c); **73**, Villalta Comella & Crusafont Pairó (1944); **74**, Villalta & Crusafont (1946a); **75**, Villalta & Crusafont (1946b); **76**, Villalta & Crusafont (1946c); **77**, Villalta Comella and Crusafont Pairó (1948); **78**, Viret and Crusafont-Pairó (1955); **79**, Villalta & Crusafont (1952); **80**, This study, based on material housed at the ICP, MGB and/or MGSB.

Table 9.2. Synthetic revised taxonomic identification and chronostratigraphic range of Miocene carnivorans from the Vallès-Penedès Basin. See Table 9.1 for further details.

Age	**Sites**	Carnivora indet	Viverridae indet	*Semigenetta sansaniensis*	*Semigenetta* cf. *sansaniensis*	*Semigenetta ripolli*	*Semigenetta grandis*	*Albanosmilus jourdani*	Felidae indet	"Felis vireti"	*Pseudaelurus quadridentatus*	*Pseudaelurus romieviensis*	*Styriofelis* sp	*Styriofelis turnauensis*	*Styriofelis lorteti*	*Machairodus aphanistus*	cf. *Promegantereon ogygia*	*Stenailurus teilhardi*
MN3	MC		■							■								
	SB													■				
MN4	CBL												■					
	CC		■										■	■				
	CJ									■								
	CS											■						
	EC												■					
	LCV		■															
	SM											■			■			
	TV																	
	VV													■				
MN5?-MN6	CAL	■																
MN7+8	ACM	■	■		■			■	■		■	■		■				
	BDA																	
	BCV1																	
	BG																	
	CBR																	
	CMA																	
	CM1			■				■			■							
	CPA																	
	CV													■				
	HPI							■			■			■				
	MB																	
	SQ							■			■							
MN7+8-MN9	CM															■		
	HP			■							■							
MN9	CB						■	■	■		■			■				
	CCN20							■			■							
	CCN22																	
	CLL1					■		■	■							■		
	CMS							■										
	CP1							■	■		■					■		
	ECM		■															
	HPS																	
	SA							■								■		
	SBL																	
	SC													■				
MN10	B40OV																	
	BS																	
	CBA																	
	CLL2																	
	CPE															■	■	
	CPL																	
	CT																	
	LTR1									■						■	■	
	ROS															■		
	SMT																	
	TF				■											■		
	TNA																■	
	TRR																	
	TSA																	
	VL																	
MN12	PI																	
	TGM																	
	TT																	■

Table 9.2 *(Continued)*

Age	Sites	Hyaenidae indet	cf. *Hyaenictis* sp.	*Hyaenictis almerai*	*Adcrocuta eximia*	*Thalassictis* sp	*Thalassictis robusta*	*Thalassictis montadai*	*Hyaenictitherium wongii*	*Plioviverrops orbignyi*	*Plioviverrops guerini*	*Protictitherium crassum*	*Protictitherium gaillardi*	? *Protictitherium llopisi*	*Leptoplesictis aurelianensis*	*Leptoplesictis filholi*
MN3	MC															
	SB															
MN4	CBL														■	
	CC														■	
	CJ															
	CS												■		■	
	EC														■	
	LCV															
	SM															
	TV															
	VV															
MN5?-MN6	CAL															
MN7+8	ACM	■						■				■	■			
	BDA															
	BCV1							■								■
	BG					■										
	CBR							■								
	CMA															
	CM1	■						■					■			■
	CPA															
	CV															
	HPI					■		■					■			
	MB							■								
	SQ					■										
MN7+8-MN9	CM															
	HP										■					■
MN9	CB												■			
	CCN20															
	CCN22	■														
	CLL1											■	■			
	CMS															
	CP1	■						■					■			
	ECM															
	HPS								■							
	SA												■			
	SBL									■						
	SC															
MN10	B40OV						■									
	BS															
	CBA													■		
	CLL2											■				
	CPE															
	CPL				■											
	CT															
	LTR1															
	ROS		■													
	SMT			■			■									
	TF															
	TNA												■			
	TRR				■		■									
	TSA												■			
	VL						■									
MN12	PI								■							
	TGM										■					
	TT				■						■					

Table 9.2 *(Continued)*

Age	**Sites**	*Amphicyon* sp.	*Amphicyon major*	*Amphicyon olisiponensis*	*Ictiocyon socialis*	*Magericyon castellanus*	*Thaumastocyon dirus*	*Hemicyon goeriachensis*	*Plithocyon conquense*	*Ursavus brevirhinus*	Ailuropodinae indet.	*Kretzoiarctos beatrix*	*Indarctos punjabiensis*	*Indarctos vireti*	*Protursus simpsoni*	*Simocyon batalleri*	?*Plesiomeles* sp.	*Plesiomeles cajali*	*Plesiomeles* aff. *cajali*	*Promephitis pristinidens*	*Mesomephitis medius*
MN3	MC	■																			
	SB																				
MN4	CBL	■																			
	CC																				
	CJ	■																			
	CS	■		■					■												
	EC	■			■																
	LCV	■																			
	SM																				
	TV																				
	VV																				
MN5?-MN6	CAL																				
MN7+8	ACM											■									■
	BDA																				
	BCV1																				
	BG																				
	CBR																				
	CMA							■													
	CM1																				
	CPA																				
	CV																				
	HPI																				
	MB																				
	SQ																				
MN7+8-MN9	CM																				
	HP																				■
MN9	CB		■														■				
	CCN20									■											■
	CCN22																				
	CLL1					■	■			■				■	■					■	■
	CMS																				
	CP1		■								■			■			■		■	■	■
	ECM																				
	HPS																				
	SA																				■
	SBL															■					
	SC																				
MN10	B40OV																				
	BS															■					
	CBA																				
	CLL2																				
	CPE																				
	CPL													■						■	
	CT																	■			
	LTR1												■								
	ROS																				
	SMT																				
	TF												■								
	TNA																				
	TRR																				
	TSA																				
	VL													■							
MN12	PI																				
	TGM																				
	TT																				

Table 9.2 *(Continued)*

Age	Sites	Mustelidae indet.	Mustelinae indet	*Martes* sp.	*Martes delphinensis*	*Martes munki*	*Martes* cf. *andersoni*	*Martes melibulla*	*Martes basilii*	*Stromeriella franconica*	*Circamustela dechaseauxi*	*Marcetia santigae*	*Ischyrictis mustelinus*	*Ischyrictis* cf. *bezianensis*	*Trochictis narcisoi*	*Hoplictis helbingi*	*Hoplictis petteri*	*Iberictis buloti*	*Palaeomeles pachecoi*	*Sabadellictis crusafonti*	*Limnonyx sinerizi*	*Trocharion albanense*
MN3	MC									■												
	SB																					
MN4	CBL																					
	CC		■																			
	CJ	■																				
	CS			■														■				
	EC					■																
	LCV																					
	SM					■																
	TV													■								
	VV																					
MN5?-MN6	CAL																					
MN7+8	ACM	■		■		■							■						■			■
	BDA																					■
	BCV1																					
	BG				■																	
	CBR																					
	CMA																					
	CM1												■						■			
	CPA																					
	CV																		■			
	HPI												■									
	MB																					
	SQ					■							■									■
MN7+8-MN9	CM																					
	HP												■						■			
MN9	CB			■												■			■			■
	CCN20																					
	CCN22																					
	CLL1							■			■	■			■		■			■		■
	CMS																					
	CP1						■		■												■	
	ECM	■																				
	HPS																					
	SA		■																			
	SBL																					
	SC																					
MN10	B40OV			■																		
	BS																					
	CBA																					
	CLL2																					
	CPE																					
	CPL																					
	CT																					
	LTR1																					
	ROS																					
	SMT																					
	TF																					
	TNA							■														
	TRR																					
	TSA																					
	VL																					
MN12	PI																					
	TGM																					
	TT																					

See locality abbreviations in Table 9.1.

Chapter 10. Conclusions

In this work, the fossil record of Miocene Carnivora (Mammalia) from the Vallès-Penedès Basin (NE Iberian Peninsula) is revised, with particular emphasis on previously unpublished remains recovered during the last decade from primate-bearing localities. The main conclusions of this dissertation are summarized below:

1. An updated chronology is provided for hominoid-bearing localities from Western Eurasia, with particular emphasis on the correlation between Vallès-Penedès sites and those from elsewhere in Western Eurasia. Of particular significance for the purposes of this work are the localities from the late Aragonian stratigraphic series of Abocador de Can Mata, which have provided a new wealth of information (both on primates and carnivorans) for the MN7+8 (a critical time interval for understanding the early evolutionary radiation of Miocene apes in Eurasia). The significance of the recent dryopithecine hominoid finds from the Vallès-Penedès Basin is reviewed from a chronological viewpoint, suggesting that these stem great apes evolved from kenyapithecines of African origin that extended their range into Eurasia after the Langhian transgression. Therefore, this work also furnishes the main biostratigraphic framework for the study of the carnivoran remains from the Vallès-Penedès Basin revised in this dissertation.

2. New dentognathic remains of *Trocharion albanense* (Mustelidae: Leptarctinae) are described from Middle to Late Miocene localitites of the Vallès-Penedès Basin. On this basis, an emended diagnosis of genus *Trocharion* is provided. A phylogenetic analysis of the extinct subfamily Leptarctinae, incorporating the new cranial features reported for *Trocharion*, indicates a very basal position for this genus within this subfamily, and suggests that the carnassial notch was lost independently in leptarctines and other mustelids.

3. New craniodental remains of the false sabertooth *Albanosmilus jourdani* (Barbourofelidae: Barbourofelini) are described from the Middle to Late Miocene localities of the Vallès-Penedès Basin. On the basis of the more derived cranial features of this species, the genus *Albanosmilus* (previously considered a junior

synonym of *Sansanosmilus*) is resurrected, and an emended diagnosis is provided. Several synonyms of the nominotypical species (*A. jourdani*) and a new combination (*Albanosmilus whitfordi*) are also provided. A cladistic analysis based on craniodental features supports the monophyly of both the Barbourofelidae and the Barbourofelini, and among the latter it supports for *Albanosmilus* an intermediate branching between the more basal *Sansanosmilus* and the more derived *Barbourofelis*. From a paleobiogeographic viewpoint, this analysis suggests that barbourofelins originated in Eurasia and that later *Albanosmilus* dispersed into North America during the Middle Miocene, giving rise to the genus *Barbourofelis* there.

4. The previously-unpublished dentognathic remains of small-bodied Felinae from the Middle Miocene of Abocador de Can Mata are described, being attributed to three distinct species from two different genera: *Styriofelis turnauensis*, *Pseudaelurus quadridentatus* and *Pseudaelurus romieviensis*. The chronostratigraphic distribution of these species in the Iberian Peninsula is reviewed and compared with that from the rest of Europe. The new material reveals previously unknown mandibular features of *P. romieviensis*, and enables refining the taxonomic validity of some putative diagnostic features that had been previously used to distinguish *P. romieviensis* from *P. quadridentatus*. Moreover, the new material of *P. romienviensis* extends the chronostratigraphic range of this species in the Vallès-Penedès Basin, in agreement with its previously-known range elsewhere in Eurasia.

5. All the available Vallès-Penedès material attributable to the scimitar-toothed cat *Machairodus aphanistus* (Felidae: Machairodontinae), including new remains from Ronda Oest Sabadell and some previously-known localities, is revised. The analysis of the craniodental material confirms most previous citations of this taxon, except for the remains previously employed to substantiate its first appearance datum in the Vallès-Penedès (Creu Conill 22), which are attributed to a hyaenid. Overall, however, the currently known range of this taxon in the Vallès-Penedès Basin (MN9-MN10) agrees well with that known elsewhere in Eurasia. The study of the (mostly previously unpublished) postcranial remains suggests a less cursorial locomotion for this taxon that in its putative descendant *Megantereon*.

6. A new genus, *Kretzoiarctos* (Ursidae: Ailuropodinae) is described, based on previously-unpublished dentognathic material from the Vallès-Penedès Basin. This material shows that the species previously referred to *Agriarctos beatrix* belongs in fact to a distinct genus. A cladistic analysis indicates that *Kretzoiarctos* represents the oldest member of the giant panda lineage (subfamily Ailuropodinae), which has significant paleobiogeographic implications for ursid evolution. Based on the phylogenetic results, a new tribe (Indarctini) is erected for other extinct ursids (genus *Indarctos*) that are the sister-taxon of members of the giant panda lineage in a strict sense (tribe Ailupodini, including the extinct *Kretzoiarctos*, *Agriarctos* and *Ailurarctos*, as well as the extant *Ailuropoda*).

7. Besides the more detailed studies summarized above, a preliminary taxonomic revision has been also undertaken for the remaining carnivoran taxa from the Miocene of the Vallès-Penedès Basin. Based on this revision, the paleodiversity of carnivorans in that basin at several taxonomic ranks is updated. Thus, before the beginning of this dissertation, a total of 12 families, 67 genera and 93 species of Miocene carnivorans were recorded in the Vallès-Penedès based on the then available literature. On the basis of the data provided in this dissertation, it is here considered that only 11 families, 41 genera and 55 species are recorded. This considerable drop in carnivoran paleobiodiversity is mostly attributable to the synonymization of multiple taxa. This example highlights the significance to undertake a taxonomic revision (based on the study of the actual fossil remains) of any group, before undertaking evolutionary paleobiological studies on paleobiodiversity dynamics or similar topics. In any case, only some groups (especially felids and some mustelids) have been reviewed in greater depth in this dissertation, so that the figures provided above are likely to change not only as new fossil remains are discovered, but also as those already available are studied in greater detail.

8. The currently available record of Miocene carnivorans from the Vallès-Penedès Basin, even after the descrease in recorded paleobiodiversity caused by their taxonomic revision, agrees with the general view that there is a biodiversity peak in the earliest Vallesian (MN9), like in other Neogene Iberian basins. Carnivoran diversity in the Vallès-Penedès clearly descreased in the late Vallesian (MN10) and

especially the Turolian (MN11-MN12), as in other Iberian basins. Available data in these other basins suggest that the faunal turnover experienced by the carnivoran guilds was progressive, mostly implying the substitution of forest-adapted forms by carnivorans more adapted to open environments. The timing of this turnover is more difficult to assess in the Vallès-Penedès Basin. Although the carnivoran paleobiodiversity drop appears more marked, this is most likely attributable to a sampling bias (since the MN10 and, especially, the MN11-MN12 are represented by a much lower number of localities compared to the MN7+8 and MN9.

LITERATURE CITED

Literature Cited

Abella, J., Domingo, M.S., Valenciano, A., Montoya, P., Morales, J. 2011. La asociación de Carnívoros de Batallones 3, Mioceno Superior del Cerro de los Batallones, cuenca de Madrid. *Paleontologia i Evolució* Memòria Especial 6, 21–24.

Abella, J., Alba, D.M., Robles, J.M., Valenciano, A., Rotgers, C., Carmona, R., Montoya, P., & Morales, J. 2012. *Kretzoiarctos* gen. nov., the oldest member of the panda clade. *PLoS ONE* 7, *e48985.*

Abella, J., Montoya, P., & Morales, J. 2014. Paleodiversity of the Superfamily Ursoidea (Carnivora, Mammalia) in the Spanish Neogene, related to environmental changes. *Journal of Iberian Geology* 40, 11–18.

Aguilar, J.-P., Agustí, J., Gibert, J. 1979. Rongeurs miocènes dans le Vallès-Penedès. 2 - Les Rongeurs de Castell de Barbera. *Paleovertebrata* 9, 17–32.

Agustí Ballester, J., Cabrera, L. 1980. Nuevos datos sobre la biozonación del Burdigaliense continental de la cuenca del Vallès-Penedès. *Acta Geológica Hispánica* 15, 81–84.

Agustí, J. 1983. Roedores (Mammalia) del Mioceno inferior de Can Martí Vell (Vallès-Penedès, Cataluña, España). *Estudios Geológicos* 39, 417–430.

Agustí, J., Moyà-Solà, S., Gibert, J. 1984. Mammal distribution dynamics in the eastern margin of the Iberian Peninsula during the Miocene. *Paléobiologie Continentale* 14, 33–46.

Agustí, J., Cabrera, L., Moyà-Solà, S. 1985. Sinopsis estratigráfica del Neógeno de la fosa del Vallès-Penedès. *Paleontologia i Evolució* 18, 57–81.

Agustí, J., Moyà-Solà, S. 1990. Mammal extinctions in the Vallesian (Upper Miocene). *Lecture Notes in Earth Sciences* 30, 425-432.

Agustí, J., Kölher, M., Moyà-Solà, S., Cabrera, L., Garcés, M., Parés, J.M. 1996. Can Llobateres: the pattern and timing of the Vallesian hominoid radiation reconsidered. *Journal of Human Evolution* 31, 143–155.

Agustí, J., Galobart, A. 1997. Noves localitats amb mamífers fòssils en el Miocè de la Conca del Vallès-Penedès. *Tribuna d'Arqueologia* 1996-1997, 9–22.

Agustí, J., Cabrera, L., Garcés, M., Parés, J.M. 1997. The Vallesian mammal succession in the Vallès-Penedès Basin (northeast Spain): paleomagnetic calibration and correlation with global events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133, 149–180.

Agustí, J., Cabrera, L., Garcés, M., Llenas, M. 1999. Mammal turnover and global climate change in the late Miocene terrestrial record of the Vallès-Penedès Basin (NE Spain). In: Agustí, J., Rook, L. & Andrews, P. (Eds.), *Hominoid Evolution and climatic change in Europe. Vol. 1: The Evolution of Neogene Terrestrial Ecosystems in Europe*, pp. 390–412. Cambridge University Press, Cambridge.

Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., Parés, J.M. 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. *Earth-Science Reviews* 52, 247–260.

Agustí, J., Sanz de Siria, A., Garcés, M. 2003. Explaining the end of the hominoid experiment in Europe. *Journal of Human Evolution* 45, 145–153.

Agustí, J., Casanovas-Vilar, I., Furió, M. 2005. Rodents, insectivores and chiropterans (Mammalia) from the late Aragonian of Can Missert (Middle Miocene, Vallès-Penedès Basin, Spain). *Geobios* 38, 575–583.

Agustí, J., Cabrera, Ll., Garcés, M. 2013. The Vallesian Mammal Turnover: A Late Miocene record of decoupled land-ocean evolution. *Geobios* 46, 151–157.

Alba, D.M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Rotgers, C., Furió, M., Angelone, C., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Obradó, P. 2006. Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l'Anoia, Cataluña), una sucesión de localidades del Aragoniense superior (MN6 y MN7+8) de la cuenca del Vallès-Penedès. Campañas 2002-2003, 2004 y 2005. *Estudios Geológicos* 62, 295–312.

Alba, D.M., Galindo, J., Casanovas-Vilar, I., Robles, J.M., Moyà-Solà, S., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Rotgers, C., Furió, M., Angelone, C. 2007. La intervenció paleontològica a la nova fase del dipòsit controlat de Can Mata (Els Hostalets de Pierola, Anoia): campanyes 2002-2003, 2004 i 2005. *Tribuna d'Arqueologia* 2006, 7–33.

Alba, D.M., Robles, J.M., Rotgers, C., Casanovas-Vilar, I., Galindo, J., Moyà-Solà, S., Garcés, M., Cabrera, L., Furió, M., Carmona, R., Bertó Mengual, J.V. 2009. Middle Miocene vertebrate localities from Abocador de Can Mata (els Hostalets de Pierola, Vallès-Penedès Basin, Catalonia, Spain): An update after the 2006-2008 field campaigns. *Paleolusitana* 1, 59–73.

Alba, D.M., Carmona, R., Bolet, A., Robles, J.M., Casanovas-Vilar, I., Furió, M., Sanisidro, Ó., Rifà, E., Balaguer, J., Checa, L., Luján, À., Tomàs, M., Moyà-Solà, S.

2010a. Intervención paleontológica en la Autovía Orbital de Barcelona B-40, tramo Olesa de Montserrat – Viladecavalls: Resultados preliminares. *Cidaris* 30, 51–59.

Alba, D.M., Robles, J.M., Rotgers, C., Casanovas-Vilar, I., Furió, M., Bertó, J.V., Carmona, R., Galindo, J., Balaguer, J., Moyà-Solà, S. 2010b. Intervenció Paleontològica a l'Abocador de Can Mata (2006-2008). *I Jornades de la Catalunya Central, 2010*, 138–141.

Alba, D.M., Casanovas-Vilar, I., Robles, J.M., Moyà-Solà, S. 2011a. Parada 3. El Aragoniense superior y la transición con el Vallesiense: Can Mata y la exposición paleontológica de els Hostalets de Pierola. *Paleontologia i Evolució* Memòria Especial 6, 95–109.

Alba, D.M., Casanovas-Vilar, I., Moyà-Solà, S., Robles, J.M. 2011b. Parada 4. El Vallesiense inferior y su transición con el Vallesiense superior: Can Llobateres. *Paleontologia i Evolució* Memòria Especial 6, 111–123.

Alba, D.M., Casanovas-Vilar, I., Robles, J.M., Marmi, J., Moyà-Solà, S. 2011c. New paleontological excavations at the Late Miocene site of Can Llobateres 1 (Vallès-Penedès Basin, NE Iberian Peninsula): preliminary results of the 2010 field campaign. *Cidaris* 30, 35–43.

Alba, D.M., Carmona, R., Bertó Mengual, J.V., Casanovas-Vilar, I., Furió, M., Garcés, M., Galindo, J., Luján, A.H. 2012. Intervenció paleontológica a l'Ecoparc de Can Mata (els Hostalets de Pierola, conca del Vallès-Penedès). *Tribuna d'Arqueologia*, 2010–2011, 115–130.

Alba, D.M., Moyà-Solà, S. 2012. A new pliopithecid genus (Primates: Pliopithecoidea) from Castell de Barberà (Vallès-Penedès Basin, Catalonia, Spain). *American Journal of Physical Anthropology* 147, 88–112.

Alba, D.M., DeMiguel, D., Morales, J., Sánchez, I.M., Moyà-Solà, S. 2014. New remains of *Dorcatherium crassum* (Artiodactyla: Tragulidae) from the Early Miocene (MN4) of Els Casots (Subirats, Vallès-Penedès Basin). *Comptes Rendus Palevol* 13, 73–86.

Alberdi Alonso, M.T. 1981. *Paleoecología del yacimiento del Neógeno continental de Los Valles de Fuentidueña (Segovia)*. Fundación Juan March, Madrid.

Alcalá, L., Sesé, C., Herráez, E., Adrover, R. 1991. Mamíferos del Turoliense Inferior de Puente Minero (Teruel, España). *Boletín de la Real Sociedad Española de Historia Natural (Sección Geología)* 86, 205–251.

Alcalá. L., Montoya, P., Morales, J. 1994. New large mustelids from the Late Miocene of the Teruel Basin (Spain). *Comptes Rendus de l'Académie des Sciences de Paris* 319, 1093–1100.

Aldana Carrasco, E.J. 1992. Los Castoridae (Rodentia, Mammalia) del Neógeno de Cataluña (España). *Treballs Museu de Geologia de Barcelona* 2, 99–141.

Almécija, S. Alba, D.M., Moyà-Solà, S. 2012. The thumb of Miocene apes: New insights from Castell de Barberà (Catalonia, Spain). *American Journal of Physical Anthropology* 148, 436–450.

Andrews, P., Harrisson, T., Delson, E., Bernor, R.L., Martin, L. 1996. Distribution and biochronology of European and Southwest Asian Miocene catarrhines. In: Bernor, R. L., Falhbusch, V., Mittmann, H.-W. (Eds.), *The evolution of Western Eurasian Neogene mammal faunas*, pp. 168–207. Columbia University Press, New York.

Anyonge, W.N. 2001. Carnivora. In: *Encyclopedia of life sciences (eLS)*. John Whiley and Sons, http://www.els.net. DOI: 10.1038/npg.els.0001558

Arnason, U., Widegren, B. 1986. Pinniped phylogeny enlightened by molecular hybridizations using highly repetitive DNA. *Journal of Molecular Evolution* 3, 356–365.

Arnason, U., Gullberg, A., Janke, A., Kullberg, M., Lehman, N., Petrov, E.A., Väinölä, R. 2006. Pinniped phylogeny and a new hypothesis for their origin and dispersal. *Molecular Phylogenetics and Evolution* 41, 345–354.

Arnason U., Gullberg A., Janke A., Kullberg M. 2007. Mitogenomic analyses of caniform relationships. *Molecular Phylogenetics and Evolution* 45, 863–874.

Ax, P. 1985. Stem species and the stem lineage concept. *Cladistics* 1, 279–187.

Bartrina, M.T., Cabrera, L., Jurado, M.J., Guimerà, J., Roca, E. 1992. Evolution of the central Catalan margin of the Valencia trough (western Mediterranean). *Tectonophysics* 203, 219–247.

Barycka, E. 2007. Evolution and systematics of the feliform Carnivora. *Mammalian Biology* 72, 257–282.

Baskin, J.A. 1981. *Barbourofelis* (Nimravidae) and *Nimravides* (Felidae) with a description of two new species from the Late Miocene of Florida. *Journal of Mammalogy* 62, 122–139.

Baskin, J.A. 1998. Procyonidae. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.), *Evolution of tertiary mammals of North America*, pp. 144–149. Cambridge University Press, New York.

Bataller, J.R. 1921. Mamífers fòssils de Catalunya. *Butlletí de la Institució Catalana d'Història Natural* 21, 81–86.

Bataller, J.R. 1924. Contribució a l'estudi de nous mamífers fòssils de Catalunya. *Arxius de l'Institut de Ciències* 12, 1–53.

Bataller Calatalyud, J.R. 1938. *Els ratadors fòssils de Catalunya*. Impremta de la Casa d'Assistència President Macià, Barcelona.

Bataller, J.R. 1941. Los yacimiento paleontológicos de Piera (Barcelona). *Boletim da Sociedade Geológica de Portugal* 1, 1–10.

Berta, A., Ray, C.E., Wyss, A.R. 1989. Skeleton of the oldest known Pinniped, *Enaliarctos mealsi*. *Science* 244, 60–62.

Begun, D.R., Moyà-Solà, S., Kölher, M. 1990. New Miocene hominoid specimens from Can Llobateres (Vallès Penedès, Spain) and their geological and paleoecological context. *Journal of Human Evolution* 19, 255–268.

Begun, D.R. 2002. The Pliopithecoidea. In: Hartwig, W.C. (Ed.), *The primate fossil record*, pp. 221–240.. Cambridge University Press, Cambridge.

Benton, M.J. 2000. Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead? *Biological Reviews* 75, 633–648.

Bininda-Edmonds, O.R.P., Gittleman, J.L., Purvis, A. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews* 74, 143–175.

Blumenbach, J.F. 1791. *Handbuch der Naturgeschichte*. Fourth Edition. Dietrich, Göttingen.

Bremer, K. 1994. Branch support and tree stability. *Cladistics* 10, 295–304.

Bryant, H.N. 1991. Phylogenetic relationships and systematics of the Nimravidae (Carnivora). *Journal of Mammalogy* 72, 56–78.

Bryant, H.N. 1996. Explicitness, stability, and universality in the phylogenetic definition and usage of taxon names: a case study of the phylogenetic taxonomy of the Carnivora (Mammalia). *Systematic Biology* 45, 174–189.

Bonaparte, C.L. 1845. Specchio generale dei sistemi erpetologico ed anfibiologico. *Atti Congresso Scienzia Italia* 6, 376–378.

Bowdich, T.E. 1821. *An analysis of natural classification of Mammalia for the use of students and travellers*. J. Smith, Paris.

Cabrera, L., Calvet, F. 1990. Sequential arrangement of the Neogene sedimentary record in the Vallés-Penedés and Valls-Reus half grabens, Iberian margins, NE Spain. *Terra Abstracts* 2, 1–110.

Carmona R., Alba, D.M., Casanovas-Vilar, I., Furió, M., Garcés, M., Bertó Mengual, J.V., Galindo, J., Luján, À.H. 2011. Intervención paleontológica en la serie del Mioceno superior del Ecoparc de Can Mata (cuenca del Vallès-Penedès, NE de la península Ibérica). In: Pérez-García, A., Gascó, F., Gasulla J.M., Escaso, F. (Eds.), *Viajando a mundos pretéritos*, pp. 77–84. Ayuntamiento de Morella, Morella.

Carroll, R.L. 1988. *Vertebrate paleontology and evolution*. W. H. Freeman and Company, New York.

Casanovas-Vilar, I., Furió, M., Agustí, J. 2006. Rodents, insectivores and paleoenvironment associated to the first-appearing hipparionine horses in the Vallès-Penedès Basin (Northeastern Spain). *Beiträge zur Paläontologie* 30, 89–107.

Casanovas-Vilar, I. 2007. *The rodent assemblages from the late Aragonian and the Vallesian (Middle to Late Miocene) of the Vallès-Penedès Basin (Catalonia, Spain)*. Doctoral dissertation, Universitat Autònoma de Barcelona.

Casanovas-Vilar, I., Agustí, J. 2007. Ecogeographical stability and climate forcing in the late Miocene (Vallesian) rodent record of Spain. *Palaeogeography, Palaeoclimatology, Palaeocology* 248, 169–189.

Casanovas-Vilar, I., Alba, D.M., Moyà-Solà, S., Galindo, J., Cabrera, L., Garcés, M., Furió, M., Robles, J.M., Köhler, M., Angelone, C. 2008. Biochronological, taphonomical and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae). *Journal of Human Evolution* 55, 589–603.

Casanovas-Vilar, I., García-Paredes, I., Alba, D.M., Van den Hoeck Ostende, L.W., Moyà-Solà, S. 2010. The European Far West: Miocene mammal isolation, diversity and turnover in the Iberian Peninsula. *Journal of Biogeography* 37, 1079–1093.

Casanovas-Vilar, I., Alba, D.M., Robles, J.M., Moyà-Solà, S. 2011a. Registro palentológico continental de la cuenca del Vallès-Penedès. *Paleontologia i Evolució* Memòria Especial 6, 55–80.

Casanovas-Vilar, I., Alba, D.M., Moyà-Solà, S. 2011b. Parada 1. Panorámica general de la cuenca y yacimiento de Els Casots (Subirats): una fauna de vertebrados del Aragoniense inferior. *Paleontologia i Evolució* Memòria Especial 6, 81–88.

Casanovas-Vilar, I., DeMiguel, D., Galindo, J., Robles, J.M., Garcés, M., Cabrera, L. 2011c. The continental Burdigalian (Early Miocene) of the Vallès- Penedès Basin (Catalonia, Spain). In: Pérez-García, A., Gascó, F., Gasulla J.M., Escaso, F. (Eds.), *Viajando a mundos pretéritos*, pp. 93–100. Ayuntamiento de Morella, Morella.

Casanovas-Vilar, I. Alba, D.M., Garcés, M., Robles, J.M., Moyà-Solà, S. 2011d. Updated chronology for the Miocene hominoid radiation in Western Eurasia. *Proceedings of the National Academy of Sciences U.S.A.* 108, 5554–5559.

Casanovas-Vilar, I., Hoek Ostende, L.W. Van Den, Furió, M., Madern, P.A. 2014. The range and extent of the Vallesian Crisis (Late Miocene): new prospects based on the micromammal record from the Vallès-Penedès basin (Catalonia, Spain). *Journal of Iberian Geology* 40, 29–48.

Checa Soler, L., Rius Font, L. 2000. Intervenció paleontològica a l'EDAR Sabadell-Riu Ripoll (Can Llobateres, Sabadell, Vallès Occidental). *Tribuna d'Arqueologia* 1999-2000, 1–7.

Chenu, J. 1851-1858. *Encyclopedie d'Histoire Naturelle ou Traité complet de cette science d'après les travaux des naturalistes les plus éminents de tous les pays et de toutes les époques: Buffon, Daubenton, Lacépède, G. Cuvier, F. Cuvier, Geoffroy Saint-Hilaire, Latreille, De Jussieu, Brongniart, etc. Ouvrage résumant les Observations des Auteurs anciens et comprenant toutes les Découvertes modernes jusqu'à nos jours. Avec: Tables Alphabétiques des noms vulgaires et scientifiques de tous les sujets décrits et figurés.* Paris: Maresq ou Gustave Havard, s.d. [1850-1858], Maresque 1857 a 1861 pour les tables.

Cope, E.D. 1875. On the supposed Carnivora of the Eocene of the Rocky Mountains. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1875, 444–448.

Cope, E.D. 1880. The badlands of the wind River and their fauna. *American Naturalist* 14, 745–748.

Colbert, E.H., Morales, M., Minkoff, E.C. 1991. *Colbert's evolution of the vertebrates: a history of the backboned animals though time.* Fifth edition. Wiley, Canada.

Cray, P.E. 1973. Marsupialia, Insectivora, Primates, Creodonta and Carnivora from the Headon beds (Upper Eocene) of Southern England. *Bulletin of the British Museum (Natural History), Geology* 23, 1–102.

Crusafont Pairó, M. 1950. *Limnonyx* un nuevo lútrido del mioceno español. *Notas y Comunicaciones del Instituto Geológico y Minero de España* 20, 129–142.

Crusafont Pairó, M. 1952. La presencia del félido *Pseudaelurus tournauensis* (Hoernes) en el Mioceno de Hostalets de Pierola y Sabadell (Vallés-Penedés). *Notas y Comunicaciones del Instituto Geológico y Minero de España* 28, 95–109.

Crusafont Pairó, M., Villalta Comella, J.F. 1952. Una nueva localidad con mamíferos fósiles del Burdigaliense continental del Penedés (nota previa). *Notas y Comunicaciones del Instituto Geológico y Minero de España* 27, 151–158.

Crusafont, M., Truyols, J. 1953. Un ensayo goniométrico sobre la carnicera inferior de los Fisípedos. *Estudios Geológicos* 18, 225–256.

Crusafont, M., Truyols, J. 1954. *Catálogo paleomastológico del Mioceno del Vallés-Penedés y de Calatayud-Teruel. Segundo Cursillo Internacional de Paleontología.* Museo de la Ciudad de Sabadell, Sabadell.

Crusafont Pairó, M., Truyols Santoja, J. 1954. Sinopsis estratigráfico-paleontológica del Vallés-Penedés. *Arrahona* 1954, 1–15.

Crusafont-Pairó, M. 1955. Données biogéographiques relevées par la paléomammalogie du Miocène espagnol. In: *Colloque International sur "Problèmes Actuels de Paléontologie",* pp. 101–108. C.N.R.C., Paris.

Crusafont, M., Villalta, J.F., Truyols, J. 1955. El Burdigaliense continental de la cuenca del Vallés-Penedés. *Memorias y Comunicaciones del Instituto Geológico* 12, 1–272.

Crusafont-Pairó, M., Truyols-Santoja, J. 1956. A biometric study of the evolution of fissiped carnivores. *Evolution* 10, 314–332.

Crusafont Pairó, M., Truyols-Santonja, J. 1957a. Un estudio de la evolución de los Carnívoros por métodos numéricos. *Estudios Geológicos* 34, 177–202.

Crusafont Pairó, M., Truyols-Santoja, J. 1957b. Estudios masterométricos en la evolución de los Fisípidos: I: Los módulos angulares "alfa" y "beta". II: Los parámetros lineales P, C y T. *Boletín del Instituto Geológico y Minero de España* 68, 85–224.

Crusafont Pairó, M., Truyols-Santoja, J. 1958. Masterometría, sintetotipo y evolución. *Boletín de la Real Sociedad Española de Historia Natural* 56, 73–84.

Crusafont Pairó, M. 1959a. Primer hallazgo en España del género *Ursavus* (Carnivora, Ursidae). *Notas y Comunicaciones del Instituto Geológico y Minero de España* 55, 137–144.

Crusafont Pairó, M. 1959b. Biometría y evolución. *Revista de la Universidad de Madrid* 8, 29–31.

Crusafont Pairó, M., Truyols Santoja, J. 1960. Sobre la caracterización del Vallesiense. *Notas y Comunicaciones del Instituto Geológico y Minero de España* 60, 109–126.

Crusafont Pairó, M. 1962. Algunos principios teóricos derivados del cálculo masterométrico. *Boletín de la Real Sociedad Española de Historia Natural* 60, 167–176.

Crusafont Pairó, M. 1964. La biota de Can Llobateres (Sabadell) y su significación biológica. *Cursillos y Conferencias del Instituto "Lucas Mallada"* 9, 177–179.

Crusafont Pairó, M., Aguirre, E. de García, J. 1968. Un nuevo yacimiento de mamíferos del mioceno de la meseta española. *Acta Geológica Hispánica* 3, 22–24.

Crusafont Pairó, M., Petter, G. 1969. Contribution a l'étude des Hyaenidae. La sous-familie des Ictitheriinae. *Annales de Paléontologie* 55, 1–41.

Crusafont-Pairó, M., Aguirre, E. 1972. *Stenailurus*, Félidé nouveau, du Turolien d'Espagne. *Annales de Paléontologie (Vertébrés)* 58, 211–225.

Crusafont-Pairó, M. 1972. Les *Ischyrictis* de la transition Vindobonien-Vallésien. *Palaeovertebrata* 5, 253–260.

Crusafont Pairó, M., Golpe Posse, J.M. 1972. Los yacimientos de mamíferos fósiles del Vallès. *Boletín Informativo del Instituto de Paleontología de Sabadell* 4, 20–24.

Crusafont-Pairó, M., Golpe-Posse, J.M. 1973a. New Pongids from the Miocene of Vallès Penedes Basin (Catalonia, Spain). *Journal of Human Evolution* 2, 17–23.

Crusafont Pairó, M., Golpe Posse, J.M. 1973b. Nuevos hallazgos de *Progenetta montadai* en el Mioceno de Cataluña. *Boletín Geológico y Minero* 84, 105–113.

Crusafont-Pairó, M. Golpe-Posse, J.M. 1974. Asociación de *Anchitherium* Mey. 1834, con *Hipparion* Christ, 1832, en el Alto Mioceno del Vallés. *Boletín de la Real Sociedad Española de Historia Natural* 72, 75–93.

Crusafont Pairó, M., Kurtén, B. 1976. Bears and bear-dogs from the Vallesian of the Vallès-Penedès Basin, Spain. *Acta Zoologica Fennica* 144, 1–29.

Crusafont-Pairó, M. 1979a. Nova troballa de l'*Ischyrictis mustelinus* (Viret, 1933). *Butlletí Informatiu de l'Institut de Paleontologia de Sabadell* 11, 17–19.

Crusafont-Pairó, M. 1979b. Novetats paleomastològiques del Vallès-Penedès. Nota preliminar. *Acta Geológica Hispánica* 14, 354–355.

Crusafont-Pairó, M., Golpe-Posse, J.M. 1981. Hallazgo de una nueva especie del género *Semigenetta (S. grandis)* del Vindoboniense terminal de Castell de Barberà (Depresión prelitoral catalana; España). *Boletín de la Real Sociedad Española de Historia Natural (Geología)* 79, 67–76.

Crusafont Pairó, M., Golpe Posse, J.M. 1982. Hallazgo de *Palaeomeles pachecoi* Vill. et. Crus., 1943, en Castell de Barberà (Vallès-Penedès). *Acta Geològica Hispànica* 17, 27–37.

de Beaumont, G. 1961. Recherches sur *Felis attica* Wagner du Pontien eurasiatique avec quelques observations sur les genres *Pseudaelurus* Gervais et *Proailurus* Filhol. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon* 6, 17–45.

de Beaumont, G. 1964. Remarques sur la classification des Felidae. *Eclogae Geologicae Helvetiae* 57, 837–845.

de Beaumont, G., Crusafont-Pairó, M. 1982. Les Félidés (Mammifères, Carnivores) du Vallésien du Vallès, Catalogne, Espagne. *Archives des Sciencies Genève* 35, 41–64.

De Bruijn, H., Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P., Morales, J., Heinzmann, E., Mayhew, D.F., van der Meulen, A.J., Schmidt-Kittler, N., Telles Antunes, M. 1992. Report of the RCMNS working group on fossil mammals, Reisenburg 1990. *Newsletters on Stratigraphy* 26, 65–118.

De Gibert, J.M. Casanovas-Vilar, I. 2011. Contexto geológico de la cuenca del Vallès-Penedès. *Paleontologia i Evolució* Memòria Especial 6, 39–45.

Domingo, M.S., Badgley, C., Azanza, B., DeMiguel, D., Alberdi, M.T. 2014. Diversification of mammals from the Miocene of Spain. *Paleobiology* 40, 196–220.

Evans, H.E. 1993. *Miller's Anatomy of the Dog. Third Edition*. Saunders, Philadelphia.

Ewer, R.F. 1973. *The carnivores (The World Naturalist Series).* Weidenfeld & Nicholson, London.

Farris, J.A. 1983. The logical basis of phylogenetic analysis. In: Platnick, N.I. & Funk, V.A. (Eds.), *Advances in cladistics: Proceedings of the Second Meeting of the Willi Hennig Society (Volume 2)*, pp. 7–36. Columbia University Press, New York.

Farris, J.A. 1989a. The retention index and the rescaled consistency index. *Cladistics* 5, 417–419.

Farris, J.A. 1989b. The retention index and homoplasy excess. *Systematic Zoology* 38, 406–407.

Felsenstein, J. 1983. Statistical Inference of Phylogenies. *Journal of the Royal Statistical Society*, 146, 246–272.

Felsenstein, J. 1985. Phylogenies and the Comparative Method. *The American Naturalist*, 125, 1–15.

Felsenstein, J. 2004. *Inferring Phylogenies*. Sinauer Associates, Inc. Sunderland, Massachusetts.

Filhol, H. 1883. Notes sur quelques Mammifères fossiles de l'époque miocène. *Archives du Muséum d'Histoire Naturelle de Lyon* 3, 1–97.

Finarelli, J.A. 2008. A total evidence phylogeny of the Arctoidea (Carnivora: Mammalia): Relationships among basal taxa. *Journal of Mammal Evolution* 15, 231–259.

Finarelli, J.A., Flynn, J.J. 2006. Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): The effects of incorporating data from the fossil record. *Systematic Biology* 55, 301–313.

Fischer von Waldheim, J. 1817. Adversia zoologica. *Mémories de la Société Impériale des Naturalistes de l'Université Impériale de Moscou* 5, 368–428.

Fleagle, J.G. 2013. *Primate adaptation and evolution. Third edition*. Academic Press, San Diego.

Flynn, J.J., Galiano, H. 1982. Phylogeny of early Tertiary Carnivora, with a description of a new species of *Protictis* from the middle Eocene of northwestern Wyoming. *American Museum Novitates* 2725, 1–64.

Flynn, J.J. 1996. Phylogeny and rates of evolution: morphological, taxic and molecular. In: Gittleman, J. (Ed.), *Carnivore behaviour, ecology and evolution,* Vol. 3, pp. 542–581. Cornell University Press, New York.

Flynn, J.J. 1998. Early Cenozoic Carnivora ("Miacoidea"). In: Janis, C.M., Scott, K.M. & Jacobs, L.L. (Eds.), *Evolution of Tertiary mammals of North America*, pp. 110–123. Cambridge University Press, New York.

Flynn, J.J., Nedbal, M.A. 1998. Phylogeny of the Carnivora (Mammalia): congruence vs. incompatibility among multiple data sets. *Molecular Phylogenetics Evolution* 9, 414–426.

Flynn, J.J., Nedbal, M.A., Dragoo, J.W., Honeycutt, R.L. 2000. Whence the red panda?. *Molecular Phylogenetics and Evolution* 17, 190–199.

Flynn, J.J., Wesley-Hunt, G.D. 2005. Carnivora. In: Rose, K.D. & Archibald, D. (Eds.), *The rise of placental mammals: Origins and relationships of the major extant clades*, pp. 175–198. Hopkins University Press, Baltimore.

Flynn, J.J., Finarelli, J.A., Zehr, S., Hsu, J., Nedbal, M.A. 2005. Molecular phylogeny of the Carnivora (Mammalia): assessing the impact of increased sampling on resolving enigmatic relationships. *Systematic Biology* 54, 317–337.

Flynn, J.J., Finarelli, J.A., Spaulding, M. 2010. Phylogeny of the Carnivora and Carnivoramorpha, and the use of the fossil record to enhance understanding of evolutionary transformations. In: Goswami, A. & Friscia A. (Eds.), *Carnivoran* *evolution: New views on phylogeny, form and function*, pp. 25–63. Cambridge University Press, Cambridge.

Flower, W.H. 1869. On the value of the characters of the base of the cranium in the classification of the order Carnivora, and on the systematic position of *Bassaris* and other disputed forms. *Proceedings of the Zoological Society of London* 37, 4–37.

Fortelius, M., Hokkanen, A. 2001. The trophic context of hominoid occurrence in the later Miocene of western Eurasia: a primate-free view. In: de Bonis, L., Koufos, G.D. & Andrews, P. (Eds.), *Hominoid evolution and climatic change in Europe. Volume 2: Phylogeny of Neogene primates of Eurasia*, pp. 19–47. Cambridge University Press, Cambridge.

Fortelius, M., Werdelin, L., Andrews, P., Bernor, R.L., Gentry, A., Humphrey, L., Mittmann, H.-W., Viranta, S. 1996. Provinciality, diversity, turnover and paleoecology in land mammal faunas of the later Miocene of Western Eurasia. In: Bernor, R.L., Fahlbusch, V. & Mittmann, H.-W. (Eds.), *The evolution of Western Eurasian Neogene mammal faunas*, pp. 414–448. Columbia University Press, New York.

Fraile, S., Pérez, B., De Miguel, D., Morales, J. 1997. Revisión de los Carnívoros presentes en los yacimientos del Neógeno español. In: Calvo J.P. & Morales, J. (Eds.), *Avances en el conocimiento del Terciario Ibérico*, pp. 77–80. UCM-CSIC, Madrid.

Frick, C. 1926. The Hemicyoninae and an American Tertiary bear. *Bulletin of the American Museum of Natural History* 56, 1–119.

Fulton, T.L., Strobeck, C. 2006. Molecular phylogeny of the Arctoidea (Carnivora): effect of missing data on supertree and supermatrix. Analyses of multiple gene data sets. *Molecular Phylogenetics and Evolution* 41, 165–181.

Galobart, A., Acosta, C.A., Vila, B. 2011. Patrocinio y mecenazgo en paleontología de vertebrados: Crusafont, Hürzeler y Can Llobateres, diez años de una colaboración inacabada. *Paleontologia i Evolució* Memòria Especial 6, 151–156.

Galindo, J. 2000. *Castellbisbal, un viatge a través del temps.* Publicacions del Museu de la Pagesia, Castellbisbal.

Garcés Crespo, M. 1995. *Magnetoestratigrafía de las sucesiones del Mioceno Medio y Superior del Vallès Occidental (Depresión del Vallès-Penedès, N.E. de España): Implicaciones biocronológicas y cronoestratigráficas*. Doctoral dissertation, Universitat de de Barcelona.

Garcés, M., Agustí, J., Cabrera, L., Parés, J.M. 1996. Magnetostratigraphy of the Vallesian (late Miocene) in the Vallès-Penedès Basin (northeast Spain). *Earth and Planetary Science Letters* 142, 381–396.

Garcés, M., Cabrera, L., Agustí, J., Parés, J.M. 1997. Old World first appearance datum of "*Hipparion*" horses: Late Miocene large-mammal dispersal and global events. *Geology* 25, 19–22.

Garrido, G., Arribas, A. 2008. Generalidades sobre los carnívoros del Villafranquiense Superior en relación con el registro fósil de Fonelas P-1. In: Arribas A. (Ed.), *Vertebrados del Plioceno superior terminal en el suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas*. *Cuadernos del Museo Geominero* 10, 85–146.

Gaudry, A. 1862. *Animaux fossiles et géologie de l'Attique*. F. Savy, Paris.

Gaubert, P., Veron, G. 2003. Exhaustive sample set among Viverridae reveals the sister-group of felids: the linsangs as a case of extreme morphological convergence within Feliformia. *Proceedings of the Royal Society London B* 270, 2523–2530.

Gaubert, P., Cordeiro-Estella, P. 2006. Phylogenetic systematics and tempo of evolution of the Viverrinae (Mammalia, Carnivora, Viverridae) within feliformians: implications for faunal exchanges between Asia and Africa. *Molecular Phylogenetics and Evolution* 41, 266–278.

Gingerich, P. 1983. Systematics of Early Eocene Miacidae (Mammalia, Carnivora) in the Clark's Fork Basin, Wyoming. *Contributions from the Museum of Paleontology University of Michigan* 26, 197–225.

Gingerich, P., Winkler, D.A. 1985. Systematics of Paleocene Viverravidae (Mammalia, Carnivora) in the Bighorn Basin and Clark's Fork Basin, Wyoming. *Contributions from the Museum of Paleontology University of Michigan* 27, 87–128.

Ginsburg, L. 1961a. Plantigrady and digitigrady in the fissiped carnivorans. *Mammalia* 25, 1–21.

Ginsburg, L. 1961b. La faune des carnivores miocènes de Sansan (Gers). *Mémoirs du Muséum national d'Histoire naturelle* 9, 1–90.

Ginsburg, L., Morales, J., Soria, D. 1981. Nuevos datos sobre los carnívoros de Los Valles de Fuentidueña (Segovia). *Estudios Geológicos* 37, 383–415.

Ginsburg, L. 1992. Les genres *Pseudarctos* et *Ictiocyon*, Amphicyonidae (Carnivora, Mammalia). *Bulletin du Muséum d'Histoire naturelle* 14, 301–317.

Ginsburg, L., Morales, J. 1998. Les Hemicyoninae (Ursidae, Carnivora, Mammalia) et les formes apparentées du Miocène inférieur et moyen d'Europe occidentale. *Annales Paléontologie* 84, 71–123.

Ginsburg, L. 1999. Order Carnivora. In: Rössner, G. & Heissig, K. (Eds.), *The Miocene land mammals of Europe*, p. 109–148. Verlag Dr. Friedrich Pfeil, München.

Golpe-Posse, J.M. 1974. Faunas y yacimientos con suiformes del Terciario español. *Paleontología i Evolución* 8, 1–87.

Golpe Posse, J.M., Santafé-Llopis, J.V., Casanovas-Cladellas, M.L. 1979. Datos sobre el Vallesiense medio-superior de los alrededores de Terrassa. *Acta Geológica Hispánica* 14, 356–361.

Golpe Posse, J.M. 1979. Los yacimientos con restos fósiles del Vindoboniense superior al Vallesiense superior de la región Sabadell-Terrassa. *Boletín de la Real Sociedad Española de Historia Natural (Geología)* 77, 199–212.

Golpe-Posse, J.M. 1981a. Datos comparativos de tres formas viverrinas del Vindoboniense superior y Vallesiense medio del Vallès-Penedès (depresión prelitoral catalana, España). *Acta Geològica Hispànica* 16, 191–194.

Golpe-Posse, J.M. 1981b. Estudios comparativo entre la mandíbula de *Semigenetta grandis* del Vindoboniense de Castell de Barberà (Depresión Prelitoral Catalana, España) y otros ejemplares europeos de *Semigenetta*. *Paleontologia i Evolució* 16, 15–24.

Golpe-Posse, J.M. 1984. Las formas melinoideas de la transición Vindoboniense superior – Vallesiense medio del Vallès-Penedès (Depresión prelitoral catalana, España). *Acta Geològica Hispànica* 19, 11–18.

Gómez-Alba, J. 1997. Catálogo razonado de los vertebrados fósiles de España del Museo de Geología de Barcelona (1882-1982). *Treballs del Museu de Geologia de Barcelona* 6, 1–289.

Gray, J.E. 1821. On the natural arrangement of vertebrose animals. *London Medical Repository* 15, 296–310.

Gray, J.E. 1825. An outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. *Annals of Philosophy* 10, 337–344.

Gray, J.E. 1843. *List of the specimens of Mammalia in the collection of the British Museum.* The Trustees [of the British Museum], London.

Gregory, W.K., Hellman, M. 1939. On the evolution and major classification of the civets (Viverridae) and allied fossil and recent Carnivora: A phylogenetic study of the skull and dentition. *Proceedings of the American Philosophical Society* 81, 309–392.

Goswami, A. 2010. Introduction to Carnivora. In: Goswami, A. & Friscia A. (Eds.), *Carnivoran evolution: New views on phylogeny, form and function*, pp. 1–24. Cambridge University Press, Cambridge.

Haeckel, E.H. 1866. *Generelle Morphologie der Organismen: allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von C. Darwin reformite Decendenz-theorie*. Georg Reimer, Berlin.

Hay, O.P. 1930. Second bibliography and catalogue of the Vertebrata of North America, Vol. 2. *Carnegie Institute of Washington Publications* 390, 1–1074.

Heinrich, R.E., Rose, K.D. 1995. Partial skeleton of the primitive carnivoran *Miacis petilus* from the early Eocene of Wyoming. *Journal of Mammalogy* 76, 148–162.

Heinrich, R.E., Rose, K.D. 1997. Postcranial morphology and locomotor behavior of two early Eocene miacoid carnivorans, *Vulpavus* and *Didymictis*. *Palaeontology* 40, 279–305.

Heinrich, R.E., Houde, P. 2006. Postcranial anatomy of *Viverravus* (Mammalia, Carnivora) and implications for substrate use in basal carnivora. *Journal of Vertebrate Paleontology* 26, 422–435.

Henry, M.D., Penny, D. 1982. Branch-and-bound algorithms to determine minimal evolutionary trees. *Mathematical Biosciences*, 59, 277–290.

Hennig, W. 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana.

Hennig, W. 1981. *Insect phylogeny*. John Wiley & Sons, Chichester.

Herman, G.T. 2009. *Fundamentals of computerized tomography: Image reconstruction from projection*. Second Edition. Springer-Verlag, London.

Hillson, S. 2005. *Teeth*. Second Edition. Cambridge University Publications, Camdridge.

Holliday, J.A., Steppan, S.J. 2004. Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity. *Paleobiology* 30, 108–128.

Hough, J. 1948. The auditory region in some members of the Procyonidae, Canidae, and Ursidae: Its significance in the phylogeny of the Carnivora. *Butlletin of the American Museum of Natural History* 92, 67–118.

Hunt, R.M. 1974. The auditory bulla in Carnivora: an anatomical basis for reappraisal of carnivore evolution. *Journal of Morphology* 143, 21–76.

Hunt, R.M. 1987. Evolution of the aeluroid Carnivora: significance of auditory structure in the nimravid cat *Dinictis*. *American Museum Novitates* 2886, 1–74.

Hunt, R.M. 1989. Evolution of the aeluroid Carnivora: Significance of the ventral promontorial process of the petrosal and the origin of basicranial patterns in the living families. *American Museum Novitates* 2930, 1–32.

Hunt, R.M. 1991. Evolution of the aeluroid Carnivora: viverrid affinities of the Miocene carnivoran *Herpestides*. *American Museum Novitates* 3023, 1–34.

Hunt, R.M. 1996. Biogeography of the order Carnivora. In: Gittleman, J.L. (Ed.), *Carnivore behavior, ecology and evolution*. Vol. 2, pp. 485–541. Cornell University Press, Ithaca.

Hunt, R.M. 1998a. Evolution of the aeluroid Carnivora: diversity of the earliest aeluroids from Eurasia (Quercy, Hsanda-Gol) and the origin of felids. *American Museum Novitates* 3252, 1–65.

Hunt, R.M., 1998b. 10. Ursidae. *Evolution of Tertiary mammals of North America. Volume 1: Terrestrial carnivores, ungulates, and ungulatelike mammals*, pp. 174–195. In: Janis, C.M., Scott, K.M. & Jacobs, L.L. Cambridge, Cambridge University Press.

Hunt, R.M., 1998c. 11. Amphicyonidae. *Evolution of Tertiary mammals of North America. Volume 1: Terrestrial carnivores, ungulates, and ungulatelike mammals*, pp. 196–227. In: Janis, C.M., Scott, K.M. & Jacobs, L.L. Cambridge, Cambridge University Press.

Hunt, R.M. 2001. Basicranial anatomy of the living linsangs *Prionodon* and *Poiana* (Mammalia, Carnivora, Viverridae), with comments on the early evolution of aeluroid carnivorans. *American Museum Novitates* 3330, 1–24.

Hunt, R.M., Tedford, R.H. 1993. Phylogenetic relationships within the aeluroid Carnivora and implications of their temporal and geographic distribution. In: Szalay, F.S., Novacek, M.J. & McKenna, M.C. (Eds.), *Mammal phylogeny: plancentals*, pp. 53–73. Springer-Verlag, New York.

Hunt, R.M., Solounias, N. 1991. Evolution of the Aeluroid Carnivora: Hyaenid affinities of the Miocene Carnivoran *Tungurictis spocki* from Inner Mongolia. *American Museum Novitates* 3030, 1–25.

Hunter, L. 2011. *Carnivores of the World*. Princeton University Press, Princeton and Oxford.

Illiger, J.K.W. 1811. *Prodromus Systematis Mammaliaum et Avium: additis terminis zoographicis utriusque classis, eorumque versione germanica.* Berolini: Sumptibus C. Salfeld, Berlin.

International Commission on Zoological Nomenclature (ICZN). 1999. *International code of zoological nomenclature*, *4th edition*. International Trust for Zoological Nomenclature, London.

Janis, C.M., Baskin, J.A., Berta, A., Flynn, J.J., Gunnell, G.F., Hunt, R.M., Martin, L.D., Munthe, K. 1998. Carnivorous mammals. In: Janis, C.M., Scott, K.M. & Jacobs, L.L. (Eds.), *Evolution of Tertiary mammals of North America*, pp. 70–90. Cambridge University Press, New York.

Jefferies, R.P.S. (1979). The origin of chordates—A methodological essay. In: House, M.R. (Ed.), *The origin of major intervebrate groups*, pp. 443–477. Academic Press, London.

Koepfli, K.P., Gomper, M E., Eizirik, E., Ho, C.C., Linden, L., Maldonado, J.E., Wayne, R.K. 2007. Phylogeny of the Procyonidae (Mammalia: Carnivora): Molecules, morphology and the Great American Interchange. *Molecular Phylogenetics and Evolution* 43, 1076–1095.

Koepfli, K.P., Deere, K.A., Slater, G.J., Begg, C., Begg, K., Grassman, L., Lucherini, M., Veron, G., Wayne, R.K. 2008. Multigene phylogeny of the Mustelidae: Resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. *BMC Biology* 6, 10.

Kretzoi, M. 1943. *Kochitis centenii* n. g. n. sp. ein altertümlicher Creodonte aus dem Oberoligozän Siebenbürgens. *Földtany Közlöny* 73, 10–17.

Kretzoi, M. 1945. Bemerkungen über das Raubtiersystem. *Annales Hististorico-Naturales Musei Nationalis Hungarici* 38, 59–83.

Kruuk, H. 2001. Carnivores. In: *Encyclopedia of Biodiversity.* Volume 1. Academic Press, New Jersey.

Lartet, É. 1851. *Notice sur la Colline de Sansan, suivie d'une récapitulation des diverses espèces d'animaux vertébrés fossiles, trouvés soit a Sansan, soit dans d'autres gisements du terrain tertiaire Miocène dans le bassin Sous-Pyréneen [Avec une liste des coquilles terrestres, lacustres et fluviatiles fossiles du mêmem terrain (par M. Noulet, l'Abbé Dupuy et M. de Boissy)].* J.-A. Portes, Paris.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata.* Laurentii Salvii, Stockholm.

Macdonald, D.W., Kays, R.W. 2005. An Introduction. In: Hopkins, J. (Ed.), *Walker's carnivores of the world*. The John Hopkins University Press, Baltimore.

MacIntyre, G.T. 1966. The Miacidae (Mammalia, Carnivora) Part 1. The systematics of *Ictidopappus* and *Protictis*. *Butlletin of American Museum of Natural History* 131, 115–210.

Major, F. 1903. New Carnivora from the middle Miocene of La Grive Saint Alban, Isère, France. *Geological Magazine* 10, 534–537.

Madurell-Malapeira, J., Robles, J. M., Casanovas-Vilar, I., Abella, J., Obradó, P., Alba, D.M. (in press). The scimitar-toothed cat *Machairodus aphanistus* (Carnivora: Felidae) in the Vallès-Penedès Basin (NE Iberian Peninsula). *Comptes Rendus Palevol.* DOI:10.1016/j.crpv.2014.05.001

Martin, L.D. 1980. Functional morphology and the evolution of cats. *Transactions of the Nebraska Academy of Sciences* 8, 141–154.

Martin, L.D. 1989. Fossil history of the terrestrial Carnivora. In: Gittleman J.L. (Ed.), *Carnivore behavior, ecology and evolution*, pp. 536–568. Cornell University Press, Ithaca.

Martin, L.D. 1998a. Nimravidae. In: Janis, C.M., Scott, K.M. & Jacobs, L.L. (Eds.), *Evolution of Tertiary mammals of North America*, pp. 228–235. Cambridge University Press, New York.

Martin, L.D. 1998b. Felidae. In: Janis, C.M., Scott, K.M. & Jacobs, L.L. (Eds.), *Evolution of Tertiary mammals of North America*, pp. 236–242. Cambridge University Press, New York.

Martínez-Navarro, B., Rook, L. 2003. Gradual evolution in the African hunting dog lineage Systematic implications. *Comptes Rendus Palevol* 2, 695–702.

Matthew, W.D. 1901. Additional observations on the Creodonta. *Butlletin of the American Museum of Natural History* 14, 1–38.

Matthew, W.D. 1909. The Carnivora and Insectivora of the Bridger basin, middle Eocene. *Memoirs of the American Museum of Natural History* 9, 289–567.

McKenna, M.C., Bell, S.K. 1997. *Classification of mammals above the species level*. Columbia University Press, New York.

Mein, P. Ginsburg, L. 2002. Sur l'âge relatif des différents dépôts karstiques miocènes de La Grive-Saint-Alban (Isère). *Cahiers scientifiques* 2, 7–47.

Morales, J., Pickford, M., Salesa, M., Soria, D. 2000. The systematic status of *Kelba*, Savage, 1965, *Kenyalutra*, Schmidt-Kittler, 1987 and *Ndmathaia*, Jacobs et al., 1987, (Viverridae, Mammalia) and a review of Early Miocene mongoose-like carnivores of Africa. *Annales de Paléontologie* 86, 243–251.

Morales, J., Salesa, M.J., Pickford, M., Soria, D. 2001. A new tribe, new genus and two new species of Barbourofelinae (Felidae, Carnivora, Mammalia) from the Early Miocene of East Africa and Spain. *Transactions of the Royal Society of Edinburgh* 92, 97–102.

Morales, J., Pozo, M., Silvia, P.G., Domingo, M.S., López-Antoñanzas, R., Álvarez Sierra, M.A., Antón, M., Martín Escorza, C., Quiralte, V., Salesa, M.J., Sánchez, I.M., Azanza, B., Calvo, J.P., Carrasco, P., García-Paredes, I., Knoll, F., Hernández Fernández, M., van den Hoek Ostende, L., Merino, L., van der Meulen, A., Montoya, P., Peigné, S., Peláez-Campomanes, P., Sánchez Marco, A., Turner, A. 2008. El sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid: estado actual y perspectivas. *Paleontologica Nova SEPAZ* 8, 41-117.

Morlo, M., Peigné, S., Nagel, D. 2004. A new species of *Prosansanosmilus*: implication for the systematic relationship of the family Barbourofelidae new rank (Carnivora, Mammalia). *Zoological Journal of the Linnean Society* 140, 43–61.

Morlo, M., Miller, E.R., El-Barkooky, A.N., 2007. Creodonta and Carnivora from Wadi Moghra, Egypt. *Journal of Vertebrate Paleontology* 27, 145–159.

Morlo, M., Peigné, S. 2010. Molecular and morphological evidence for Ailuridae and a review of its genera. In: Goswami, A. & Friscia A. (Eds.), *Carnivoran evolution: New views on phylogeny, form and function*, pp. 92–140. Cambridge University Press, Cambridge.

Moyà-Solà, S. 1983. Los Boselaphini (Bovidae, Mammalia) del Neógeno de la Península Ibérica. *Publicacions del Departament de Geologia de la Universitat Autónoma de Barcelona* 18, 1–236.

Moyà-Solà, S., Agustí, J. 1990. Bioevents and mammal successions in the Spanish Miocene. In: Lindsay, E.H., Fahlbush, V. & Mein, P. (Eds.), *European Neogene mammal chronology*, pp. 357–373. Plenum Press, New York.

Moyà-Solà, S., Rius Font, L. 1993. El jaciment paleontològic dels Casots (Subirats, Alt Penedès). *Tribuna d'Arqueologia* 1991-1992, 7–12.

Moyà-Solà, S., Kölher, M., Alba, D.M. 2001. *Egarapithecus narcisoi*, a new genus of Pliopithecidae (Primates, Catarrhini) from the Late Miocene of Spain. *American Journal of Physical Anthropology* 114, 312–324.

Moyà-Solà, S., Kölher, M., Alba, D.M., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Cabrera, L., Garcés, M., Almécija, S., Beamud, E. 2009. First partial face and upper dentition of the Middle Miocene hominoid *Dryopithecus fontani* from Abocador de Can

Mata (Vallès-Penedès Basin, Catalonia, NE Spain): Taxonomic and phylogenetic implications. *American Journal of Physical Anthropology* 139, 126–145.

Munthe, K. 1998. *Canidae.* In: Janis, C.M., Scott, K.M. & Jacobs, L.L. (Eds.), *Evolution of Tertiary mammals of North America. Volume 1: Terrestrial carnivores, ungulates, and ungulatelike mammals*, pp. 124–143. Cambridge University Press, Cambridge.

Navas, E., Martinell, J., Domènech R., Batllori, J. 1994. Correlación biostratigráfica entre las sucesiones miocénicas marinas de Sant Pau d'Ordal y Sant Llorenç d'Hortons (Depressión del Vallès-Penedès, Barcelona). *Acta Geológica Hispánica* 29, 149–168.

Neff, N.A. 1983. *The basicranial anatomy of the Nimravidae (Mammalia: Carnivora): Character analyses and phylogenetic inferences*. Ph.D. dissertation, The City University of New York.

Novacek, M.J. 1992. Mammalian phylogeny: shaking the tree. *Nature* 356, 121–125.

Nowak, R.M. 2003. *Walker's marine mammals of the world.* Sixth edition. The John Hopkins University Press. London.

Pales, L., García, M.A. 1981. *Atlas ostéologique des mamiféres*. Ed. CNRS, Paris.

Peigné, S. 2003. Systematic review of European Nimravinae (Mammalia, Carnivora, Nimravidae) and the phylogenetic relationships of Palaeogene Nimravidae. *Zoologica Scripta* 32, 199–229.

Peigné, S., Salesa, M.J., Antón, M., Morales, J. 2005. Ailuid carnivoran mammal Simocyon from the late Miocene of Spain and the systematics of the genus. *Acta Palaeontologica Polonica* 50, 219–238.

Petter, G. 1963. Contribution a l'étude des mustélidés des bassins Néogènes du Vallès-Penedès et de Calatayud-Teruel (Espagne Orientale). *Memoires de la Société Géologique de France* 43, 1–44.

Petter, G. 1964. Deux mustélidés nouveaux du pontien d'Espagne Orientale. *Bulletin du Muséum National d'Histoire Naturelle* 36, 270–278.

Petter, G. 1967. Mustélidés nouveaux du Vallesian de Catalogne. *Annales de Paléontologie* 53, 19–23.

Petter, G. 1976. Étude d'un nouvel ensemble de petits carnivores du Miocène d'Espagne. *Géologie Méditerranéenne* 3, 135–154.

Pineda-Muñoz, S., Casanovas-Vilar, I., Alba, D.M., Carmona, R., Rifà, E. 2011. Cricetinae (Rodentia) from site B40OV/S5C (Vallès-Penedès Basin, NE Iberian Peninsula). In: Pérez-García, A., Gascó, F., Gasulla J.M. & Escaso, F. (Eds.), *Viajando a mundos pretéritos*, pp. 289–296. Ayuntamiento de Morella, Morella.

Pocock, R.I. 1917. The classification of existing Felidae. *Annals of the Magazine of Natural History* 20, 329–350.

Pocock, R.I. 1929. Tigers. *Journal of the Bombay Natural History Society* 33, 505–541.

Polly, P.D., Wesley-Hunt, G.D., Heinrich, R.E., Davis, G., Houde, P. 2006. Earliest known carnivoran auditory bulla and support for a recent origin of crown-group Carnivora (Eutheria, Mammalia). *Palaeontology* 49, 1019–1027.

Pons-Moyà, J. 1990. Presencia de carnívoros turolosienses en el Vallesiense terminal (MN10) de Terrassa (Catalunya). *Paleontologia i Evolució* 23, 199–203.

Reeves, R.B., Stewart, S., Leatherwood, S. 1992. *The Sierra Club handbook of seals and sirenians*. Sierra Club Books, San Francisco.

Riedman, M. 1990. *Pinnipeds: seals, sea Lions, and walruses*. University of California Press, Berkeley.

Robles, J.M., Alba, D.M., Moyà-Solà, S. 2009. The morphology of the upper fourth premolar in *Trocharion albanense* Major, 1903 (Mustelidae: Leptarctinae) and the independent loss of the carnassial notch in leptarctines and other mustelids. *Paleolusitana* 1, 403–409.

Robles, J.M., Alba, D.M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Rotgers, C., Almécija, S., Carmona R. 2010a. New craniodental remains of *Trocharion albanense* Major, 1903 (Carnivora, Mustelidae), from the Vallès-Penedès Basin (Middle to Late Miocene, Barcelona, Spain). *Journal of Vertebrate Paleontology* 30, 547–562.

Robles, J.M., Alba, D.M., Carmona, R., Rotgers, C., Galindo, J., Balaguer, J., Almécija, S., Moyà-Solà, S. 2010b. Nuevos hallazgos de *Sansanosmilus jourdani* (Filhol 1883) (Carnivora: Barbourofelidae) del Mioceno Medio de la serie estratigráfica del Abocador de Can Mata (cuenca del Vallès-Penedès, Barcelona, España). *Cidaris* 30, 265–271.

Robles J.M., Alba, D.M., Casanovas-Vilar, I., Galindo, J., Cabrera, L., Carmona, R., Moyà-Solà. S. 2011. On the age of the paleontological site of Can Missert (Terrassa, Vallès-Penedès Basin, NE Iberian Peninsula). In: Pérez-García, A., Gascó, F., Gasulla J.M. & Escaso, F. (Eds.), *Viajando a mundos pretéritos*, pp. 339–346. Ayuntamiento de Morella, Morella.

Robles, J.M., Alba, D.M., Fortuny, J., De Esteban-Trivigno, S., Rotgers, C., Balaguer, J., Carmona, R., Galindo, J., Almécija, S., Bertó, J.V., Moyà-Solà, S. 2013a. New craniodental remains of the barbourofelid *Albanosmilus jourdani* (Filhol, 1883) from the Miocene of the Vallès-Penedès Basin (NE Iberian Peninsula) and the phylogeny of the Barbourofelini. *Journal os Systematic Paleontology* 11, 993–1022.

Robles, J.M., Madurell-Malapeira, J., Abella, J., Rotgers, C., Carmona, R., Almécija, S., Balaguer, J., Alba, D.M. 2013b. New *Pseudaelurus* and *Styriofelis* remains (Carnivora: Felidae) from the Middle Miocene of Abocador de Can Mata (Vallès-Penedès Basin). *Comptes Rendus Palevol* 12, 101–113.

Robles, J.M., Madurell-Malapeira, J., Casanovas-Vilar, I., Abella, J., Alba, D.M. 2013c. The scimitar-toothed cat *Machairodus aphanistus* (Carnivora, Felidae) in the Vallès-Penedès Basin (NE Iberian Peninsula): new remains and taxonomic revision [Abstract]. *Journal of Vertebrate Paleontology* 33 Suppl. 1, 200.

Robles, J.M., Abella, J., Madurell-Malapeira, J., Alba, D.M. (unpublished manuscript). Miocene carnivorans from the Vallès-Penedès Basin.

Roca, E., Guimerà, J. 1992. The Neogene structure of the eastern Iberian margin: structural constraints on the crustal evolution of the Valencia Trough (Western Mediterranean). *Tectonophysics* 203, 203–218.

Rotgers, C., Alba, D.M. 2011. The genus *Anchitherium* (Equidae: Anchitheriinae) in the Vallès-Penedès Basin (Catalonia, Spain). In: Pérez-García, A., Gascó, F., Gasulla J. M. & Escaso, F. (Eds.), *Viajando a mundos pretéritos*, pp. 347–354. Ayuntamiento de Morella, Morella.

Rotgers, C., Alba, D.M., Robles, J.M., Casanovas-Vilar, I., Galindo, J., Bertó, J.V., Moyà-Solà, S. 2011. A new species of *Anchitherium* (Equidae: Anchitheriinae) from the Middle Miocene of Abocador de Can Mata (Vallès-Penedès Basin, NE Iberian Peninsula). *Comptes Rendus Palevol* 10, 567–576.

Roth, C. 1987. *Die Raubtierfauna aus den miozänen Spaltenfüllungen Petersbusch 2 und Erketshofen 2. Taxonomie-Stratigraphie-Ökologie*. Ph.D. Dissertation, Institute für Geowissenschaften (Paläontologie), Johannes Gutenberg-Universität Mainz.

Roth, C. 1988. *Leptoplesictis* Major, 1903 (Mammalia, Carnivora, Viverridae) aus dem Orleanium und Astaracium/Miozän von Frankreich und Deutschland. *Paläontologische Zeitschrift* 62, 333–343.

Roth, J., Wagner, A. 1854. Die fossilen knochenüberreste von Pikermi in Griechenland. *Abhandlungen der Mathematisch-Physikalischen Classe der Königlich Bayersichen Akademie der Wissenschaften* 7, 371–464.

Salesa, M.J., Montoya, P., Alcalá, L., Morales, J. 2003. The genus *Paramachairodus* Pilgrim, 1913 (Felidae, Machairodontinae) in the Spanish Upper Miocene. *Coloquios de Paleontología* Volumen Extraordinario 1, 603–615.

Salesa, M.J., Antón, M., Turner, A., Morales, J. 2005a. Inferred behaviour and ecology of the primitive sabre-toothed cat *Paramachairodus ogygia* (Felidae, Machairodontinae) from the Late Miocene of Spain. *Journal of Zoology* 268, 243–254.

Salesa, M.J., Antón, M., Turner, A., Morales, J. 2005b. Aspects of the functional morphology in the cranial and cervical skeleton of the sabre-toothed cat *Paramachairodus ogygia* (Kaup, 1832) (Felidae, Machairodontinae) from the Late Miocene of Spain: implications for the origins of the machairodont killing bite. *Zoological Journal of the Linnean Society* 144, 363–377.

Salesa, M.J., Antón, M., Morales, J., Peigné, S. 2012. Systematics and phylogeny of the small felines (Carnivora, Felidae) from the Late Miocene of Europe: a new species of Felinae from the Vallesian of Batallones (MN10, Madrid, Spain). *Journal of Systematic Palaeontology* 10, 87–102.

Sanderson, J.G., Watson, P. 2011. *Small wild cats: The animal answer guide*. The Johns Hopkins University Press. Baltimore.

Sato, J.J., Hosoda, T., Wolsan, M., Tsuchiya, K., Yamamoto, M., Suzuki, H. 2003. Phylogenetic relationships and divergence times among Mustelids (Mammalia: Carnivora) based on nucleotide sequences of the Nuclear Interphotoreceptor Retinoid binding protein and Mitochondrial Cytochrome *b* Genes. *Zoological Science* 20, 243–264.

Sato, J.J., Hosoda, T., Wolsan, M., Suzuki, H. 2004. Molecular phylogeny of arctoids (Mammalia: Carnivora) with emphasis on phylogenetic and taxonomic positions of the ferret-badgers and skunks. *Zoological Sciencie* 21, 111–118.

Sato, J.J., Wolsan, M., Suzuki, H., Yamaguchi, Y., Hiyama, K., Kobayashi, M., Minami, S. 2006. Evidence from nuclear DNA sequences sheds light on the phylogenetic relationships of Pinnipedia: single origin with affinity to Musteloidea. *Zoological Science* 23, 125–146.

Savage, D.E. 1977. Aspects of vertebrate paleontological stratigraphy and geochronology. In: Kaufman, E.G. & Hazel, J.E. (Eds.), *Concepts and methods in biostratigraphy*, pp. 427–442. Dowden, Hutchinson and Ross, Stroudsburg.

Sechrest, W., Brooks, T.M., da Fonseca, G.A.B., Konstant, W.R., Mittermeier, R.A., Purvis, A., Rylands, A.B., Gittleman, J.L. 2002. Hotspots and the conservation of evolutionary history. *Proceedings of the National Academy of Sciences U.S.A.* 99, 2067–2071.

Schlosser, M. 1904. Notizen über einige Säugethiere aus dem Miocän von Württemberg und Bayern. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie B* 19, 485–502.

Schlosser, M. 1923. Säugetiere. In Broili, F. & Schlosser, M. (Eds.). *K. A. von Zittel, Grundzüge der Paläontologie, neu bear-beitet*, pp. 402–689. M. R. Oldenbourg, Munich.

Schlosser, M. 1924. Tertiary vertebrates from Mongolia. *Palaeontologia Sinica* 1, 1–133.

Schmidt-Kittler, N. 1976. Raubtiere aus dem Jungtertiär Kleinasiens. *Palaeontolographica A* 155, 1–131.

Schultz, C.B., Schultz, M.R., Martin, L.D. 1970. A new tribe of saber-toothed cats (Barbourofelini) from the Pliocene of North America. *Bulletin of the University of Nebraska State Museum* 9, 1–31.

Schmidt-Kittler, N. 1981. Zur Stammesgeschichte der marderverwandten Raubtiegruppen (Musteloidea, Carnivora). *Eclogae Geologica Helvetica* 74, 753–801.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85, 1–350.

Smith, J.B., Dodson, P. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology* 23, 1–12.

Solé, F., Gheerbrant, E., Godinot, M. 2013. The "miacids" (Carnivoraformes, Mammalia) from Early Eocene locality of Le Quesnoy (MP7, France); first occurrence of Vassacyon in Europe. *Comptes Rendus Palevol* 12, 191–202.

Soltis, P.S., Soltis, D.E. 2003. Applying the bootstrap in phylogeny reconstruction. *Statistical Science* 18, 256–267.

Spaulding, M., Flynn, J.J. 2009. Anatomy of the postcranial skeleton of "*Miacis*" *uintensis* (Mammalia: Carnivoramorpha). *Journal of Vertebrate Paleontology* 29, 1212–1223.

Spaulding, M., Flynn, J.J., Stucky, R.K. 2010. A new basal carnivoramorphan (Mammalia) from the "Bridger B" (Black's Fork Member, Bridger Formation, Bridgerian Nalma, Middle Eocene) of Wyoming, USA. *Palaeontology* 53, 815–832.

Spaulding, M., Flynn, J.J. 2012. Phylogeny of the Carnivoramorpha: The impact of postcranial characters. *Journal of Systematic Palaeontology* 10, 653–677.

Swofford, D.L. 2003. PAUP* 4.0. Sinauer Associates, Sunderland, Massaachusetts.

Swofford, D.L., Sullivan, J. 2009. Phylogeny inference based on parsimony and other methods using PAUP*. In: Lemey, P., Salemi, M. & Vandamme, A.-M. (Eds.), *The* *phylogenetic handbook. A practical approach to phylogenetic analysis and hypothesis testing*, pp. 267–312. Cambridge University Press, Cambridge.

Tedford, R.H. 1976. Relationship of pinnipeds to other carnivores (Mammalia). *Systematic Zoology* 25, 363–374.

Tedford, R.H. 1978. History of dog and cats: a view from the fossil record. In: *Nutrition and management of dogs and cats*. Ralston Purina Co, St. Louis.

Thenius, E. 1977. Zur systematischen Stellung von *Protursus* (Carnivora, Mammalia). *Anzeiger der Österreichischen Akademie der Wissenchaften, mathematisch-naturwissenschaflichen Klasse* 3, 37–41.

Tomiya, S. 2011. A new basal caniform (Mammalia: Carnivora) from the middle Eocene of North America and remarks on the phylogeny of early carnivorans. *PLoS ONE* 6, e24146.

Tomiya, S. 2013. New carnivoraforms (Mammalia) from the middle Eocene of California, USA, and comments on the taxonomic status of "*Miacis*" *gracilis*. *Palaeontologia Electronica* 16, 1–29.

Toula, F. 1884. Über *Amphicyon*, *Hyaemoschus* und *Rhinoceros* (*Aceratherium*) von Göriach bei Turnau in Steiermark. *Sitzungsberichte der Königlich Akademie der Wissenschaften Mathematisch-Naturwissenschaftlichen* 90, 406–428.

Tomàs, M., Alba, D.M., Robles, J.M., Rotgers, C., Carmona, R., Galindo, J., Almécija, S., Bertó, J.V., Casanovas-Vilar. I., Balaguer, B., Moyà-Solà, S. 2010. Small suoids from the Middle Miocene of Abocador de Can Mata (Vallès-Penedès Basin, NE Iberian Peninsula): A preliminary assessment. In: Pérez-García, A., Gascó, F., Gasulla J.M. & Escaso, F. (Eds.), *Viajando a mundos pretéritos*, pp. 390–398. Ayuntamiento de Morella, Morella.

Trouessart, É.L. 1885. Catalogue des Mammifères vivants et fossiles. Fasc. IV–Carnivores (Carnivora). *Bulletin de la Societé d'Études Scientifiques d'Angers* 15, 1–108.

Tseng, Z.J., Takeuchi, G.T., Wang, X. 2010. Discovery of the upper dentition of *Barbourofelis whitfordi* (Nimravidae, Carnivora) and an evolution of the genus in California. *Journal of Vertebrate Paleontology* 30, 244–254.

Turner, A., Antón, M. 1997. *Big cats and their fossil relatives: an illustrated guide*. Columbia University Press, New York.

Valenciano, A., Abella, J., Sanisidro, O., Álvarez-Sierra, M.A., Morales, J. 2013, in press. A complete skull and mandible of *Eomelllivora piveteaui* Ozansoy, 1965 (Carnivora, Mammalia) from Batallones-3 (MN10), Upper Miocene (Madrid, Spain). *Journal of Vertebrate Paleontology.*

Van Valen, L. 1969. The multiple origins of the placental carnivores. *Evolution* 23, 1–11.

Vaughan, T.A., Ryan, J.M., Czaplewski, N.J. 2011. Carnivora. In: Vaughan, T.A., Ryan, J.M. & Czaplewski, N.J. (Eds.), *Mammalogy.* Fifth Edition, pp. 293–320. Jones and Bartlett Publishers, Sudbury.

Veron, G. 1994. *Méthodes de recherche en biotaxonomie des mammifères carnivores. Confrontation des méthodes de phylogénie traditionnelle et moléculaire dans la recherche de la position systématique* de Cryptoprocta ferox *(Aeluroidea)*. Doctoral dissertation, Muséum National d'Histoire Naturelle, Paris.

Veron, G. 1995. La position systématique de *Cryptoprocta ferox* (Carnivora). Analyse cladistique des caractères morphologiques de carnivores Aeluroidea actuels et fossiles. *Mammalia* 59, 551–582.

Veron, G. 2010. Phylogeny of the Viverridae and "viverrid-like" feliforms. In: Goswami, A. & Friscia A. (Eds.), *Carnivoran evolution: New views on phylogeny, form and function*, pp. 64–91. Cambridge University Press, Cambridge.

Vicente i Castells, J. 1987. Noves troballes al jaciment de mamífers de Cases de la Valenciana (Gelida, Alt Penedès). *Butlletí del Centre d'Estudis de la Natura del Barcelonès Nord* 3, 130–131.

Villalta Comella, J.F. de, Crusafont Pairó, M. 1941. Noticia preliminar sobre la fauna de carnívoros del Mioceno continental del Vallés-Penedés. *Boletín de la Real Sociedad Española de Historia Natural. Sección (Geología)* 39, 201–208.

Villalta Comella, J.F. de, Crusafont Pairó, M. 1943a. Los Vertebrados del Mioceno continental de la cuenca del Vallès-Penedès. (Prov. de Barcelona): I) Insectívoros. II) Carnívoros. *Boletín del Instituto Geológico y Minero de España* 46, 147–314.

Villalta Comella, J.F. de, Crusafont Pairó, M. 1943b. *Indarctos vireti* nova sp., un nuevo úrsido del grupo de los hemiciónidos del mioceno superior del Vallés-Panadés. Consejo Superior de Investigaciones Científicas, Madrid.

Villalta Comella, J.F., Crusafont Pairó, M. 1944. Nuevos carnívoros del Vindoboniense de la cuenca del Vallés-Panadés. *Notas y Comunicaciones del Instituo Geológico y Minero de España* 13, 53–88.

Villalta, J.F., Crusafont, M. 1946a. Les gisements de Mamifères du Néogène espagnol. III. Bassin du Vallés-Penadés (Catalogne). Pontien. *Comptes Rendus Sommaires de la Société Géologique de France,* 224–227.

Villalta, J.F., Crusafont, M. 1946b. Les gisements de Mammifères du Néogène espagnol. II. Bassin de Vallès-Pénadès (Catalogne), Vindobonien, Hostalets de Pierola. *Comptes Rendus Sommaires de la Société Géologique de France,* 133–134.

Villalta, J.F., Crusafont, M. 1946c. Les gisements de Mammifères du Néogène espagnol. I. Bassin du Valles-Panaeés [sic] (Catalogne) Vindobonien. Sant Quirze de Galliners. *Comptes Rendus Sommaires de la Société Géologique de France,* 49–51.

Villalta Comella, J.F. de, Crusafont Pairó, M. 1948. Nuevas aportaciones al conocimiento de los carnívoros pontienses del Vallès-Penedès. In: *Miscelánea Almera*. *Publicaciones del Instituto* Geológico 7, 81–121.

Villalta, J.F. de. Crusafont, M. 1952. *Grivasmilus* remplaçant *Albanosmilus* (=*Sansanomilus*). *Comptes Rendus des Seances de la Société Géologique de France* 14, 308–309.

Viret, J. 1951. Catalogue critique de la faune des Mammifères miocènes de la Grive Saint-Alban (Isère). Première partie: Chiroptères, Carnivores, Edentés pholidotes. *Nouvelles Archives du Museum d'Histoire Naturelle de Lyon* 3, 1–102.

Viret, J., Crusafont-Pairó, M. 1955. *Plesiomeles Cajali* n. gen. n. sp. un Méliné du Vallésien d'Espagne. *Eclogae Geologicae Helvetiae* 48, 447–452.

Vrana, P.B., Milinkovitch, M.C., Powell, J.R., Wheeler, W.C. 1994. Higher level relationships of the artoid Carnivora based on sequence data and total evidence. *Molecular Phylogenetics and Evolution* 3, 47–58.

Wang, X., Tedford, R.H. 1994. Phylogenetic systematics of the Hesperocyoninane (Carnivora: Canidae). *Bulletin of the American Museum of Natural History* 221, 1–207.

Wang, X., Whistler, D.P., Takeuchi, G.T. 2005a. A new basal skunk *Martinogale* (Carnivora, Mephitinae) from late Miocene Dove Spring Formation, California, and origin of New World mephitines. *Journal of Vertebrate Paleontology* 25, 936–949.

Wang, X., McKenna, M.C., Dashzeveg, D. 2005b. *Amphicticeps* and *Amphicyonodon* (Arctoidea, Carnivora) from Hsanda Gol Formation, Central Mongolia and Phylogeny of Basal Arctoids with Comments on Zoogeography. *American Museum Novitates* 3483, 1–57.

Werdelin, L., Solounias, N. 1991. The Hyaenidae: Taxonomy, systematics and evolution. *Fossils and Strata* 30, 1–104.

Wesley-Hunt, G.D., Flynn, J.J., 2005. Phylogeny of the Carnivora: Basal relationships among the carnivoramorphans, and assessment of the position of carnivora. *Journal of Systematic Palaeontology* 31, 1–28.

Wesley-Hunt, G.D., Werdelin, L., 2005. Basicranial morphology and phylogenetic position of the upper Eocene carnivoramorphan *Quercygale*. *Acta Palaeontologica Polonica* 504, 837–846.

Williams, B.A. 2007. Comparing levels of homoplasy in the primate skeleton. *Journal of Human Evolution* 52, 480–489.

Wilson, D.E., Reeder, D.M. 1993. *Mammals species of the world, Second Edition*. Smithsonian Intitution Press, Washington, D. C.

Wolsan, M. 1993. Phylogeny and classification of early European Mustelida (Mammalia: Carnivora). *Acta Theriologica* 38, 345–384.

Wolsan, M., Bryant, H.N. 2004. Phylogenetic nomenclature of carnivoran mammals. In: *First International Phylogenetic Nomenclature Meeting, Paris, Muséum National d'Histoire Naturelle*, pp. 32–33.

Wortman, J.L. 1901. Studies of Eocene Mammalia in the Marsh collection, Peabody Museum. *American Journal of Science* 162, 281–296.

Wortman, J.L., Matthew, W.D. 1899. The ancestry of certain members of the Canidae, the Viverridae, and Procyonidae. *Bulletin of the American Museum of Natural History* 12, 109–139.

Wozencraft, W.C. 1989. Phylogeny of the Recent Carnivora. In: Gittleman, J. (Ed.), *Carnivore behaviour, ecology and evolution, Vol. 3*, pp. 495–535. Cornell University Press, New York.

Wozencraft, W.C. 2005. Order Carnivora. In: Wilson, D.E. & Reeder, D.M. (Eds.), *Mammal Species of the World*, *Third Edition*, pp. 532–628. Smithsonian Institution Pres, Washington

Wyss, A.R., Flynn, J.J. 1993. A phylogenetic analysis and definition of the Carnivora. In: Szalay, F.S., Novacek, F.S. & McKenna, M.C. (Eds.), *Mammal phylogeny: Placentals*, pp. 32–52. Springer-Verlag, New York.

Yoder, A.D., Burns, M.M., Zehr, S., Delefosse, T., Veron, G., Goodman, S.M., Flynn, J.J. 2003. Single origin of Malagasy Carnivora from an African ancestor. *Nature* 421, 734–737.

Yonezawa, T., Nikaido, M., Kohno, N., Fukumoto, Y., Okada, N., Hasegawa, M. 2007. Molecular phylogenetic study on the origin and evolution of Mustelidae. *Gene* 396, 1–12.

Young, J.Z. 1971. *La vida de los vertebrados*. Omega, Barcelona.

Yu, L., Li, Q., Ryder, O.A., Zhang, Y. 2004. Phylogenetic relationships within mammalian order Carnivora indicated by sequences of two nuclear DNA genes. *Molecular Phylogenetics and Evolution* 33, 694–705.

Yu, L., Zhang, Y.P. 2006. Phylogeny of the caniform carnivora: evidence from multiple genes. *Genetica* 127, 65–79.

Zittel, K.A. 1893. *Traité de Paléontologie III, Palaeozologie Verterbata (Pisces, Amphibia, Reptilia, Aves).* O. Doin, Paris.

APPENDIXES

Appendix 1. *Kretzoiarctos* gen. nov., the oldest member of the giant panda clade

Reproduced from:

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Kretzoiarctos gen. nov., the Oldest Member of the Giant Panda Clade

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Abstract

The phylogenetic position of the giant panda, *Ailuropoda melanoleuca* (Carnivora: Ursidae: Ailuropodinae), has been one of the most hotly debated topics by mammalian biologists and paleontologists during the last century. Based on molecular data, it is currently recognized as a true ursid, sister-taxon of the remaining extant bears, from which it would have diverged by the Early Miocene. However, from a paleobiogeographic and chronological perspective, the origin of the giant panda lineage has remained elusive due to the scarcity of the available Miocene fossil record. Until recently, the genus *Ailurarctos* from the Late Miocene of China (ca. 8–7 mya) was recognized as the oldest undoubted member of the Ailuropodinae, suggesting that the panda lineage might have originated from an *Ursavus* ancestor. The role of the purported ailuropodine *Agriarctos*, from the Miocene of Europe, in the origins of this clade has been generally dismissed due to the paucity of the available material. Here, we describe a new ailuropodine genus, *Kretzoiarctos* gen. nov., based on remains from two Middle Miocene (ca. 12–11 Ma) Spanish localities. A cladistic analysis of fossil and extant members of the Ursoidea confirms the inclusion of the new genus into the Ailuropodinae. Moreover, *Kretzoiarctos* precedes in time the previously-known, Late Miocene members of the giant panda clade from Eurasia (*Agriarctos* and *Ailurarctos*). The former can be therefore considered the oldest recorded member of the giant panda lineage, which has significant implications for understanding the origins of this clade from a paleobiogeographic viewpoint.

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Introduction

The Fossil Record of the Giant Panda Lineage

The extant giant panda from central Asia, *Ailuropoda melanoleuca* [1], differs from other living ursids by the presence of several craniodental adaptations to durophagy (i.e., feeding tough plant material, mainly bamboo) [1,2,3,4]. These adaptations are already present, to a large extent, in the Plio-Pleistocene relatives of *A. melanoleuca* (*Ailuropoda microta* and *Ailuropoda wulingshanensis*) [2,4], which displayed a larger distribution, from northern China to Southeast Asia [5,6,7], than the living giant panda. Despite long-lasting disputes about the phylogenetic position of *Ailuropoda*, especially due to dietary-driven convergence in the dentition with the lesser panda (*Ailurus fulgens*) [2,3], it is currently well-established on molecular grounds that the former corresponds to the living sister-taxon of other extant bears [8,9,10,11,12,13], being classified in its own subfamily (Ailuropodinae) [11,13] or tribe (Ailuropodini) [14]. Molecular data have estimated the divergence time between ailuropodines and other bears to correspond to the Early Miocene (ca. 22 mya [8], 19 mya [12] or 18 mya [2]). However, from a paleontological perspective, ailuropodine origins are still largely uncertain, due to the paucity of the available Miocene record [14]. It is generally considered that *Ailuropoda* descended from the Asian, Late Miocene ursid *Ailurarctos* [5,7,14]. The latter genus is first recorded by *Ai. yuanmouensis* from the Chinese locality of Yuanmou (8.2-7.2 mya) [15], being subsequently recorded by *Ai. lufengensis* from Lufeng (6.9-5.8 mya) [5,6,7,14,15]. *Ailurarctos* has been considered to be descended from an unidentified Miocene species of *Ursavus* [4,5,6,7,14], although no formal cladistic analysis had been thus far provided to substantiate such phylogenetic hypothesis.

Besides *Ailurarctos*, the extinct genus *Agriarctos*, from the Miocene of Europe [5,16,17,18], has been also attributed to the Ailuropodinae. Until recently, the scarcity of available *Agriarctos* material precluded a secure assessment of its phylogenetic affinities with the Late Miocene *Ailurarctos*, which already displays incipient adaptations to durophagy, being customarily considered the oldest undoubted member of the giant panda lineage [2,4,5,7,14]. The type species of *Agriarctos*, *Ag. gaali*, was originally based on a mandibular fragment with p3-m2 [16] from the Turolian (MN12, Late Miocene) locality Hatvan (Hungary) [19]. *Ag. vighi* was also created by Kretzoi (1942), after an m1 from the Hungarian locality of Rózsaszentmárton. With no other material for comparison, provisionally we consider these two species as valid, until a more detailed study of these fossils is carried out. Although some authors attributed the holotype of *A. gaali* to *Indarctos* cf. *vireti* [19], more recently the validity of the former genus and species have been supported [20], being characterized by a strong development of the distal cusps of the premolars (usually poorly developed or absent in most of the Ursidae) and by the mesial position of the m1 metaconid [20]. *Agriarctos* was first transferred to the Ailuropodinae several decades ago [17,18], by further including material from the Late Miocene localities of Soblay (MN10, France; [21]) and Wissbergh (= Gau-Weinheim; MN9, Germany), previously attributed to *Ursavus depereti* [22,23,24]. The remains from Soblay differ from *Ursavus* by the lengthening of the upper carnassial, due to the presence of a parastyle [22,23]. They can be therefore attributed to the genus *Agriarctos* [17,20], even if indirectly (i.e., *Agriarctos* cf. *gaali*) (18), since a direct comparison with the *Ag. gaali* holotype is not possible due to the lack of upper dentition in the latter.

Most recently, an older, new species of this genus, *Agriarctos beatrix*, was described on the basis of dental remains from the late Aragonian (MN8, Middle Miocene) locality of Nombrevilla 2 (NOM2, Calatayud-Daroca Basin, Spain) [20], formerly attributed to *Ursavus primaevus* [25]. Given the lack of lower dentition, however, a direct comparison with *Ag. gaali* from the type locality was not feasible. On the basis of a new mandible of the same species, recovered in a similarly-aged (MN8) locality from the Abocador de Can Mata (ACM) local stratigraphic series (Vallès-Penedès Basin, Spain), here we show that *"Agriarctos" beatrix* is distinct enough as to be attributed to a different genus, *Kretzoiarctos* gen. nov. This new genus represents the oldest and most basal member of the ursid clade currently represented by *Ailuropoda*, thus being of utmost significance for understanding the origin of the giant panda lineage from both a chronological and paleobiogeographic perspectives.

Age and Geological Background

The local stratigraphic series of ACM (els Hostalets de Pierola, Catalonia, Spain), situated in the Vallès-Penedès Basin (NE Iberian Peninsula), is a 250 m-thick stratigraphic composite succession including more than 200 fossil vertebrate localities and spanning about 1 myrs (from ca. 12.5 to 11.5 mya; late Aragonian, Middle Miocene) [26,27,28,29]. The new material described in this paper (IPS46473) corresponds to an isolated find from sector ACM/C6-Camí, in a stratigraphic horizon situated 2 m above the formally-defined locality ACM/C6-A1. Based on litho- and magnetostratigraphic correlation [27,30], both ACM/C6-A1 and the layer where IPS46473 was found are correlated to subchron C5r.2n, with an interpolated estimated age of 11.6 mya. Although no associated small mammal remains are available for IPS46473, its age indicates that this find belongs to the *Megacricetodon ibericus* + *Democricetodon crusafonti* concurrent range local biozone [29,31], which can be correlated to the MN8 sensu Mein and Ginsburg [32]. The locality of Nombrevilla 2 (NV2), situated in the Calatayud-Daroca Basin, can be correlated to the same biozone, spanning from ca. 11.8-11.2 mya [29,31], given the presence of *M. ibericus* and *D. crusafonti* together with the lack of the hipparionine equid *Hippotherium* [25].

Systematic Paleontology

Order Carnivora Bowdich, 1821; suborder Caniformia Kretzoi, 1942; infraorder Arctoidea Flower, 1869; parvorder Ursida Tedford, 1976; superfamiliy Ursoidea Fischer von Waldheim, 1814; family Ursidae Fischer von Waldheim, 1814; subfamily Ailuropodinae Grevé, 1894; tribe Ailuropodini Grevé, 1894; *Kretzoiarctos* gen. nov.

Etymology: Dedicated to the paleontologist Miklós Kretzoi and from the Greek *'arctos'* (bear).

Type species: *Kretzoiarctos beatrix* (Abella et al., 2011) comb. nov. [20].

Diagnosis: as for the type species.

Differential Diagnosis

Kretzoiarctos shares many morphological characters with the other middle and late Miocene European (*Ursavus*, *Indarctos* and *Agriarctos*) and Asian (*Ailurarctos*) ursid genera, from which it is distinguished by a unique combination of features. *Kretzoiarctos* differs from *Ursavus* in the relative development of the upper premolars and lower molars. Thus, the upper carnassial in *Ursavus* is triangular and always lacks a parastyle, whereas in *Kretzoiarctos* it shows a well-developed parastyle (although not yet separated from the paracone). In turn, the lower carnassial in *Ursavus* has a well-developed sectorial blade in the trigonid, whereas in *Kretzoiarctos* the m1 displays blunt and low cuspids. Moreover, the m2 in *Ursavus* is relatively shorter than in *Kretzoiarctos* because of the lesser-developed talonid. *Kretzoiarctos* differs from *Agriarctos* in the following features: smaller dental size; less developed lower premolars without strong accessory cusps; P4 with a less developed parastyle, a less complex and more mesially-situated protocone, much less developed basal labial cingulum, more labiolingually-compressed labial cusps (parastyle, paracone and metastyle), and P4 slightly longer than the M1 (instead of being similar in length). Finally, *Kretzoiarctos* can be easily distinguished from *Indarctos* by the smaller size of the former. *Indarctos vireti* is the smallest species of this genus and the only one that could be mistaken for *Kretzoiarctos*, although they can be distinguished because *I. vireti* has no trace of parastyle and no accessory cusps in the premolars.

Kretzoiarctos beatrix (Abella et al., 2011) comb. nov

Synonyms: *Ursavus depereti* (in ref. [33], p. 78); *Ursavus primaevus* (in ref. [25], p. 31); *Agriarctos beatrix* (in ref. [20], p. 188).

Holotype: left P4, NV-2-42 (Figure 1; 3a–c) from NV II.

Paratype: right M1, NV-2-40 (Figure 1; 4a–c) from NV II.

The hypodigm also includes the new material described here: partial right mandible with c1–m2 and associated P4, IPS46473 (Figure 1; 1–2 and Figure 2) from ACM/C6-Camí.

Type locality: Nombrevilla 2 (NV II; Calatayud-Daroca Basin, Spain).

Other localities: ACM/C6-Camí (Vallès-Penedès Basin, Spain).

Chronological range: the type locality has an age of ca. 11.8-11.2 mya [34], whereas ACM/C6-Camí has an estimated age of 11.6 mya, both localities thus being correlated to the MN8 *sensu* Mein and Ginsburg [32] (late Aragonian, Middle Miocene).

Emended Diagnosis

Small-sized ailuropodine species. P4 with a well-developed protocone situated opposite to the paracone, and parastyle of moderate size but well-individualized from the protocone. M1 with a highly-developed metastyle and lingual cingulum poorly-differentiated from the protocone and hypocone [20]. Robust mandibular corpus, deepest under the m1 and m2. Low-crowned and curved lower canine. Lower premolars (p2–p4) with a single, duniform main cusp, and reduced mesial and distal accessory cusps, not separated by any diastema. Long and low-crowned m1, with the metaconid and protoconid of similar height, long and shallow talonid basin, and no cusp at the paraconid-hypoconid valley. Relativelly long m2 with well-developed trigonid and talonid basins.

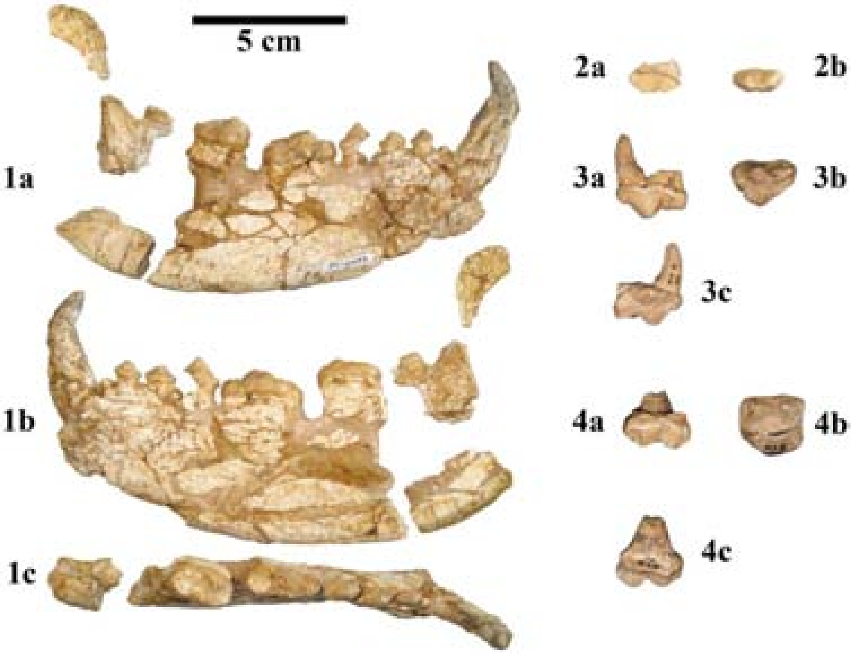

Figure 1. Dentognathic material of *Kretzoiarctos* gen. nov. *beatrix*. 1, Right mandible with canine and p2–m3 IPS46473 from ACM/C6-Camí in labial (a), lingual (b) and occlusal (c) views; 2, Broken P4 IPS46473 in labial (a) and occlusal (b) views; 3, Left P4 NV-2-42 (holotype) in labial (a), occlusal (b) and lingual (c) views; 4, Right M1 NV-2-42 (paratype) in labial (a), occlusal (b) and lingual (c) views from Nombrevilla 2.
doi:10.1371/journal.pone.0048985.g001

Description of the New Material

IPS46473 corresponds to a partial right mandible that preserves the canine and the lower cheek teeth (see measurements in Table 1). The mandibular corpus is short, displays a rounded ventral outline and is taller under the m1–m2 than at the symphyseal region. Despite some damage, a relatively tall and verticalized coronoid process may be reconstructed. The lower canine, which is slightly displaced out from its alveolus, is low-crowned and curved. The premolars (p2–p4) have a single main cusp that displays a duniform shape, as well as poorly-developed mesial and distal accessory cusps. There is no diastema between the lower premolars. The m1 is long and low-crowned; the metaconid and the protoconid are similar in heigh; the talonid basin is long and shallow; no cusp can be observed within the paraconid-hypoconid valley. The m2 is long, and both the trigonid and talonid basins are shallow but wide. The associated P4 is quite damaged, and only the paracone and metastyle can be observed; however, it is possible to ascertain that it was a long upper carnassial with a well-developed labial cingulum; the parastyle is preserved but it cannot be clearly observed due to breakage; both the paracone and metastyle are low and wide.

Results

Nomenclatural Statement

An LSID number was obtained for the new taxon (Genus *Kretzoiarctos*):

urn:lsid:zoobank.org:act:96C5EE3D-3C7B-4D5B-80FD-95C242753DFA.

Cladistic Analysis

A cladistic analysis based on a morphologic data matrix for living and fossil ursids recovered a single most parsimonious tree of 157 steps (Figure 3). Besides the outgroup (the canid *Canis lupus*), the basal-most taxon is *Zaragocyon daamsi*, a representative of the Hemicyionidae–stem Ursoidea not included within the Ursidae [35]. The analysis therefore recovers the monophyly of the Ursidae, represented by three consecutive members of its stem lineage (*Ballusia elmensis*, *Ursavus primaevus* and *Ursavus brevirhinus*, the latter suggesting that the genus *Ursavus* is paraphyletic), and two major clades: the Ailuropodinae, including the extant giant panda (*Ailuropoda*); and the Ursinae + Tremarctinae, including all the extand ursids except *Ailuropoda*. Among the latter, the extant *Tremarctos ornatus* appears as the basal most species, followed by *Melursus ursinus*. Among the Ailuropodinae, two distinct subclades can be distinguished: that composed by *Indarctos* species (*I. vireti*, *I. arctoides* and *I. punjabiensis*), which are here included in a distinct tribe, Indarctini tribe nov. (type genus *Indarctos*); and the one including the remaining ailuropodines (tribe Ailuropodini). The Indarctini appear as the sister-taxon of the Ailuropodini, comprising the European genera *Agriarctos* and *Kretzoiarctos*, as well as the Asian *Ailuropoda* and *Ailurarctos*. The three extinct ailuropodin genera are recovered as a monophyletic clade, sister taxon of the extant *Ailuropoda*.

A bootstrap analysis (Figure 3) shows that most of the clades recovered by the most parsimonious tree are relatively well supported (i.e., bootstrap values higher than 50%). The monophyly of the Ursidae total group (bootstrap value 79) and of the Ursidae crown-group (bootstrap value 66) are well supported, whereas in contrast the successive stem position of *Ursavus* species is not supported. Among crown ursids, the dichotomy between Ailuropodinae (bootstrap value 82) and the clade composed by Tremarctinae + Ursinae (bootstrap value 82) is also well supported. Within the latter, only the position of the ursines *Helarctos malayanus* and *Ursus thibetanus* are not supported by the 50% mayority rule bootstrap analysis (see Discussion). Within the Ailuropodinae, no clade is supported by the 50% mayority rule tree recovered by the bootstrap analysis. The lack of resolution among this subfamily may be attributed to the retention of many plesiomorphies shared with both the successive stem ursids *Ursavus*

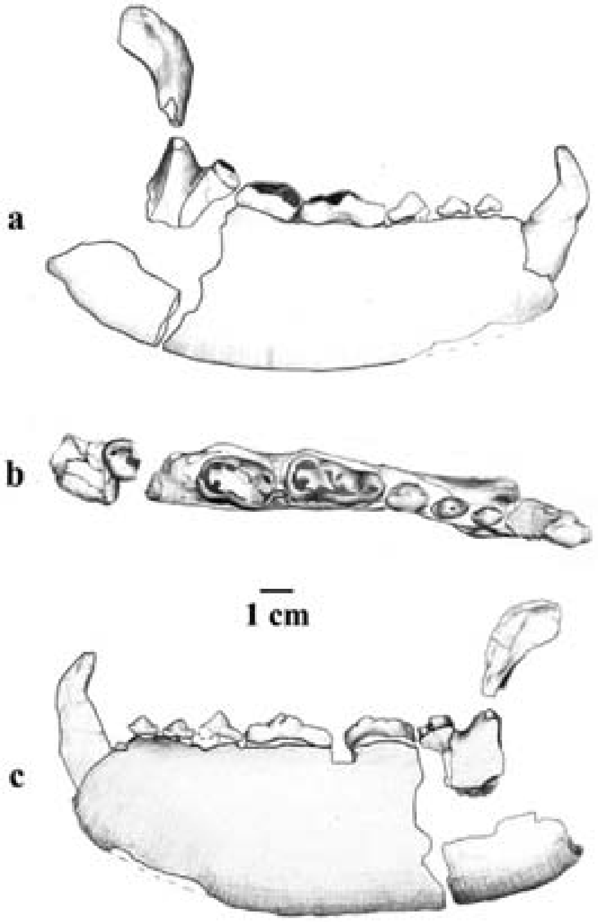

Figure 2. Drawing of the new material of *Kretzoiarctos* gen. nov. *beatrix* from ACM/C6-Camí. a, labial; b, occlusal; c, lingual. Artwork by Marta Palmero.
doi:10.1371/journal.pone.0048985.g002

and *Ballusia*, as well as with the other most primitive members of the Ailuropodinae (*Indarctos*, *Kretzoiarctos* and *Agriarctos*). However, most importantly, the inclusion of *Kretzoiarctos* and the other putative extinct ailuropodines in this subfamily is well supported not only by the most parsimonious cladogram but also by the bootstrap analysis. Accordingly, the new genus *Kretzoiarctos* emerges as the oldest member of the panda lineage (either the Ailuropodini and the Ailuropodinae) thus far recorded, thus enabling to track the fossil record of this subfamily of bears back to the MN8 (11.8-11.2 mya).

Discussion

The results of our cladistic analysis of the Ursoidea mostly agree well with molecular analyses performed on extant ursids [13,36,37], especially regarding the fact that the giant panda appears as the sister-taxon of all remaining members of this family. There are a few particular points that should be taken into account. The first is the position of *Melursus ursinus*, considered a member of the Ursinae, but not showing a clear position within this clade [13]. *M. ursinus* displays a very autapomorphic craniodental morphology adapted to myrmecophagy [38], characterized by reduced teeth and even lacking several incisors. Accordingly, the basal position of *Melursus* recovered by our analysis–restricted to dental, cranial and mandibular features–even though it does not differ much from the genetic-based analysis–could be interpreted as an artifact, reflecting its very autapomorphic dietary complex relative to the remaining Ursinae. A similar anomalous result is obtained by our analysis regarding tha lack of support of the *Ursus* clade, whose monophyly is supported by molecular studies [13]. Like above, the divergent dietary adaptations displayed among the ursine bears [39] could be the cause of this ambiguity.

Table 1. Dental measurements (in mm) of *Kretzoiarctos beatrix* from ACM/C6-Camí (this study) and Nombrevilla 2 (from ref. 20).

Catalogue No.	Tooth	Length	Width
IPS46473	Right lower canine	14.73	8.84
IPS46473	Right p2	7.67	4.83
IPS46473	Right p3	5.33	8.87
IPS46473	Right p4	–	6.64
IPS46473	Right m1	22.64	10.80
IPS46473	Right m2	17.74	11.28
IPS46473	Right m3	–	9.73
NV-2-42 (holotype)	Left P4	18.5	13.0
NV-2-40 (paratype)	Rright M1	17.2	15.4

doi:10.1371/journal.pone.0048985.t001

With regard to Ailuropodinae, our analysis indicates that this subfamily constitutes a monophyletic clade, sister-taxon to that including the remaining ursid subfamilies (Tremarctinae and Ursinae), in agreement with molecular analyses [13]. According to our results, the Ailuropodinae would be characterized by the following synapomorphies: a tall coronoid process; a high articular process; and alisphenoid canal present. Most of the remaining characteristics of this group correspond to primitive features that have been subsequently lost in both the Tremarctinae and the Ursinae, including among others: the development of the premolars; the well-developed carnassials; the wide molars; and the curved tooth row. These primitive characters are not informative for distinguishing ailuporodines from stem ursids, although they can be used to distinguish the former from the two other, more derived subfamilies of crown ursids. Along with these features, in the Ailuropodinae there is a tendency towards an increased dental complexity, as reflected by the presence of a well-developed parastyle and a complex protocone, which is a synapomorphy shared by all ailuropodines except the primitive *Indarctos vireti*. A list of all the apomorphies is given in Table S2.

The most parsimonious tree delivered by our cladistic analysis recovers two distinct ailuropodine subclades, which are here distinguished at the tribe level (Ailuropodini and Indarctini). Alternatively, these subclades could be distinguished at the subfamily rank. However, it should be taken into account that the monophyly of these tribes, unlike that of the subfamily Ailuropodinae, is not supported by the bootstrap analysis, so that merely distinguishing them at the tribe level is a more conservative option. Additional studies based on more complete material would be required in order to confirm their monophyly. If confirmed, or in case one of them was shown to occupy a more basal position than the other within the Ursidae, then it might be preferable to separate them at the subfamily level. The Indarctini includes the species of the genus *Indarctos* [40,41,42], which was widely distributed though Northern Africa, Eurasia and North and Central America during the Late Miocene (MN9-MN13; [40,43]).

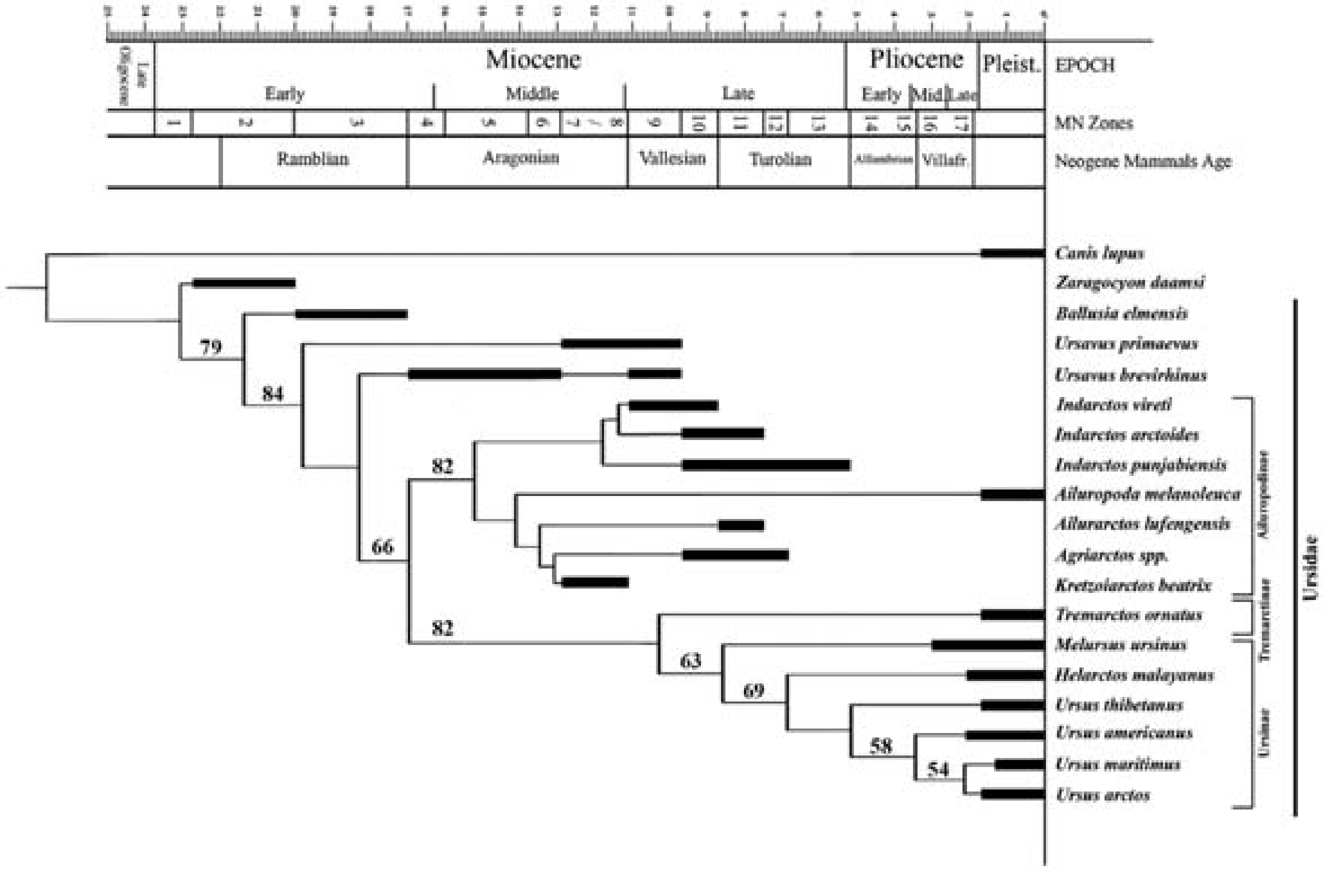

Figure 3. Single most parsimonious cladogram recovered by the cladistic analysis using the branch-and-bound method. See the data matrix employed in Table S1. *Agriarctos* spp. includes *A. gaali*, *A. vighi* and *A. depereti*. Numbers above each clade indicate bootstrap support over 50%. The cladogram further incorporates the known stratigraphic range for each taxon. Cladogram metrics: tree length, 159 steps; Consistency Index, 0.553; Retention Index, 0.710; Homoplasy Index, 0.447.
doi:10.1371/journal.pone.0048985.g003

These species include *I. vireti* (Iberian Peninsula, MN9) and *I. arctoides* (Europe MN10-11), with a relatively limited temporal range and geographic distribution, as well as *I. punjabiensis* (MN10-13), with a Holarctic distribution, and the endemic insular *I. laurillardi* from Baccinello (MN12), whose taxonomic status is yet to be determined. According to our results, the Indarctini still share several plesiomorphic traits with the Ailuropodini (non-reduced carnassials, all premolars present, wide molars, etc.), whereas some of the common characters, such as the developed pterygoideus muscles, the high coronoid process and the development of the zygomaticomandibularis muscle against the reduction of the masseteris, are derived characters present in the ursids with less meat in their diet [44]. The Ailuropodini, comprising the extant giant panda and the remaining fossil Ailuropodinae–including *Kretzoiarctos*–, can be distinguished from the Indarctini by a set of derived dental features (elongated P4, presence of a labial parastyle in the P4, development distal and mesial accessory cusps in the premolars), which we interpret as adaptations towards a more herbivorous diet. The single living representative of this group, the giant panda, markedly differs from the remaining living bears by the particular features of its masticatory apparatus [1,2,3,4], which had been previously tracked backwards in time until the Late Miocene genera *Agriarctos* from Europe [16] and *Ailurarctos* from Asia [5]. This agrees well with our cladistic results, according to which the two latter genera, together with *Kretzoiarctos*, are basal members of the Ailuropodini. The new genus described here, however, further enables to push back in time the origin of the giant panda lineage to the late Middle Miocene.

Conclusions

A new genus of extinct ursid belonging to the giant panda lineage, *Kretzoiarctos* gen. nov. (Ursidae: Ailuropodinae: Ailuropodini), is here described on the basis of new fossil remains from the Spanish site ACM/C6-Camí (Vallès-Penedès Basin). This new material allows a more precise taxonomic approach of the type material from the also Spanish locality of Nombrevilla 2 (Calatayud-Daroca Basin), previously attributed to the Late Miocene genus *Agriarctos*. With a late Middle Miocene age, *Kretzoiarctos* represents the oldest known member not only of the tribe Ailuropodini, but also of the whole subfamily Ailuropodinae (Ailuropodini + Indarctini), substantially preceding in time the other taxa that had been previously attributed to this group. Given that *Kretzoiarctos* is only known from the Iberian Peninsula (Calatayud-Daroca and Vallès-Penedès basins), a Western European origin of the giant panda lineage (Ailuropodinae) is now tentatively supported by the results of this paper. It should be taken into account, however, that the fossil record of this group is still too scarce and fragmentary, as evidenced by the various ghost lineages that must be inferred based on the Early Miocene divergence times for ailuropodines suggested by molecular data. The fossil remains of *Kretzoiarctos* reported here, however, at least conclusively document the occurrence of ailuropodines by the Middle

Miocene of Eurasia, with *Ballusia* and *Ursavus* displaying a successive basal position with regard to crown ursids as a whole.

Materials and Methods

Cladistic Analysis

The data matrix of craniodental features employed in the cladistic analysis, including 82 characters and 19 taxa (see Table S1), was coded on the basis of original specimens of osteological and fossil material, casts, and published figures and descriptions. For *Canis lupus*, *Ursus arctos*, *Ursus americanus*, *Tremarctos ornatus*, *Ailuropoda melanoleuca, Ursavus brevirhinus*, *Indarctos vireti*, *I. arctoides* and *I. punjabiensis*, we had direct access to skulls and mandibles. For *Ursus thibetanus* and *Helarctos malayanus*, we relied on casts of mandibles and skulls. For the remaining species, we used either photographs or images from scientific papers. The character description can be consulted in the Text S1. The matrix was generated using MacClade 4.08a OS X, and was analyzed using PAUP* (Version 4.0b10 for Macintosh [45]. A maximum-parsimony analysis was performed using the branch-and-bound method, with *Canis lupus* as the outgroup. Even though *C. lupus* is not a member of the Ursidae, its cranial, mandibular and dental morphologies are supposed to be similar to the ancestor of the Arctoidea, and therefore a quite accurate choice as an outgroup for this analysis. In order to test clade robusticity, a bootstrap analysis with 1,000 replicates was performed using the branch-and-bound search option.

Studied Material

IPS46473 is a nearly complete right mandible with canine and p2-m3 series (Figure 1; 1a-c and Figure 2) associated to a broken P4 (Figure 1; 2a–b) from ACM/C6-Camí. These specimens are housed at the Institut Català de Paleontologia Miquel Crusafont (ICP; Sabadell, Catalonia, Spain). The material from Nombrevilla 2 (NV 2) includes an upper carnassial and an M1 (Figure 1, 3–4) and it is housed in the Museo Nacional de Ciencias Naturales – Consejo Superior de Investigaciones Científicas (MNCN-CSIC), Madrid [20].

Nomenclatural Statement

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub:B572EF80-998C-45D4-8364-14C0C7F299D9. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

Supporting Information

Table S1 Data matrix of craniodental features employed in the cladistic analysis, including 82 characters and 19 taxa.
(NON)

Table S2 List of the apomorphies found in the cladistic analysis. Note: the changes of states are shown for each taxon. Note: Character number start in 0. Therefore Character 1 in the matrix would be character 0 in this list.
(PDF)

Text S1 Character description.
(PDF)

Acknowledgments

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Author Contributions

Conceived and designed the experiments: JA PM JM. Performed the experiments: JA JMR AV CR RC. Analyzed the data: JA DMA JMR AV. Contributed reagents/materials/analysis tools: JA DMA JMR AV. Wrote the paper: JA DMA.

References

1. Chorn J, Hoffmann RS (1978) *Ailuropoda melanoleuca*. Mammalian Species 110: 1–6.
2. Figueirido B, Serrano-Alarcón FJ, Slater GJ, Palmqvist P (2010) Shape at the cross-roads: homoplasy and history in the evolution of the carnivoran skull towards herbivory. Journal of Evolutionary Biology 23: 2579–2594.
3. Figueirido B, Serrano-Alarcón FJ, Palmqvist P (2011) Geometric morphometrics shows differences and similarities in skull shape between the red and giant pandas. Journal of Zoology. doi:10.1111/j.1469-7998.2011.00879.x.
4. Figueirido B, Palmqvist P, Pérez-Claros JA, Wong W (2011) Cranial shape transformation in the evolution of the giant panda (*Ailuropoda melanoleuca*). Naturwissenschaften 98: 107–116.
5. Qiu Z, Qi G (1989) Ailuropod found from the Late Miocene deposits in Lufeng, Yunnan. Vertebrata PalAsiatica 27: 153–169.
6. Huang WP (1993) The skull, mandible and dentition of giant pandas (*Ailuropoda*): morphological characters and their evolutionary implications. Vertebrata PalAsiatica 31: 191–207.
7. Jin C, Ciochon RL, Dong W, Hunt RM Jr, Liu J, et al. (2007) The first skull of the earliest giant panda. Proceedings of the National Academy of Sciences, U.S.A. 104: 10932–10937.
8. Bininda-Emonds ORP, Gittleman JL, Purvis A (1999) Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora. Biological Reviews 74: 143–175.
9. Bininda-Emonds ORP (2004) Phylogenetic position of the giant panda: historical consensus through supertree analysis. In: Lindburg D, Baragona D, editors. Giant pandas, biology and conservation. Berkeley: University of California Press. 11–35.
10. Waits LP (2004) Phylogenetic placement of the giant panda based on molecular data. In: Lindburg D, Baragona D, editors. Giant pandas, biology and conservation. Berkeley: University of California Press. 36–37.
11. Fulton TL, Strobeck C (2006) Molecular phylogeny of the Arctoidea (Carnivora): Effect of missing data on supertree and supermatrix analyses of multiple gene data sets. Molecular Phylogenetics and Evolution 41: 165–181.
12. Krause J, Unger T, Noçon A, Malaspinas AS, Kolokotronis SO, et al. (2008) Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary. BMC Evolutionary Biology 8: 220.
13. Pagès M, Calvignac S, Klein C, Paris M, Hughes S, et al. (2008) Combined analysis of fourteen nuclear genes refines the Ursidae phylogeny. Molecular Phylogenetics and Evolution 47: 73–83.
14. Hunt RM Jr (2004) A paleontologist's perspective on the origin and relationships of the giant panda. In: Lindburg D, Baragona D, editors. Giant pandas, biology and conservation. Berkeley: University of California Press. 45–52.
15. Qi G, Dong W, Zheng L, Zhao L, Gao F, et al. (2006) Taxonomy, age and environment status of the Yuanmou hominoids. Chinese Science Bulletin 51: 704–712.
16. Kretzoi M (1942) Zwei neue Agriotheriiden asu dem ungarischen Pannon. Foldtani Kozlony 72: 350–353.
17. Thenius E (1979) Zur systematischem und phylogenetischen Stellung des Bambusbaren: *Ailuropoda melanoleuca* David (Carnivora, Mammalia). Z. Saugetierk 441: 286–305.

18. Ginsburg L, Morales J (1998) Les Hemicyoninae (Ursidae, Carnivora, Mammalia) et les formes apparentées du Miocène inférieur et moyen d'Europe occidentale. Ann Paléontol 84 (1): 71–123.
19. Bernor RL, Feibel C, Viranta S (2003) The Vertebrate Locality of Hatvan, Late Miocene (Middle Turolian, MN12), Hungary. In: Petculescu A, Ştiucă E, editors. Advances in Vertebrate Paleontology Hen to Panta. Bucharest: Romanian Academy Emil Racovită Institute of Speleology. 105–112.
20. Abella J, Montoya P, Morales J (2011) A New species of Agriarctos (Ailuropodinae, Ursidae, Carnivora) in the locality of Nombrevilla 2 (Zaragoza, Spain). Estudios Geológicos 67(2): 187–191.
21. Ménouret B, Mein P (2008) Les Vertébrés du Miocène supérieur de Soblay (Ain, France). Documents des laboratoires de géologie Lyon 165: 1–97.
22. Viret J, Mazenot G (1948) Nouveaux restes de mammifères dans le gisement de lignite pontien de Soblay (Ain). Annales de Paléontologie 34: 19–56.
23. Viret J (1949) Observations complementaires sur quelques mammiferes fossiles de Soblay. Eclogae Geologicae Helvetiae 42: 469–476.
24. Tobien H. (1955) Neue und wenig bekannte Carnivoren aus den Unterpliozänen Dinotheriensanden Rheinhessens. Notizbl. hess. L. Amt Bodenforsch. 83: 7–31.
25. Álvarez-Sierra MA, Calvo J-P, Morales J, Alonso-Zarza A, Azanza B, et al. (2003) El tránsito Aragoniense-Vallesiense en el área de Daroca-Nombrevilla (Zaragoza, España). Coloquios de Paleontología (Volumen Extraordinario) 1: 25–33.
26. Alba DM, Moyà-Solà S, Casanovas-Vilar I, Galindo J, Robles JM, et al. (2006) Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l'Anoia, Cataluña), una sucesión de localidades del Aragoniense superior (MN6 y MN7+8) de la cuenca del Vallès-Penedès. Campañas 2002–2003, 2004 y 2005. Estudios Geológicos 62: 295–312.
27. Alba DM, Robles JM, Rotgers C, Casanovas-Vilar I, Galindo J, et al. (2009) Middle Miocene vertebrate localities from Abocador de Can Mata (els Hostalets de Pierola, Vallès-Penedès Basin, Catalonia, Spain): An update after the 2006–2008 field campaigns. Paleolusitana 1: 59–73.
28. Alba DM, Casanovas-Vilar I, Robles J-M, Moyà-Solà S (2011) Parada 3. El Aragoniense superior y la transición con el Vallesiense: Can Mata y la exposición paleontological de els Hostalets de Pierola. Paleontologia i Evolució, Memòria especial núm 6: 95–109.
29. Casanovas-Vilar I, Alba DM, Garcés M, Robles JM, Moyà-Solà S (2011) Updated chronology for the Miocene hominoid radiation in Western Eurasia. Proceedings of the National Academy of Sciences, U.S.A. 108, 5554–5559.
30. Moyà-Solà S, Köhler M, Alba DM, Casanovas-Vilar I, Galindo J, et al. (2009) First partial face and upper dentition of the Middle Miocene hominoid *Dryopithecus fontani* from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, NE Spain): taxonomic and phylogenetic implications. American Journal of Physical Anthropology 139: 126–145.
31. Casanovas-Vilar I, Alba DM, Robles JM, Moyà-Solà S (2011) Registro paleontológico continental del Mioceno de la cuenca del Vallès-Penedès. Paleontologia i Evolució, Memòria especial núm 6: 55–80.
32. Mein P, Ginsburg L (2002) Sur l'âge relatif des différents dépôts karstiques miocènes de La Grive-Saint-Alban (Isère). Cahiers scientifiques 2: 7–47.
33. Fraile S, Perez B, De Miguel I, Morales J (1997) Revisión de los carnívoros presents en los yacimientos del Neógeno español. In: Calvo JP, Morales J, editors. Avances en el conocimiento del Terciario Ibérico. Madrid: Universidad Complutense-C.S.I.C. 77–80.
34. Garcés W, Krijgsman M, Peláez-Campomanes P, Alvarez-Sierra MA, Daams R (2003) *Hipparion* dispersal in Europe: magnetostratigraphic constraints from the Daroca area (Spain). COLPA Vol Extra: 171–178.
35. McKenna MC, Bell SK (1997) Classification of Mammals Above the Species Level. New York: Columbia University Press. 631 p.
36. Nash WG, Wienberg J, Ferguson-Smith MA, Menninger JC, O'Brien SJ (1998) Comparative genomics: tracking chromosome evolution in the family Ursidae using reciprocal chromosome painting. Cytogenet. Cell. Genet. 83: 182–192.
37. Agnarsson I, Kuntner M, May-Collado L (2010) Dogs, cats, and kin: A molecular species-level phylogeny of Carnivora. Molecular Phylogenetics and Evolution 54: 726–745.
38. Erdbrink DP (1953) A review of fossil and recent bears of the old world. Deventer. Drukkerij Jan De Lange. 89–122.
39. Ewer RF (1973) The carnivores. Ithaca: Cornell University Press. 494 p.
40. Montoya P, Alcalá L, Morales J (2001) *Indarctos* (Ursidae, Mammalia) from the Spanish Turolian (Upper Miocene). *Scripta Geol.* 122: 123–151.
41. Baryshnikov GF (2002) Late Miocene Indarctos punjabiensis atticus (Carnivora, Ursidae) in Ukraine with survey of *Indarctos* records from the former USSR. Russian J. Theriol 1 (2): 83–89.
42. Koufos GD (2011) The Miocene carnivore assemblage of Greece. Estudios Geológicos 67(2): 291–320.
43. Ginsburg L (1999). Order Carnivora In: Rössner GE, Heissig K, editors. The Miocene Land Mammals of Europe. München: Verlag Dr. Friedrich Pfeil. 109–148.
44. Davis DD (1955) Masticatory apparatus in the spectacled bear (*Tremarctos ornatus*). Fieldiana: Zoology, Chicago. 37: 25–46.
45. Swofford DL (2003) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

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Ursavus_brevirhinus :

No autapomorphies

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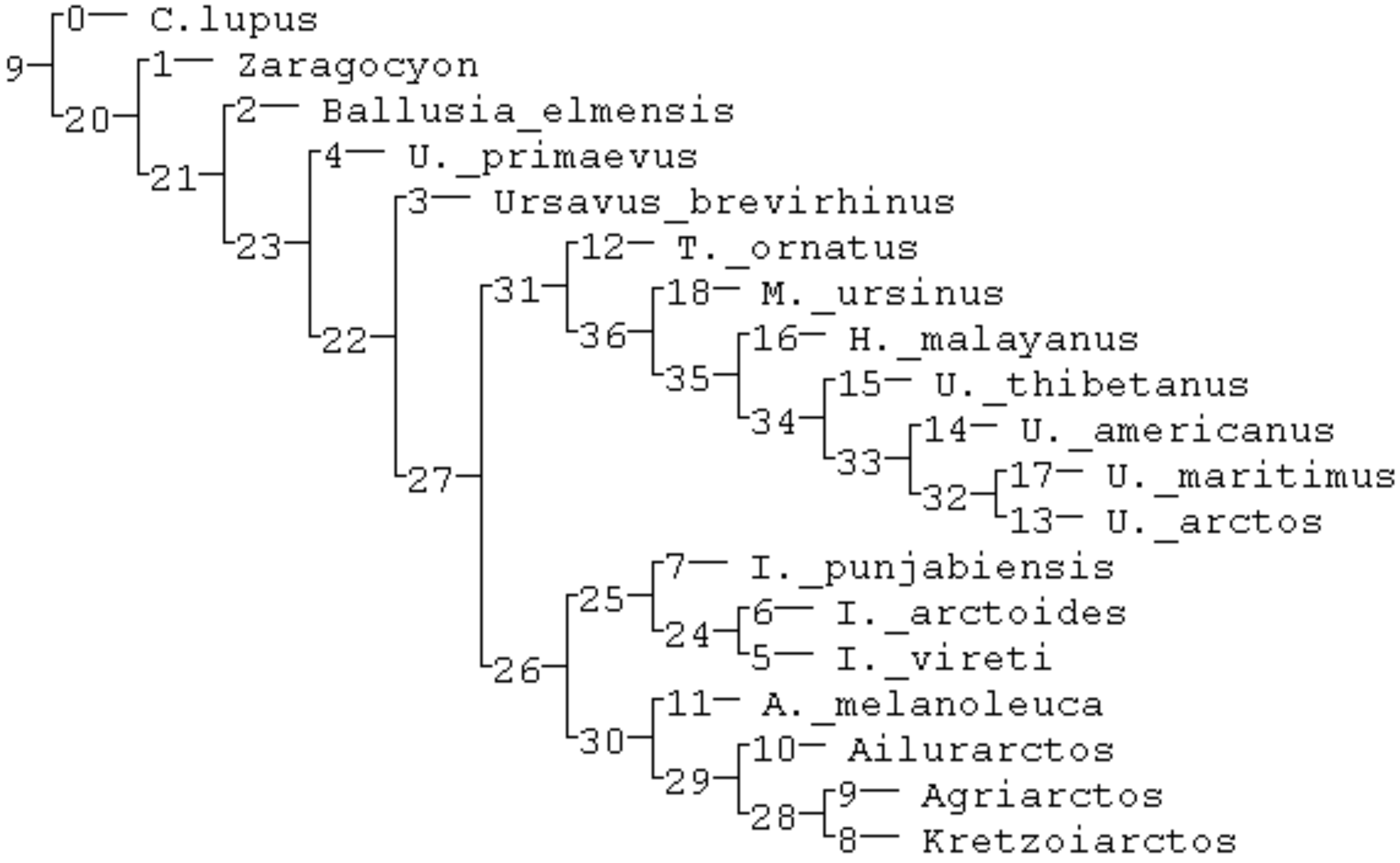
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24
5 I._vireti
26
11 A._melanoleuca
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10 Ailurarctos
29
9 Agriarctos
28
8 Kretzoiarctos

Character Description:

1. Development in heigh of the lower canines. The canines in most of bears are not as developed as in other carnivorans. However, they display an important reduction in some of lineages such as the Ailuropodinae. This character is an important feature that may indicate herbivore adaptations.
State 0. Canine at least twice as high as the remaining maxillary and mandibular teeth.
State 1. Canine less than twice as high as the remaining maxillary and mandibular teeth.

2. Relative premolar development, compared to the remaining teeth. The premolars in most bears, especially the Ursinae, display a reduction in both number and morphology. However, there are other lineages that display the complete set of premolars or even a more complicated morphology and enamel structure.
State 0. All premolars relatively large, with developed accessory cusps.
State 1. Morphology of the premolars less complicated, without developed accessory cusps in some of them.
State 2. Both reduced morphology of the premolars and loss of at least one premolar.

3. Height of the coronoid process. The coronoid process development is a good indicator of the relationship between the *temporalis* and the *masseteris* muscles. The presence of a tall, verticalized coronoid is usually related to a more herbivorous diet.
State 0. Coronoid process does not reach twice the height of the mandibular ramus and it is relatively wide.
State 1. Coronoid process doubles the height of the mandibular ramus and it is verticalized and relatively slender.

4. Articular process position. The position of the articular process may vary among different species due to the biomechanics of the feeding complex. Therefore a higher articular process may be related to a more hypocarnivorous diet.
State 0. Same height as the tooth row.
State 1. Higher than the tooth row.

5. Articular process mediolateral width. This character that is considered to be related to the biomechanics of the lateral movement of the mandible.
State 0. Short (poorly developed).
State 1. Long (well-developed).

6. Angular process. The position of this process is also linked to the feeding complex biomechanics, and more precisely to the position and development of the *digastricus* muscle.
State 0. Short, not projected caudally and with a small insertion for the *digastricus* muscle.
State 1. Long, caudally projected and with a large insertion for the *digastricus* muscle.

7. Development of the insertion of the *masseteris superficialis* muscle in the mandible.
State 0. Large, ventrally closing the masseteric fossa.
State 1. Small, not ventrally closing the masseteric fossa.

8. Development of the insertion of the *pterygoideus* (*internus* and *externus*) muscles.
State 0. Small, not covering wide areas of the mandible.

State 1. Large, occupying large areas of the mandible, both in the articular process and in the ventrocaudal region.

9. Development of the insertion of the *digastricus* muscle.
State 0. Lined-up with the dentary bone.
State 1. Lingually projected, forming a curve towards the inner part of the mandible.

10. Development of the insertion of the *zygomaticomandibularis* muscle.
State 0. Short, not covering all the rostral part of the ascending ramus.
State 1. Long and developed. closing the whole masseteric fossa in the rostral edge.

11. Shape of the ventral outline of the jaw in lateral view.
State 0. Curved; most of the ventral outline of the dentary bone is convex in shape.
State 1. Straight.

12. Shape of the ventral outline of the jaw in lateral view, proximal to the insertion of the *digastricus* muscle.
State 0. Straight.
State 1. Forming a step between the ventral edge and the beginning of the angular process.

13. Postcanine groove in the jaw, found in the surface of the mandible, caudal to the canine.
State 0. Absent.
State 1. Present.

14. Apical morphology of the coronoid process. Even though the apex of the coronoid is somehow curved in most carnivores, its angle can be used as a character that is linked to the projection of the uppermost fibres of the *temporalis* muscle.
State 0. Slightly curved.
State 1. Apex angle close to 45º .

15. Lateral morphology of the tooth row. This character is somehow linked to the biomechanics of the feeding complex, as it affects bite strength throughout the mouth.
State 0. Curved, forming a sigmoidal shape.
State 1. Straight.

16. Jaw bone height at the level of the m1. Although this character can vary throughout the ontogeny of the animals, it can also give very important information about differences in the feeding complex and bite strength between several taxa.
State 0. Low, not reaching thrice the height of the m1.
State 1. High, exceeding more than thrice the height of the m1.

17. Mandibular symphysis ventral morphology. This character reflects the strength of the union between the two hemimandibles.
State 0. Curved.
State 1. Marked chin.

18. Premasseteric fossa. This character is only observed in some Ursoidea, such as the Hemicyonidae and the Tremarctinae; although two main types of morphologies can be detected, we code them as the same structure. In the Hemicyionidae it is located below the m1, while in the Tremarctinae it is located in a more caudal position and it is separated from the masseteric fossa by a well-developed insertion of the *zygomaticomandibularis* muscle.
State 0. Absent.
State 1. Present.

19. Position of m3. The rearrangements of the masticatory apparatus of some bears tend to modify the morphology of the ascending ramus as well as the relative position of the last lower molar in lateral view.
State 0. In front of the coronoid process, well-separated from the ascending ramus.
State 1. Included in the coronoid process, touching the ascending ramus.
State 2. Behind the coronoid process, partly or completely covered by the coronoid process.

20. Development of the distal cuspid of the i3. This character reflects its relative size compared to the incisor's main cuspid.
State 0. Small; less than half the size of the main cuspid.
State 1. Large; at least half the size of the main cuspid.

21. p1.
State 0. Present.
State 1. Absent.

22. p1-p4 diastema. This character is only observed in those species that have lost one or more premolars.
State 0. Absent.
State 1. Present.

23. p2.
State 0. Present.
State 1. Absent.

24. p3.
State 0. Present.
State 1. Absent.

25. Distal accessory cuspid of the p4.
State 0. Present.
State 1. Absent.

26. Lingual ridge of the p4, running from the main cuspid towards the lingual wall.
State 0. Absent.
State 1. Present.

27. Morphology of the paraconid of the m1 (discernible when not completely worn).
State 0. Sharp, i.e. meaning cutting edges as found in hypercarnivores.

State 1. Bunodont, i.e. meaning blunt cusps.

28. Position of the paraconid of the m1 relative to the protoconid. Although the paraconid primitively displays a mesiolingual position relative to the protoconid, most bears have switched it labially, and some (such as the Ursinae) have further closed the trigonid valley.
State 0. Mesiolingual.
State 1. Labial.

29. Heigh of the m1 protoconid relative to the paraconid.
State 0. Protoconid clearly higher than the paraconid.
State 1. Protoconid equal or subequal in heigh compared to the paraconid.

30. Morphology of the m1 protoconid. This character would be related to the action of the carnassial as an active cutting blade.
State 0. Sharp, if a clear blade is observed in the cuspid.
State 1. Bunodont, if no clear blade is observed.

31. Size of the m1 metaconid relative to the remaining trigonid cuspids.
State 0. Reduced, i.e., not individualized from the protoconid and relatively small in size.
State 1. Large, i.e., individualized from the proconid and relatively well-developed in size.

32. m1 Pre-metaconid. This cuspid, when present, displays a mesial position relative to the metaconid and a lingual position relative to the protoconid, and somehow closes the trigonid on its lingual side.
State 0. Absent.
State 1. Present.

33. Morphology of the labial part of the m1 talonid.
State 0. Narrow, without expansion.
State 1. Widened, creating an expansion.

34. Mesial angle of the m1 paraconid. It is measured in relation to the line formed by the basal-most part of the tooth crown.
State 0. High, close to 90º.
State 1. Low, clearly lower than 90º.

35. Lingual ridge of the m1 protoconid. This cristid, which runs from the protoconid towards the lingual part of the crown, is observed in some taxa together with the mesial and distal ridges.
State 0. Absent.
State 1. Present.

36. Trigonid valley of the m1. In some taxa, a closed valley is observed within the trigonid between paraconid, protoconid and metaconid.
State 0. Present.
State 1. Absent.

37. Morphology of the distal wall of the m1 trigonid.
State 0. Vertical.
State 1. Inclined.

38. Relative length of the m1 talonid relative to the trigonid.
State 0. Short.
State 1. Long.

39. m1 pre-hypoconid. This cuspid, when present, is located on the labial wall between the protoconid and the hypoconid.
State 0. Absent.
State 1. Present.

40. Morphology of the m1 crown base. In some bears, the basal portion of the crown (next to the roots) of the lower carnassials displays a rounded, swollen shape.
State 0. Straight.
State 1. Swollen, with a rounded base.

41. Morphology of the mesial ridge of the m1 paraconid in occlusal view. This character indicates the direction of the mesial cristid of the lower carnassials, which in some taxa is curved lingually.
State 0. Straight, directed towards the mesial part of the m1.
State 1. Curved, directed towards the lingual wall of the m1.

42. Morphology of the m1 talonid valley. This character whether the valley of the talonid is completely surrounded by cuspids and ridges or not.
State 0. Open, not completely surrounded by cuspids and/or ridges.
State 1. Closed, completely surrounded by cuspids and/or ridges.

43. Morphology of the m1 talonid valley. This character reflects the depth of the distal valley of the m1.
State 0. Relatively deep and forming a V-shape valley.
State 1. Shallow, not forming a v-shape valley.

44. Position of the m1 hypoconid in occlusal view.
State 0. Isolated, not forming part of the lingual cristid.
State 1. Forming part of the lingual cristid.

45. m1 distal ridge. This cristid, when well-developed, closes the talonid valley on its distal portion.
State 0. Absent or poorly-developed, not closing the talonid valley distally.
State 1. Marked, closing the talonid valley between the entoconid complex and the hypoconid.

46. Relative size of the m2 compared to the size of the lower carnassial.
State 0. Relatively small, less than half the size of the m1,.
State 1. Relatively large, at least half the size of the m1.

47. Size of the m2 paraconid in relation to the rest of the cuspids of the trigonid.
State 0. Small or absent.
State 1. Large, sub-equal in size.

48. m2 pre-metaconid. This cuspid, when present, is located mesial to the metaconid, but cannot be homologized with the paraconid,which is reduced in most bears.
State 0. Absent.
State 1. Present.

49. Relative size of the m2 talonid compared to the trigonid.
State 0. Shorter than the trigonid.
State 1. Longer than the trigonid.

50. Most developed cusp in the m2. This character reflects the relative size between the two better-developed cuspids of the m2 (protoconid and metaconid).
State 0. Protoconid.
State 1. Metaconid.

51. Development of the m2 trigonid valley compared to the total length of the talonid valley.
State 0. Small, less than half the size of the m2 talonid valley.
State 1. Large, at least half the size the m2 talonid valley.

52. m2 pre-entoconid. This cuspid is present in taxa that have a relatively complex m2 (with multiplication of cuspids), usually mesial to the entoconid.
State 0. Absent.
State 1. Present.

53. Relative development of the m2 labial cingulum relative the development of the remaining cingulids.
State 0. Small, not surrounding the whole labial wall of the m2.
State 1. Large, raning the whole labial wall (from the mesial to the distal sides) of the m2.

54. m3 development compared to the m2.
State 0. Reduced, less than ¼ the size of the m2.
State 1. Large, at least ¼ of the size of the m2.

55.
m3 morphology in mesial view.
State 0. Rounded or ovoid.
State 1. Subtriangular, with one clear tip (usually on its distal side).

56. P2.
State 0. Present.
State 1. Absent.

57. P3.
State 0. Present.
State 1. Absent.

58. P4 development relative to the M1.
State 0. Large, subequal in size.
State 1. Reduced, clearly smaller than the M1.

59. P4 parastyle.
State 0. Absent.
State 1. Present, but small.
State 2. Present but well-developed and individualized from the paracone.

60. P4 protocone relative size in occlusal view.
State 0. Small, much smaller than the remaining cusps of the trigon.
State 1. Large, similar in size with the paracone and metastyle.

61. Morphology in terms of relative morphology of the P4 protocone.
State 0. Simple, only one cusp.
State 1. Complex, with more than one cusp and/or surrounded by a cingulum.

62. Position of the P4 protocone relative to the paracone.
State 0. Mesial, close to the level of the paracone.
State 1. Distally projected, situated close to the paracone-metastyle notch level.

63. Labial expansion of the P4 at the level of the paracone-metastyle notch. This feature, when present, gives the upper carnassial a more compact shape than the usual triangular shape.
State 0. Absent.
State 1. Present.

64. Relative size of the M1 paracone and metacone.
State 0. Paracone higher than the metacone.
State 1. Both cusps sub-equal in size.

65. M1 hypocone.
State 0. Absent.
State 1. Present.

66. M1 occlusal outline.
State 0. Square (sub-equal length and breadth).
State 1. Rectangular (longer than broad).

67. M1 distal valley. This valley is situated between the hypocone and the metacone, and hence it is only observed when the hypocone is present.
State 0. Absent.
State 1. Present.

68. Development in depth of the M1 central valley, which corresponds to the trigon valley.
State 0. Deep, forming a V-shaped valley.
State 1. Shallow, not forming a V-shaped valley.

69. Relative development of the M1 lingual cingulum compared to the size of this tooth.
State 0. Well-developed,covering all the lingual wall.
State 1. Poorly developed, not covering all the lingual wall, or absent.

70. M2 relative size compared to the M1.
State 0. Reduced, similar in size or smaller than the M1.
State 1. Developed, longer than the M1.

71. Size and development of the M2 talon.
State 0. Absent or small.
State 1. Present but moderately-development, not being longer than the trigonid.
State 2. Present and well-developed, being longer than the trigonid

72. Reduction of the incisors.
State 0. Absent (all incisors present).
State 1. Present (I1 lacking and I2 reduced).

73. Enamel structure in the molars.
State 0. Smooth.
State 1. Rough.

74. Origin of the zygomatic arch in lateral view.
State 0. At the level of the M1.
State 1. At the level of the M2.

75. Rostral maximum width of the skull.
State 0. Attained at the level of the P4.
State 1. Attained at the level of the upper canines.

76. Morphology of the sagittal crest in lateral view.
State 0. Caudally projected towards the cervical vertebra.
State 1. Obliquely-inclined and moderately-developed, but not surpassing the level of the nuchal crest.
State 2. Dorsally-projected, with its highest level not situated in the dorsal-most part of the crest.

77. Development of the mastoid process. This character is related to the capability of moving the skull up and down (ventral-dorsal movement) relative to the cervical vertebrae.
State 0. Reduced, i.e., non-protruding, flattened, not surpassing the lower level of the zygomatic arch.
State 1. Wel-developed, i.e., protruding and being laterally and ventrally projected.

78. Development of the paraoccipital process.
State 0. Reduced, not surpassing the ventral level of the mastoid process.
State 1. Large and ventrally projected, longer or subequal in size compared to the mastoid process.

79. Position of the end of the hard palate in ventral view.
State 0. At about the level of the last molar.

State 1. Caudally-situated relative to the last molar (separated from it at least by the length of the M2).

80. Alisphenoid canal.
State 0. Present.
State 1. Absent.

81. Morfology of the zygomatic arch in lateral view.
State 0. Narrow, with it central portion never being wider than its rostral or caudal parts, and with a small insertion for the *zygomaticomandibularis* muscle.
State 1. Wide, with its central portion sometimes being wider than its rostral and/or caudal parts, and with an enlarged insertion for the *zygomaticomandibularis* muscle.

82.Morfology of the zygomatic arch in lateral view.
State 0. Curved, displaying a dorsally convex and ventrally concave profile, and with an increased insertion for the *zygomaticomandibularis* muscle.
State 1. Straight, with its dorsal and ventral profiles being approximately aligned with the skull's main (rostrocaudal) long axis, and without a developed insertion for the *zygomaticomandibularis* muscle.

Appendix 2. Miocene carnivorans from the Vallès-Penedès Basin

Reproduced from:

Robles, J.M., Abella, J., Madurell-Malapeira, J. & Alba, D.M. (unpublished manuscript). Miocene carnivorans from the Vallès-Penedès Basin.

Miocene carnivorans from the Vallès-Penedès Basin

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Abstract

An updated revisiew of Miocene Carnivora (Mammalia) from the Vallès-Penedès Basin (NE, Iberian Peninsula) is provided, based on both the available literature as well as the revision of both published and unpublished fossil remains housed in several institutions. Eight species taxa are reported for the first time from this basin: 3 Amphicyonidae (*Amphicyon olisiponensis*, *Magericyon castellanus* and *Thaumastocyon dirus*), 1 Hemicyonidae (*Plithocyon conquense*), 1 Mustelidae (*Ischyrictis* cf. *bezianensis*), 1 Felidae (cf. *Promegantereon ogygia*), 1 Viverridae (*Leptoplesictis filholi*) and 1 Hyaenidae (*Hyaenictitherium wongii*). Up to 55 carnivoran species (belonging to 41 genera from 11 families) are recognized in the Miocene of the Vallès-Penedès Basin. The best represented families are the Mustelidae (13 genera and 17 species), the Hyaenidae (6 genera and 10 species), the Felidae (6 genera and 8 species) and the Amphicyonidae (4 genera and 5 species). The remaining families recorded in this basin are the Viverridae, Barbourofelidae, Ursidae, Hemicyonidae, Ailuridae, Mephitidae and Herpestidae. Among the carnivoran species recorded in the Miocene of the Vallès-Penedès, eight of them are endemics: 5 Mustelidae (*Martes melibulla*, *Marcetia santigae*, *Trochictis narcisoi*, *Hoplictis petteri* and *Sabadellictis crusafonti*), 2 Mephitidae (*Plesiomeles cajali* and *Promephitis pristinidens*) and 1 Felidae (*Stenailurus teilhardi*). In the Vallès-Penedès Basin, the order Carnivora is first reported in the MN3 with a moderate diversity, reaching a peak during the MN9, and decreasing afterwards (at least partly due to biases of the available fossil record).

Keywords: Mammalia, Carnivora, Taxonomy, Species diversity.

Introduction

The order Carnivora is widely represented in the Miocene of the Vallès-Penedès Basin. Its presence was first documented by Bataller (1921), who mentioned some remains attributed to *Hyaenictis graeca* (currently *Hyaenictis almerai*, subsequently erected by Villalta Comella and Crusafont Pairó 1948). Shortly thereafter, Bataller (1924, 1941) reported additional carnivorans in the faunal lists of new localities from the same basin. During the 1940s, Josep F. de Villalta-Comella and Miquel Crusafont-Pairó continued these preliminary studies, and published the first compilation of carnivorans from the Vallès-Penedès Basin (Villalta Comella and Crusafont Pairó 1941). During the following years, many other carnivoran, especially from localities in the Penedès sector of the basin, such as Piera (Torrentet de Traginers), Masquefa and els Hostalets de Pierola (especially from locality Can Mata 1), were published. These finds led to the erection of new taxa, such as *Ischyrictis mustelinus*, *Palaeomeles pachecoi* and *Thalassictis montadai* (Villalta Comella and Crusafont Pairó 1941, 1943a,b, 1944, 1946a,b,c). In some of these papers, new carnivoran remains from previously known localities, such as Sant Quirze, were described (Villalta Comella and Crusafont Pairó 1941, 1944, 1945), thus complementing the list of carnivoran taxa recorded in the basin (Villalta Comella and Crusafont Pairó 1948).

During the 1950s, Jaume Truyols teamed up with Crusafont and Villalta, by further strengthening not only the stratigraphic framework of the Vallès-Penedès Basin (Crusafont Pairó and Truyols Santoja 1954; Crusafont et al. 1955), but also the morphometric approach towards a better knowledge on the carnivorans from this basin (Crusafont Pairó and Truyols Santoja 1956, 1957a,b, 1958, 1966a,b; Crusafont Pairó 1959b, 1962). Crusafont and Villalta continued reporting new carnivorans from the Vallès-Penedès Basin throughout the 1950s, sometimes in collaboration with Truyols or other foreing researchers (Villalta and Crusafont 1952; Crusafont Pairó and Villalta Comella 1952; Viret and Crusafont-Pairó 1955; Crusafont Pairó 1950, 1952; Crusafont and Truyols 1953, 1954; Crusafont-Pairó and Truyols-Santoja 1956, 1957a,b, 1958; Crusafont Pairó 1959a,b). Late in the 1950s, the collaboration between Crusafont and Villalta was interrupted, but publications dealing with carnivorans continued to be published by Crusafont and co-workers in the 1960s, being mostly (but not exclusively) focused on the locality of Can Llobateres (Crusafont Pairó 1959a, 1964; Crusafont Pairó and Truyols Santoja 1960).

By this time, the french paleontologist Germain Petter began to publish new studies on the mustelids from the Vallès-Penedès Basin (Petter 1963, 1964, 1967), publishing his last contribution in the following decade (Petter 1976). Simultaneously, Crusafont and co-workers continued to publish on the carnivorans from new Vallès-Penedès localities (Crusafont Pairó 1962, 1964; Crusafont-Pairó and Truyols Santoja 1966a,b; Crusafont-Pairó et al. 1968), and the collaboration between Crusafont and Petter culminated in the joint publication of the fossil Hyaenidae from the Iberian Peninsula (Crusafont Pairó and Petter 1969). Further studies on carnivorans during the 1970s by Crusafont and collaborators included the revision of the genus *Ischyrictis* in the Vallès-Penedès Basin (Crusafont-Pairó 1972), the publication of new felines, such as *Stenailurus teilhardi* from Torrentet dels Traginers (Crusafont-Pairó and Aguirre 1972), and the description of other new remains from the Vallès sector of the basin (Crusafont-Pairó 1979a,b). It is particularly noteworthy a revision of the families Ursidae and Amphicyonidae by Crusafont Pairó and Kurtén (1976), and also remarkable the incorporation of Crusafont's student, Juana María Golpe-Posse, to the study of carnivorans and other fossil vertebrates from the Vallès-Penedès Basin by this time (Crusafont-Pairó and Golpe-Posse 1972, 1973a,b; Golpe-Posse 1974, 1981a,b, 1984; Golpe-Posse et al. 1979). The last contributions on Vallès-Penedès carnivorans by Crusafont, soon before his death, were performed in collaboration with Golpe-Posse and Gérard de Beaumont (Crusafont-Pairó and Golpe-Posse 1981, 1982; de Beaumont and Crusafont-Pairó 1982).

From 1982 onwards, no specific contributions were published on fossil carnivorans from the Vallès-Penedès Basin during that decade, although some taxonomic attributions were updated (Agustí et al. 1984, 1985). Some carnivoran reports were subsequently published in faunal lists during the 1990s (Pons-Moyà 1990; Moyà-Solà and Rius Font 1993; Agustí and Galobart 1997; Agustí et al. 1997; Gómez-Alba 1997; Galindo 2000) and the 2000s, the latter mostly related to preventive paleontological works (Checa Soler and Rius Font 2000; Alba et al. 2006, 2007, 2009, 2010, 2011a,b, 2012); Casanovas-Vilar et al. 2006, 2007, 2008, 2011a,b,c; Carmona et al. 2011). Most recently, several carnivoran taxa from the Vallès-Penedès have been revised, with particular emphasis in the new material from ACM (Robles et al. 2009, 2010a,b, 2013a,b; Abella et al. 2012; Madurell-Malapeira et al. under review). Here we revise the fossil record of the Miocene carnivorans from the Vallès-Penedès Basin, based on both the published literature and the revision of available paleontological collections.

Materials and Methods

The results of the revision of Vallès-Penedès carnivoran remains from the Miocene summarized in this work are organized in a systematic fashion in the following section. Only the most usesul taxonomic ranks (order, family, subfamily and genus) are specified, and within each genus, the species recorded in the Vallès-Penedès Basin are listed. For each species (or lowest possible rank attribution), the chronostratigraphic range and known localities are given (further specifying within brackets the type locality, if it is from the Vallès-Penedès Basin). Other considerations, regarding available material, problems in taxonomic attribution, and/or the main characteristics of each taxon, are succinctly provided as remarks.

Abbreviations

Institutional abbreviations. ICP, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Catalonia, Spain); IPS, acronym of the ICP collections, MGB, Museu de Geologia de Barcelona (Museu de Ciències Naturals de Barcelona); MGSB, Museu de Geologia del Seminari de Barcelona.

Paleontological localities abbreviations. ACM, local stratigraphic series of Abocador de Can Mata (els Hostalets de Pierola); C1 to C8, Cells 1 to 9 (ACM sectors); B40OV local stratigraphic series of Autovia Orbital de Barcelona, stretch Olesa de Montserrat; S5 (ROS sector); BCV, Barranc de Can Vila (ACM sector); BDA, Decanting Pond of Rainwater (ACM sector); BG, Barranc Gran (els Hostalets de Pierola), BS, Bòvila Sagués (Terrassa); CAL, Ca n'Almirall (Sant Llorenç d'Hortons); CBA, Can Baiona (Viladecavalls); CB, Castell de Barberà (Barberà del Vallès); CBL, Costablanca (Castellbisbal); CBR, Can Barra (Sant Quirze del Vallès); CC, Can Canals (El Papiol); CCN20, Creu Conill (Terrassa); CJ, Can Julià (Gelida); CLL, Can Llobateres (Sabadell); CMA, Can Marcet (els Hostalets de Pierola), CM, Can Mata (els Hostalets de Pierola); CM1 (Can mata 1) (els Hostalets de Pierola), CMS, Can Missert (Terrassa); CPA, Can Parellada (Masquefa); CPE, Can Parellada (Terrassa); CPL, Can Purull (Viladecavalls); CP, Can Poncic (Sant Quirze del Vallès); CS, Els Casots (Subirats); CT, Can Trullàs (Viladecavalls); CV, Can Vila (els Hostalets de Pierola); EC, El Canyet (Castellbisbal); ECM, local stratigraphic series of Ecoparc de Can Mata (els Hostalets de Pierola); HP, Hostalets de Pierola indetermined (els Hostalets de Pierola); HPI, Hostalets de Pierola Inferior (els Hostalets de Pierola); HPS, Hostalets de Pierola Superior (els Hostalets de Pierola); LCV, Les Cases de la Valenciana (Gelida); LTR, La Tarumba (Viladecavalls); MB, Mas Bernic (Masquefa), MC, Molí Calopa (Rubí); PI, Piera (Piera), ROS, local stratigraphic series of Ronda Oest de Sabadell (Sabadell); SA, Santiga (Barberà del Vallès); SB, Sant Andreu de la Barca (Sant Andreu de la Barca); SBL, Sabadell indetermined (Sabadell); SC, Serra d'en Camero (Sabadell); SM, Sant Mamet (Sant Cugat del Vallès); SMT, Sant Miquel del Taudell (Viladecavalls); SQ, Trinxera del Ferrocarril (Sant Quirze del Vallès); TF, Torrent de Febulines (Terrassa); TGM, Torrent del Gall Mullat (Piera); TNA, Trinxera Nord de l'Autopista (Terrassa); TSA, Trinxera Sud de l'Autopista (Terrassa); TRR, Terrassa (Terrassa), TT, Torrentet de Traginers (Piera); TV, Torrent de Vilaroc (Rubí); VL, Viladecavalls (Viladecavalls), VV, Vinya Vella (Esparreguera).

Systematic paleontology

Order **Carnivora** Bowdich, 1821
Family **incertae sedis**

Carnivora indet. Range: middle Aragonian to late Aragonian (MN5?/MN6–MN7+8). Sites: ACM (ACM/BDA8, ACM/C1-E6, ACM/C2-A, ACM/C2-Aa, ACM/C2-Ba, ACM/C2-Bb, ACM/C2-B3, ACM/C3-A, ACM/C3-Af, ACM/C3-Ai, ACM/C3-B, ACM/C3-C, ACM/C4-A, ACM/C4-Ad, ACM/C4-Ap, ACM/C4-A3, ACM/C4-C, ACM/C4-Cd, ACM/C4-C1, ACM/C5-Ad, ACM/C5-C2, ACM/C5-Dd, ACM/C5-Di, ACM/C5-D2, ACM/C5-D4, ACM/C5-D7, ACM/C6-A1, ACM/C6-Cd, ACM/C7-A1, ACM/C7-A2, ACM/C7-B, ACM/C8-Ad, ACM/C8-Ae, ACM/C8-Aj, ACM/C8-Al, ACM/C8-A3, ACM/C8-Ba, ACM/C8-Bc, ACM/C8-Bh, ACM/C8-Bk, ACM/C8-Bo, ACM/C8-Bp, ACM/C8-Bs, ACM/C8-Bu, ACM/C8-Bx, ACM/C8-By, ACM/C8-Ba', ACM/C8-Bc', ACM/C8-B2) and CAL.

There are only a few citations of Carnivora indet. from the literature, corresponding to the remains from CAL (Golpe-Posse 1974; Agustí et al. 1984, 1985). The revision undertaken by the authors of the ICP, MGB and MGSB collections indicates the presence of a high number of fragmentary fossils attributable to Carnivora indet. from many Vallès-

Penedès localities, ranging from the MN4 to the MN7+8. However, only those localities in which no carnivoran has been identified at the family rank (or below) have been reported above.

Suborder **Feliformia** Kretzoi, 1945

Family **Viverridae** Gray, 1821

Viverridae indet. Range: Ramblian to early Vallesian (MN3–MN9). Sites: ACM/C1-E10, ACM/C5-A6, CC, ECM, LCV, MC. Bibliographic citations and synonyms: Viverridae indet. in Crusafont and Truyols (1954), Crusafont et al. (1955), Golpe-Posse (1974), Agustí et al. (1984) and Alba et al. 2012; *Herpestes* cf. *dissimilis* in Golpe-Posse (1974).

The Vallès-Penedès remains from various localities previously attributed to Viverridae indet. (Crusafont and Truyols 1954; Crusafont et al. 1955; Golpe-Posse 1974), ?*Semigenetta* sp. (Golpe-Posse 1974; Crusafont-Pairó and Golpe-Posse 1981), *Herpestes* cf. *dissimilis* (Golpe-Posse 1974) or *Progenetta gaillardi* (Crusafont Pairó and Kurtén 1976; Golpe-Posse et al. 1979) are difficult to attribute to genus, because they mainly consist in postcranial and isolated dental remains; moreover, in some cases (Golpe-Pose 1974) these reports consists only in faunal lists with no associated catalog numbers, which makes it impossible to revise the material. Here we further report the presence of viverrids at varios ACM and ECM localities, which might be identified as more complete remains become available, although more detailed studies are required to provide an attribution to genus.

Subfamily **Viverrinae** Gray, 1821

Genus ***Semigenetta*** Helbing, 1927

***Semigenetta sansaniensis* (Lartet, 1851).** Range: late Aragonian to early Vallesian (MN7+8–MN9). Sites: CM1, HP. Bibliographic citations and synonyms: *Plesictis* sp. in Bataller (1941), Villalta Comella and Crusafont Pairó (1941, 1943a), Villalta and Crusafont (1946b) and Crusafont and Truyols (1954); *Viverra sansaniensis* in Bataller (1941), Villalta Comella and Crusafont Pairó (1941, 1943a), Crusafont-Pairó and Golpe-Posse (1981) and Golpe-Posse (1981a); ?*Plesictis mutatus* in Villalta Comella and Crusafont Pairó (1944), Villalta and Crusafont (1946b), Crusafont-Pairó and Golpe-Posse (1981) and Golpe-Posse (1974; 1981a,b); *Semigenetta sansaniensis* in Villalta and

Crusafont (1946b), Crusafont-Pairó (1953), Crusafont and Truyols (1954), Golpe-Posse (1974), Golpe-Posse (1981a,b) and Agustí et al. (1984, 1985); *Semigenetta mutata* in Crusafont and Truyols (1954) and Golpe-Posse (1974).

***Semigenetta* cf. *sansaniensis*.** Range: late Aragonian to late Vallesian (MN7+8–MN10). Main sites: ACM/C4-C2, ACM/C6-A and TF. Bibliographic citations and synonyms: cf. *Semigenetta* sp. in Alba et al. (2007).

***Semigenetta ripolli* Petter, 1976.** Range: early Vallesian (MN9). Sites: CLL1 [type locality]. Bibliographic citations and synonyms: *Semigenetta mutata* in Crusafont Pairó and Truyols Santoja (1960), Crusafont (1964), Crusafont-Pairó and Golpe-Posse (1973), Golpe-Posse (1974), Crusafont Pairó and Kurtén (1976) and Crusafont-Pairó and Golpe-Posse (1981); *Semigenetta ripolli* in Petter (1976), Golpe-Posse (1981a,b) and Alba et al. (2011b).

***Semigenetta grandis* Crusafont-Pairó and Golpe-Posse, 1981.** Range: early Vallesian (MN9). Sites: CB [type locality]. Bibliographic citations and synonyms: *Semigenetta grandis* in Crusafont-Pairó and Golpe-Posse (1981) and Golpe-Posse (1981a,b); Viverridae indet. in Crusafont Pairó and Golpe-Posse (1972) and Golpe-Posse (1974).

The genus *Semigenetta* is recorded in the Vallès-Penedès by three different species: *Se. sansaniensis*, from the MN7+8 of the localities of HP and CM1 (els Hostalets de Pierola); *Se. grandis*, from the MN9 from CB; and *Se. ripolli*, from the MN9 of CLL1. *Semigenetta sansaniensis* is widely recorded throughout the Aragonian of Europe, in localities such as Vieux-Collonges, Sansan, La Grive or Steinheim (Viret 1951; Ginsburg 1961; Heizmann 1973; Nagel 2003). Two different species are recorded during the early Vallesian of the Vallès-Penedès Basin: *Se. ripolli*, previously attributed to *Se. mutata* (Crusafont-Pairó and Truyols Santoja 1960; Crusafont 1964; Crusafont-Pairó and Golpe-Posse 1973; Golpe-Posse (1974), subsequently erected by Petter (1976) based on remains from CLL1, and more recently reported from the similarly-aged Iberian locality of Masía de la Roma MR 604 (Montoya et al. 2001); and *Se. grandis*, originally described by Crusafont-Pairó and Golpe-Posse (1981) based on material from CB, and subsequently reported from Rudabánya in Hungary (Werdelin 2004). Compared to the two other Vallès-Penedès species, *Se. ripolli* is characterized by its smaller size and several occlusal features (elongated lower premolars, with a mesially-situated accessory cuspulid in the p2, and an elongated mandibular corpus; Petter 1976), whereas *Se. grandis* is the largest species of the genus, further differing from the other species by a more carnivorous dentition (Crusafont-Pairó and Golpe-Posse 1981). The presence of *Semigenetta* cf. *sansaniensis* can be further ascertained at ACM and TF based on unpublished dental remains that displays features of the species in the m1 such as a high protoconid, a more reduced metaconid, and a short talonid, being lower, less reduced and longer respectively, in species of the early and middle Miocene, such in *Se. repelini* Helbing, 1927 (MN5; Montoya et al. 2001). However, more detailed comparisons will be required in the future to further precise the taxonomic attribution of these remains.

Family **Barbourofelidae** Schultz et al., 1970

Genus ***Albanosmilus*** Kretzoi, 1929

***Albanosmilus jourdani* Filhol, 1833.** (Figs. 1C–E, 2G–H) Range: late Aragonian to early Vallesian (MN7+8–MN9). Sites: ACM/C3-Ak, ACM/C4-C2, ACM/C6-Ak, ACM/C6-C, ACM/C7-A, ACM/C8-B/C, CB, CCN20, CLL1, CM1, CMS, CP1, HPI, SA and SQ. Bibliographic citations and synonyms: *Machairodus ogygius* in Bataller (1924); *Machairodus andresi* in Villalta Comella and Crusafont Pairó (1941); *Albanosmilus jourdani* in Villalta Comella and Crusafont Pairó (1943a,b), Villalta and Crusafont (1946b,c), Crusafont-Pairó (1953, 1979b) and Robles et al. (2013b); *Albanosmilus jourdani* var. *andresi* in Villalta Comella and Crusafont Pairó (1943a); *Grivasmilus jourdani* in Villalta and Crusafont (1952), Crusafont and Truyols (1954), Crusafont Pairó and Truyols Santoja (1954), Crusafont-Pairó and Golpe-Posse (1973a,b), Crusafont Pairó and Kurtén (1976) and Golpe-Posse (1974); *Machairodus* sp. in Crusafont and Truyols (1954) and Crusafont Pairó (1964); *Sansanosmilus jourdani vallesiensis* in de Beaumont and Crusafont-Pairó (1982); *Sansanosmilus jourdani* in Agustí et al. (1984, 1985, 1997), Agustí and Galobart (1998), Alba et al. (2006, 2007, 2009, 2011a,b), Casanovas-Vilar et al. (2008, 2011a) and Robles et al. (2010b); Felidae indet. in de Beaumont and Crusfont-Pairó (1982); *Machairodus* sp. in Crusafont and Truyols (1954) and Crusafont Pairó (1964).

The genus *Albanosmilus* was recently resurrected by Robles et al. (2013b), who reviewed the craniodental Vallès-Penedès material of its type species (*A. jourdani*). This is the only barbourofelin species currently recorded in the Iberian Peninsula. Based on the emended diagnosis provided by Robles et al. (2013b), this sabertoothed carnivoran is characterized by a short and broad muzzle, complete postorbital closure (postorbital bar), sinuous and high mandibular corpus (highest at the level of p4), large and U-shaped genial flange at the level of the postcanine diastema in adults, upper canine and cheek-teeth with crenulated borders, tetracuspid P3, and P4 with residual or absent protocone. *Albanosmilus jourdani* is recorded until the MN9, coexisting in time and space (e.g., CLL1) with the true sabertoothed felid (machairodontine) *Machairodus aphanistus*. A closely related (potentially synonymous) species of the same genus, *Albanosmilus whitfordi*, it recorded from North America, suggesting that sometime in the Middle to Late Miocene *Albanosmilus* dispersed into North America, giving rise to the clade of *Barbourofelis* spp. (Robles et al. 2013b).

Family **Felidae** Fischer von Waldheim, 1817

Felidae indet. Range: late Aragonian to early Vallesian (MN7+8-MN9). Main Sites: ACM/C6-C3, ACM/C6-C, ACM/C8-A, ACM/C8-B, ACM/C4-A1, CB, CLL1 and CP1.

Here we report unpublished postcranial remains (housed at the ICP and MGSB) of small to medium-sized felids from various Middle to Late Miocene localities of the Vallès-Penedès Basin, in which no other small-bodied felid has been reported. Further study is required to provide a more detailed assignment for these postcranial remains.

Subfamily **Felinae** Fischer von Waldheim, 1817

***“Felis” vireti* (nomen dubium).** Range: Ramblian to late Vallesian (MN3–MN10). Sites: CJ, LTR1 and MC. Bibliographic citations and synonyms: *Felis vireti* in Crusafont and Truyols (1954), Crusafont et al. (1955), Crusafont-Pairó (1963), Golpe-Posse (1974) and Agustí et al. (1984); Viverridae indet. in Golpe-Posse (1974) and Agustí et al. (1984, 1985).

Crusafont and Truyols (1954) first employed the name *Felis vireti* for felid remains from CJ and MC, attributing the authorship to Crusafont and Villalta. However, the name was not formally erected until Crusafont et al. (1955), on ‘provisional’ grounds. The authors did not explicitly designate a holotype, but it is clear from their text that they considered it to be a distal humeral fragment from CJ, whereas a proximal ulnar fragment from MC was merely attributed to the same taxon. Crusafont et al. (1955) hypothesized that the taxon represented at CJ might be the same as represented by a felid P4 from La Romieu described by Roman and Viret (1934), subsequently attributed to Viverridae indet. by de Beaumont (1961). Subsequently, Golpe-Posse (1974) further reported the presence of this taxon at LTR1. de Beaumont (1961) refrained to attribute the Vallès-Penedès remains, previously attributed to *Felis vireti* by Crusafont et al. (1955) and Golpe-Posse (1974), to the Felidae, because of the scarcity of the available remains. It is unknown what remains from LTR1 were previously attributed to *Felis vireti*, but those from CJ and MC most likely belong to one of the felines recorded during the early Aragonian in the basin (see below). According to the Code (ICZN 1999, Article 15.1), names proposed conditionally before 1961 are nomenclaturally valid, so that *Felis vireti* is not a nomen nudum. However, unless dental material from the type locality is recovered, it seems impossible to determine with certainty the taxonomic affinities of this nominal taxon, being a potential junior synonym of various species of *Styriofelis* Kretzoi, 1929 (see below). Accordingly, *"Felis" vireti* is here considered a nomen dubium.

Genus ***Pseudaelurus*** Gervais, 1850

***Pseudaelurus quadridentatus* (Blainville, 1843).** (Fig. 2C–D) Range: late Aragonian to early Vallesian (MN7+8–MN9). Sites: ACM/C4-C2, ACM/C6-C3, ACM/C8-Bd', CB, CCN20, CM1, CP1, HP, HPI and SQ. Bibliographic citations and synonyms: Felidae indet. in Villalta Comella and Crusafont Pairó (1941); *Pseudaelurus quadridentatus* in Bataller (1941), Villalta Comella and Crusafont Pairó (1941, 1943a), Villalta and Crusafont (1946b), Crusafont-Pairó (1953), Crusafont and Truyols (1954), Crusafont-Pairó and Golpe-Posse (1973a), Golpe-Posse (1974), Petter (1976), Alba et al. (2007), Robles et al. (2013a); *Pseudaelurus marini* in Villalta Comella and Crusafont Pairó (1943a), Villalta and Crusafont (1946b), Crusafont-Pairó (1953), Crusafont and Truyols (1954), Golpe-Posse (1974) and Agustí et al. (1985).

***Pseudaelurus romieviensis* (Roman and Viret, 1934).** (Fig. 2E–F) Range: early Aragonian to late Vallesian (MN4–MN7+8). Main sites: ACM/C4-A1, ACM/C5-C, ACM/C8-B, CS and SM. Bibliographic citations and synonyms: *Pseudaelurus* sp. Alba et al. (2006, 2009, 2011a) and Casanovas-Vilar et al. (2008); *Pseudaelurus romieviensis* in Casanovas-Vilar et al. (2011b) and Robles et al. (2013a); *Prosansanosmilus* sp. in Casanovas-Vilar et al. (2011c).

This genus includes multiple feline species widely recorded from Eurasia and North America but not Africa (Ginsburg 1999; Rothwell 2003; Werdelin and Peigné 2010), although North American species might have independently evolved from a more primitive ancestor (thereby rendering *Pseudaelurus*, as currently defined, as paraphyletic; Werdelin et al. 2010). *Pseudaelurus quadridentatus* (the type species of the genus) has been considered as the basal-most member of the clade of true sabertoothet cats of the family Machairodontinae (Werdelin et al. 2010; Turner et al. 2011; Salesa et al. 2012; Robles et al. 2013a), but until this is further confirmed by future phylogenetic studies for *P. romieviensis* also (or the latter is distinguished at the genus rank), here we refrain from formally classifying *Pseudaelurus* within the Machairodontinae. In any case, the lack of very bucco-lingually compressed upper canines enables to distinguish the two species of *Pseudaelurus* from the machairodontine felids recorded at the Vallès-Penedès Basin (see below). Like elsewhere in Europe, two medium-sized species (larger than *Styriofelis* spp.) of *Pseudaelurus* are recorded in the Vallès-Penedès Basin (Robles et al. 2013a): *P. romieviensis*, from the MN4 to the MN7+8; and *P. quadridentatus*, from the MN7+8 to the MN9. Robles et al. (2013a) recently reported dentognathic material of both species from various ACM localities, and first documented the retention of p2 in *P. romieviensis*, which like the development of the mesial accessory cuspulid of the p4 cannot be employed as a diagnostic criterion between the two *Pseudaelurus* species (contra Heizmann 1973). *Pseudaelurus romieviensis* is characterized by its smaller size as well as by a lower carnassial with a well-developed talonid (Roman and Viret 1934; Heizmann 1973; Robles et al. 2013a), whereas *P. quadridentatus* is distinguished by it larger size and various occlusal details, such as lesser-developed m1 talonid without a distinct metaconid as well as lower-crowned and more inflated lower premolars (Robles et al. 2013a). Previously, the presence of *Pseudaelurus* in the early Vallesian was based only on the remains of *P. quadridentatus* from CB (Petter 1976) and Los Valles de Fuentidueña (Fraile et al. 1997), but here we further report the presence of this species at CP1 and CCN20, based on unpublished remains housed at the ICP.

Genus ***Styriofelis*** Kretzoi, 1929

***Styriofelis* sp.** Range: early Aragonian (MN4). Sites: CBL, CC and EC. Bibliographic citations and synonyms: “small Carnivora” in Crusafont Pairó et al. (1968) and Golpe-Posse (1974); *Pseudaelurus turnauensis* in Crusafont Pairó and Truyols Santoja (1954), Crusafont Pairó (1959c) and Golpe-Posse (1974); ?*Pseudaelurus* sp. (small size) in Galindo (2000); *Pseudaelurus* sp. in Casanovas-Vilar et al. (2011c).

***Styriofelis turnauensis* (Hoernes, 1882).** Range: Ramblian to early Vallesian (MN3–MN9). Sites: ACM/C5-A6, CB, CC, CV, HPI, SB, SC and VV. Bibliographic citations and synonyms: *Pseudaelurus transitorius* in Bataller (1941), Villalta Comella and Crusafont

Pairó (1941, 1943a), Villalta and Crusafont (1946b) and Golpe-Posse (1974); *Pseudaelurus turnauensis* in Crusafont Pairó (1952), Crusafont and Truyols (1954), Crusafont et al. (1955), Crusafont Pairó and Truyols Santoja (1960), Golpe-Posse (1974), Petter (1976), Agustí and Galobart (1998), Alba et al. (2007) and Casanovas-Vilar et al. (2011a); *Pseudaelurus* sp. in Agustí et al. (1984) and Casanovas-Vilar et al. (2011c); *Styriofelis turnauensis* in Robles et al. (2013a).

Styriofelis lorteti **(Gaillard, 1899).** Range: early Aragonian (MN4). Sites: SM. Bibliographic citations and synonyms: *Pseudaelurus* (*Schizailurus*) *lorteti* in Crusafont et al. (1955); *Pseudaelurus lorteti* in Crusafont and Truyols (1954), Crusafont Parió and Truyols Santoja (1954), Golpe-Posse (1974) and Agustí et al. (1984).

The small-sized feline genus *Styriofelis* is widely distributed across the Miocene of Eurasia, being considered the basal-most member of the clade of conical-toothed cats, i.e., Pantherinae + Felinae (Werdelin et al. 2010; Turner et al. 2011; Salesa et al. 2012; Robles et al. 2013a). For many years, the species currently included in this genus were attributed by many authors to genus *Pseudaelurus* (e.g., Viret, 1951; Crusafont et al. 1955; de Beaumont 1961, 1978; Crusafont-Pairó and Ginsburg 1973; Petter 1976), in spite of the fact that Kretzoi (1929, 1938) had previously erected the genera *Styriofelis* Kretzoi, 1929 (for *S. turnauensis*, with *Pseudaelurus transitorius* Depéret, 1892 being its junior synonym) and *Miopanthera* Kretzoi, 1938 (for *S. lorteti*), and that Viret (1951) had erected subgenus *Schizailurus* Viret, 1951 (for *S. lorteti* as its type species, and further including *S. turnauensis*). Currently, *Syriofelis* is considered distinct from *Pseudaelurus*, with *Schizailurus* being an objective junior synonym of *Miopanthera*, and the latter being a subjective junior synonym of *Pseudaelurus* (Werdelin et al. 2010; Salesa et al. 2011, 2012; Robles et al. 2013a). Recently, Robles et al. (2013a) reported new small feline material from ACM localities, and recognized the presence of two *Styriofelis* species in the Vallès-Penedès Basin. *Styriofelis lorteti* is only recorded from the MN4 locality of SM (Crusafont and Truyols 1954; Crusafont et al. 1955), being thus more chronologically more restricted in this basin than elsewhere in Iberia (Robles et al. 2013a); in contrast, *S. turnauensis* is much more widely recorded in the Vallès-Penedès Basin, ranging from the MN3 to the MN9, in agreement with the record of this species elsewhere (it is first recorded in the MN2, which is not represented at the Vallès-Penedès; Robles et al. 2013a). Although these two species overlap in size, *S. turnauensis* can be distinguished from *S. lorteti* based on the less developed m1 talonid and its generally smaller size (Robles et al. 2013a). Several unpublished fragmentary long bones from SM (MN4) are here attributed to *S. lorteti*, given their larger size compared to the postcranial material from VV attributed to *S. turnauensis* (Crusafont et al. 1955). *Styriofelis vallesiensis* Salesa et al., 2012, recently erected from the MN10 of Batallones-3 (Salesa et al. 2012), and distinguished from other species of *Styriofelis* by its considerably smaller size, is currently not recorded at the Vallès-Penedès Basin. Besides the early Aragonian remains of *"Felis" vireti* (nomen dubium), which might belong to *Styriofelis* (see discussion above), other feline remains of similar age, previously reported by Crusafont Pairó et al. (1968) and Golpe-Posse (1974), have been merely attributed here to *Styriofelis* sp. A species assignment is not possible for the remains from CBL, CC and EC, due to the fragmentary nature and/or poor preservation of the available remains. In turn, those from CBL, previously attributed to *Pseudaelurus* sp. and Carnivora indet. (small size) by Golpe-Posse (1974) and Galindo (2000), display uncommon features (biradiculate p2 and retention of m2), which require additional study to further ascertain their taxonomic significance.

Subfamily **Machairodontinae** Gill, 1872

Genus ***Machairodus*** Kaup, 1833

***Machairodus aphanistus* (Kaup, 1832)**. Range: early to late Vallesian (MN9–MN10). Sites: CLL1, CM CP1, CPE, LTR1, ROS-D3, SA, and TF. Bibliographic citations and synonyms: *Amphimachairodus giganteus* in Pons-Moyà (1990); *Felis* sp. in Bataller (1941) and (partim) in Villalta Comella and Crusafont Pairó (1948); *Machairodus* sp. in Crusafont and Truyols (1954), Golpe-Posse (1974), Crusafont-Pairó (1979b) and Agustí et al. (1984, 1985); *Pseudaelurus* sp. in Crusafont and Truyols (1954); *Machairodus aphanistus* in Crusafont Pairó (1959a), Crusafont Pairó and Truyols Santoja (1960), Crusfafont (1964), Crusafont-Pairó and Golpe-Posse (1973a), Golpe-Posse (1974), Crusafont Pairó and Kurtén (1976), Golpe-Posse et al. (1979); de Beaumont and Crusafont-Pairó (1982), Agustí et al. (1997), Alba et al. (2011b), Robles et al. (2013c) and Madurell-Malapeira et al. (under review).

The genus *Machairodus* is the only representative of machairodontine tribe Machairodontini in the Vallès-Penedès Basin, where it is recorded by the type species of the genus, *M. aphanistus*, from both early and late Vallesian localities (Golpe-Posse et al. 1979; de Beaumont and Crusafont-Pairó 1982; Pons-Moyà 1990; Fraile et al. 1997; Robles et al. 2013c). Most recently, Madurell-Malapeira et al. (under review) revised the available remains of this taxon from the Vallès-Penedès Basin, including the report of previously unpublished (mostly postcranial) material. Although the genus is widely recorded by several species in Eurasia, North America and Eurasia, in Europe generally only *M. aphanistus* is recognized, being restricted to the Vallesian (MN9–MN10), whereas Turolian (MN10–MN13) homotheriin remains are generally attributed to *Amphimachairodus giganteus* (Wagner, 1848) (de Beaumont 1975; Bernor et al. 1988; Antón et al. 2004; Peigné et al. 2005a; Spassov et al. 2006; Madurell-Malapeira et al. under review), although the two species are apparently recorded in the MN11 of Europe and Turkey (Morlo et al. 1997; Peigné et al. 2005a,b; Spassov et al. 2006). Although the type locality of *M. aphanistus* is Eppelsheim (MN9), the species is best known from the abundant and complete craniodental and postcranial remains from Batallones-1 (Antón et al. 2004; Salesa et al. 2005; Turner et al. 2011). It is characterized by very flattered upper canines, lower canines with oval cross-section, large lower premolars with a complete set of accessory cuspids, a well-developed metaconid-talonid complex in the m1, a thick and high mandibular corpus, a high and posteriorly inclined coronoid process, an undeveloped mandibular flange, a well developed sagittal crest, a narrow skull, a lower and curved zygomatic arch, an elongated temporal fossa, a well-developed paraoccipital process, a relatively small mastoid process, a nasofrontal suture intermediate between the pantherine (pointed) and the dervied machairodontine (straight) condition, and a large but low postorbital process (Antón et al. 2004). According to Agustí et al. (1997), the first record of *M. aphanistus* in the Vallès-Penedès Basin would correspond to the earliest Vallesian locality of CCN22, but this citation is most likely based on a fossil specimen attributable to a hyaenid (Madurell-Malapeira et al. under review; see also below). Nevertheless, the presence of this taxon in the earliest Vallesian is attested by a talus from HP reported by Madurell-Malapeira et al. (under review), although dating uncertainties preclude to conclusively discount the record of this species already in the latest Aragonian.

Genus ***Promegantereon*** Pilgrim, 1913

cf. *Promegantereon ogygia*. (Fig. 3Y–A') Range: late Vallesian (MN10). Sites: CPE, LTR1 and TNA. Bibliographic citations and synonyms: *Felis antediluviana* in Villalta Comella and Crusafont Pairó (1943a), Villalta and Crusafont (1946a), Crusafont and Truyols (1954), Crusafont Pairó and Truyols Santoja (1960), Golpe-Posse (1974) and Agustí et al. (1984); *Paramachairodus* sp. in Golpe-Posse et al. (1979); *Paramachaerodu*s *orientalis* in Pons-Moyà (1990).

The name of this machairodontine genus of tribe Smilodontini has been frequently spelled out as *"Paramachairodus"* in the past (e.g., Salesa et al. 2003), but as noted by Salesa et al. (2010), there is no reason for not retaining the original spelling *Paramachaerodus*. Two species of this are recorded in Europe, *Paramachaerodus orientalis* and *Paramachaerodus maximiliani*, following the revision by Salesa et al. (2010), who removed the MN9–MN11 species *Promegantereon ogygia* (Kaup, 1832) (not recorded in the Vallès-Penedès Basin) from this genus and reassigned it to *Promegantereon* Kretzoi, 1938. The latter genus can be distinguished from *Paramachaerodus* on the basis of the lack of canine crenulations, the P3 with a marked distolingual expansion, the P4 withouth ectostyle and with well-developed protocone, buccolingually wide and biradiculated M1, and larger m1 talonid (Salesa et al. 2010). According to the latter authors, *Pa. maximiliani* (MN13 of the Iberian Peninsula) would differ from the type species of the genus, *Pa. orientalis* (MN11–MN12 of Europe) by its somewhat larger size as well as the longer P3 with a moderate distolingual expansion. In the Vallès-Penedès Basin, smilodontin sabertooths are only recorded by fragmentary and poorly-preserved remains, including a mandibular fragment with p4 and partial m1 from LTR1, attributed by Villalta Comella and Crusafont Pairó (1943a) to *Felis antediluviana* Kaup, 1832 (currently considered a synonym of *Pro. ogygia*; Salesa et al. 2010), as well as a fragmentary p4 from TNA attributed to *Paramachairodus* sp. by Golpe-Posse et la. (1979), and latter attributed to *Paramachaerodus orientalis* (Pons-Moyà 1990). Although the Vallès-Penedès remains only overlap in time with the known distribution of *Pro. ogygia*, a secure attribution is not possible, because the p4 is not diagnostic, and the m1 of the mandibular fragment from LTR1 is not completely preserved.

Genus ***Stenailurus*** Crusafont-Pairó and Aguirre, 1972

Stenailurus teilhardi **Crusafont-Pairó and Aguirre, 1972.** (Fig. 1I–K) Range: early Turolian (MN12). Sites: TT [type locality]. Bibliographic citations and synonyms: *Felis* sp. in Bataller (1941); *Machairodus* sp. in Crusafont and Truyols (1954); ?*Metailurus* sp. in Crusafont-Pairó (1953) and Crusafont and Truyols (1954); probably ?*Paramachairodus orientalis* in Villalta and Crusafont (1946a); *Stenailurus teilhardi* in Crusafont-Pairó and Aguirre (1972), Golpe-Posse (1974), Agustí et al. (1985) and Casanovas-Vilar et al. (2011a).

This monotypic genus from tribe Metailurini was originally erected by Crusafont-Pairó and Aguirre (1972) based on material from the MN11 locality of TT in the area of Piera, and has not been subsequently reported from elsewhere, in spite of the fact that other metailurins have been recorded from the Iberian Peninsula (Alcalá and Montoya 1990; Alcalá 1994; Fraile et al. 1997; Morales and Soria 1979). The available remains of this taxon (a rostral fragment with left I1-C1 and P3-P4 (partial) and right C1) display some derived features of the machairodontine tribe Metailurini (such as the more mesially-situated P4 protocone relative to the parastyle and bigger upper canines), but still retains some primitive features (presence of P2) that are lacking in other metailurins (Crusafont-Pairó and Aguirre 1972; Turner and Antón 1997). Without more complete cranial and mandibular remains remains, it is difficult to further assess the phylogenetic relationships of this taxon, because *St. teilhardi* contains at the same time primitive and derived features among the Metailurini.

Family **Hyaenidae** Gray, 1821

Hyaenidae indet. Range: late Aragonian (MN7+8). Sites: ACM/C3-A6, ACM/C4-C2, ACM/C6-C2, ACM/C6-C3, CCN22, CM1 and CP1. Bibliographic citations and synonyms: *Machairodus* sp. in Agustí and Galobart (1998); *Machairodus aphanistus* (partim) in Agustí et al. (1997).

Hyaenid remains from CCN22 (Agustí et al. 1997; Agustí and Galobart 1998) were initially assigned to *Machairodus* and *Machairodus aphanistus* based on unspecified material that, according to our survey of the ICP collections, can only correspond to a partial P4 (the protocone is not preserved) that must be attributed to a medium-sized hyaenid (Madurell-Malapeira et al. under review).

Subfamily **Hyaeninae** Gray, 1821

Genus ***Hyaenictis*** Gaudry, 1861

cf. *Hyaenictis* sp. Range: late Vallesian (MN10). Sites: ROS-D.

***Hyaenictis almerai* Villalta Comella and Crusafont Pairó, 1948.** (Fig. 2I–J) Range: late Vallesian (MN10). Sites: SMT [type locality]. Bibliographic citations and synonyms: *Hyaenictis graeca* in Bataller (1921, 1924) and Villalta Comella and Crusafont Pairó (1941, 1943a); *Hyaenictis almerai* (nomen nudum) in Villalta and Crusafont (1946c);

Hyaenictis almerai in Villalta Comella and Crusafont Pairó (1948), Crusafont and Truyols (1954), Crusafont-Pairó (1955), Crusafont Pairó and Truyols Santoja (1960), Golpe-Posse (1974) and Agustí et al. (1984).

This monotypic genus was erected by Villalta Comella and Crusafont Pairó (1948) based on a mandible from SMT in the area of Viladecavalls, previously attributed to *Hyaenictis graeca* Gaudry, 1861 by Bataller (1921, 1924), and has not been subsequently reported from elsewhere. In spite of the scarcity of the available remains, the lack of p1, the shorter mandibular corpus, the absence of m1 metaconid, and the presence of m2 indicate that this species is distinct from other Miocene hyaenids (Villalta Comella and Crusafont Pairó 1948; Werdelin and Solounias 1991). On the other hand, the species does not comfortably fit in either *Hyaenictis* (type species *Hyaenictis graeca* Gaudry, 1861) or *Chasmaporthetes* Hay, 1921, and might eventually require a different genus of its own (Werdelin and Solounias 1991). The unpublished remains from the ROS-D, a partial cranium and the associated partial left and right mandibles (IPS62078), display many primitive features, such as the retention of p1 and m2, three mental foramina and a biscuspid m1 talonid. This specimen is clearly different from *Adcrocuta eximia* (widely recorded in the Vallès-Penedès Basin) on the basis of the well-developed P4 protocone, the buccolingually narrower lower premolars and the presence of m2. The features displayed by this specimen suggest its inclusion in cursorial hunting-hyena ecomorphotype sensu Werdelin and Solounias (1991). Here we tentatively refer this specimen to genus *Hyaenictis*, pending more detailed studies.

Genus ***Adcrocuta*** Kretzoi, 1938

***Adcrocuta eximia* (Roth and Wagner, 1854).** (Fig. 1F–H) Range: late Vallesian to early Turolian (MN10–MN12). Sites: CPL, TRR and TT. Bibliographic citations and synonyms: *Crocuta eximia* in Villalta and Crusafont (1946a), Villalta Comella and Crusafont Pairó (1948), Crusafont-Pairó (1953, 1955), Crusafont and Truyols (1954), Crusafont Pairó and Truyols Santoja (1954) and Crusafont Pairó and Truyols Santoja (1960); *Percrocuta eximia* in Golpe-Posse (1974); *Adcrocuta eximia* in Agustí et al. (1984, 1985, 1997) and Casanovas-Vilar et al. (2011a).

The genus *Adcrocuta* includes a single species, with various described subspecies that would not be taxonomically valid according to Werdelin and Solounias (1991). *Adcrocuta eximia* is the earliest hyaenid species displaying well-developed adaptations for breaking bones, thus being included in the bone-cracking ecomorphotype by Werdelin and Solounias (1991). The postcranial remains recovered from the Turolian site of Pikermi (Greece) indicate that *Ad. eximia* was a powerful but probably not fast moving animal (Turner et al., 2008). This species is widely recorded in the Late Miocene of Iberia and elsewhere in Europe (Villalta Comella and Crusafont Pairó 1948, Werdelin and Solounias, 1991; Turner et al., 2008; Koufos, 2011), being characterized by a short and broad skull, a very large P4 compared with the P3 and with a reduced protocone, a buccolingually wide M1, a long m1 relative to the p4, and lower premolars without a mesial accessory cuspulid (Villalta Comella and Crusafont Pairó 1948; Werdelin and Solounias 1991; Turner et al., 2008). Almost all the material ascribed here to this species was previously published by Villalta Comella and Crusafont Pairó (1948), although the isolated C1 from CPL reported by these authors has not been located in the ICP collections. A partial juvenile cranium from TT (IPS8965) attributed to this taxon preserves the dp3-dp4 series, which shows great affinities with the decidual teeth of the extant *Crocuta crocuta* (Werdelin and Solounias 1990; Koufos 2012; J.M.-M. pers. obs.). The chronostratigraphic range of *Ad. eximia* in the Vallès-Penedès (MN10–MN12) fits well with, although it is more restricted than, that elsewhere in Europe (MN10–MN13; Werdelin and Solounias 1991).

Subfamily **Ictitheriinae** Trouessart, 1897

Genus ***Thalassictis*** Nordmann, 1850

***Thalassictis* sp.** Range: late Aragonian (MN7+8–MN9). Site: BG, HPI and SQ. Bibliographic citations and synonyms: *Hyaena eximia* in Bataller (1924); *Ictitherium* sp. in Bataller (1941), Villalta Comella and Crusafont Pairó (1943a), Villalta and Crusafont (1946b), Crusafont and Truyols (1954) and Golpe-Posse (1974); probably Hyaenidae indet. in Crusafont and Truyols (1954), Golpe-Posse (1974) and Agustí et al. (1984).

***Thalassictis robusta* Nordmann, 1858.** Range: late Vallesian (MN10). Sites: B40OV/S5, SMT, TRR and VL. Bibliographic citations and synonyms: *Ictitherium robustum* in Villalta Comella and Crusafont Pairó (1941, 1943a), Villalta and Crusafont (1946a), Crusafont-Pairó (1953), Crusafont and Truyols (1954), Crusafont Pairó and Truyols Santoja (1960), Golpe-Posse (1974) and Agustí et al. (1984): *Thalassictis robusta* in Alba et al (2010).

***Thalassictis montadai* (Villalta Comella and Crusafont Pairó, 1943a).** (Fig. 1L–N) Range: late Aragonian to early Vallesian (MN7+8–MN9). Sites: ACM/BCV1, ACM/C4-

A1, ACM/C4-C2, ACM/C5-D1, ACM/C6-C3, CBR, CM1 [type locality], CP1, HPI and MB. Bibliographic citations and synonyms: *Ictitherium montadai* in Bataller (1941), Villalta Comella and Crusafont Pairó (1943a), Villalta Comella and Crusafont Pairó (1941), and Villalta and Crusafont (1946b), Crusafont-Pairó (1953), Crusafont and Truyols (1954), Crusafont Pairó and Truyols Santoja (1954) and Crusafont Pairó and Truyols Santoja (1960); *Progenetta montadai* in Crusafont Pairó and Petter (1969), Crusafont Pairó and Golpe Posse (1973b), Crusafont Pairó and Kurtén (1976) and Agustí et al. (1985); *Ictitherium montadai vallesiensis* in Crusafont Pairó and Truyols Santoja (1960) and Crusafont-Pairó (1963); *Progenetta montadai vallesiensis* in Crusafont Pairó and Petter (1969) and Golpe-Posse (1974); *Progenetta montadai montadai* and *Progenetta montadai urgellensis* in Crusafont Pairó and Golpe Posse (1973b) and Golpe-Posse (1974); *Miohyaena montadai* in Agustí et al. (1984); *Thalasictis montadai* in Alba et al. (2006, 2007, 2009, 2011a,b) and Casanovas-Vilar et al. (2008, 2011a).

In the Vallès-Penedès Basin, the genus *Thalassictis* is represented by two species: *T. montadai*, from the late Aragonian and early Vallesian; and *T. robusta*, from the late Vallesian. Some remains from MN7+8 (BG and SQ), previously attributed to Hyaenidae indet., *Ictitherium* sp. and *Hyaena eximia* by Bataller (1924, 1941), Golpe-Posse (1974) and Agustí et al. (1984, 1985), among others, are left unassigned to species, because they are too fragmentary, although they only overlap in chronostratigraphic range with *T. montadai*. The species of *Thalassictis* recorded in the Vallès-Penedès Basin (*T. montadai* and *T. robusta*) are widely distributed in the Iberian Peninsula and elsewhere in Europe (Crusafont Pairó and Golpe Posse 1973b; Viret 1951; Werdelin and Solounias 1991; Turner et al. 2008), being distinguished from other hyaenids—such as *Hyaenictitherium wongii* (Zdansky, 194), see below—by the presence of conical and robust lower and upper premolars, a strong mandibular corpus with a short diastema, oval M1 and robust zigomatic arches (Villalta Comella and Crusafont Pairó 1943a; Werdelin and Solounias 1991). *Thalassictis robusta* can be distinguished from *T. montadai* based on size, with *T. robusta* being smaller than *T. montadai*, and by the protoconid higher than the paraconid in the m1 of *T. montadai* (Villalta Comella and Crusafont Pairó 1943a; Werdelin and Solounias 1991). *Thalassictis montadai* was originally described by Villalta Comella and Crusafont Pairó (1943a), based on material from CM1, as *Ictitherium montadai*, having been subsequently attributed to *Thalassictis* by Werdelin and Solounias (1991). These authors mainly referred to it fossil hyaenid remains from the Aragonian (MN7+8) and, with some doubts, also from the Vallesian (MN9) (Werdelin and Solounias 1991; Turner et al. 2008). In fact, the chronostratigraphic range of *T. montadai* in the Vallès-Penedès Basin fits well with that elsewhere in Western Eurasia, where it is recorded from various MN9 localities (such as as Rudabánya in Hungary, and Sinap 4 and 94 in Turkey), and the same can be said for *T. robusta*, which is recorded from the MN9 to MN11 in Germany (Werdelin and Solounias 1991; Morlo 1997).

Genus ***Hyaenictitherium*** Kretzoi, 1938

***Hyaenictitherium wongii* (Zdansky, 1924).** Range: late Aragonian to early Turolian (MN9–MN12). Sites: HPS and PI. Bibliographic citations and synonyms: *Ictitherium hipparionum* in Villalta Comella and Crusafont Pairó (1943a), Villalta and Crusafont (1946a), Crusafont and Truyols (1954) and Crusafont Pairó and Truyols Santoja (1960).

Here we attribute the hyaenid remains from HPI, previously attributed to *Ictitherium hipparionum* (currently *Thalassictis hipparionum*) by Villalta Comella and Crusafont Pairó (1943a), to *Hyaenictitherium wongii*, which is recorded in HPS (MN9) and PI (MN12). The distinction between *Hy. wongii* and *Thalassictis montadai*, the latter recorded in the late Aragonian and early Vallesian of the Vallès-Penedès Basin, is based on the presence of more derived dental features in the former, such as the structure of m1 (which has a paraconid and protoconid of equal height) and the more isolated P4 protocone. However, *Hy. wongii* is more primitive than *T. robusta*, which is also recorded in the basin during the late Vallesian (MN10; Villalta Comella and Crusafont Pairó 1943a; Crusafont and Petter 1969). In particular, *Hy. wongii* has narrower premolars than *T. robusta*, as well as a lower-crowned m1, with a relatively longer talonid and a paraconid higher than the protoconid (Villalta Comella and Crusafont Pairó 1943a; Crusafont and Petter 1969; Werdelin and Solounias 1991). These dental characters also enable the distinction of *Hy. wongii* from *Ictitherium viverrinum*, and further indicate that former citations of *Ictitherium hipparionum* from the Vallès-Penedès Basin (Villalta Comella and Crusafont Pairó 1943a; Villalta and Crusafont 1946a) correspond in fact to the genus *Hyaenictitherium* (Werdelin and Solounias 1991).

Genus ***Plioviverrops*** Kretzoi, 1938

***Plioviverrops orbignyi* (Gaudry, 1862).** Range: early Vallesian (MN9). Sites: SBL. Bibliographic citations and synonyms: *Ictitherium orbignyi* in Villalta Comella and

Crusafont Pairó (1941, 1943a), Villalta and Crusafont (1946a), Crusafont Pairó and Truyols Santoja (1960), Crusafont Parió and Truyols Santoja (1954), Crusafont and Truyols (1954) and Golpe-Posse (1974).

***Plioviverrops guerini* (Villalta Comella and Crusafont Pairó, 1948).** Range: late Aragonian to early Turolian (MN7+8–MN12). Sites: HP, TGM [type locality] and TT. Bibliographic citations and synonyms: *Herpestes crassus* in Bataller (1941); *Herpestes* cf. *crassus* in Villalta Comella and Crusafont Pairó (1941, 1943a) and Villalta and Crusafont (1946b); *Herpestes guerini* (nomen nudum) in Villalta and Crusafont (1946a); *Herpestes guerini* in Villalta Comella and Crusafont Pairó (1948) and Crusafont Pairó (1953); *Plioviverrops guerini* in Golpe-Posse (1974) and Agustí et al. (1985).

The genus *Plioviverrops* is recorded at the Vallès-Penedès Basin by two different species: *Pl. guerini* and *Pl. orbignyi*. The former was originally erected by Villalta Comella and Crusafont Pairó (1948) as *Hespestes guerini*, based on material from the Turolian of Piera and Concud, and subsequently reported from HP (Villalta Comella and Crusafont Pairó 1943a, 1946a) as well as from other Iberian localities from the Turolian (Golpe-Posse 1974; Alcalá et al. 1991; Salesa et al. 2012). *Plioviverrops orbignyi*, in turn, is widely distributed throughout the European Late Miocene (Werdelin and Solounias 1991), although in the Vallès-Penedès it is only recorded at SBL (Villalta Comella and Crusafont Pairó 1941, 1943a). *Plioviverrops guerini* is characterized by the lack of mesial accessory cuspulid in the p3, eloganted talonids in the lower cheek teeth, and tetracuspid m1 with a metaconid higher than the paraconid (Villalta Comella and Crusafont Pairó 1948). The remains of *Pl. orbignyi* reported in the literatue as belonging to Villalta's collection (Villalta Comella and Crusafont Pairó 1943a) could not be examined for this study, since they were not found among the ICP collections. However, based on the descriptions and measurements provided by Villalta Comella and Crusafont Pairó (1943a), these remains are clearly distinguishable from *Pl. guerini*.

Genus ***Protictitherium*** Kretzoi, 1938

***Protictitherium crassum* (Depéret, 1892).** (Fig. 4F–H) Range: late Aragonian to late Vallesian (MN7+8–MN10). Sites: ACM/C1-E7, ACM/C1-E9, ACM/C1-F, ACM/C3-Ak, ACM/C4-Ae, ACM/C4-A1, ACM/C4-C2, ACM/C5-A5, ACM/C5-C, ACM/C6-C, ACM/C8-B/C, CLL1 and CLL2. Bibliographic citations and synonyms: *Progenetta crassa* in Crusafont and Truyols (1954), Crusafont Pairó and Truyols Santoja (1960), Golpe-Posse

(1974) and Crusafont Pairó and Kurtén (1976); *Progenetta* cf. *crassa* in Crusafont Pairó and Truyols Santoja (1960), Crusafont (1964) and Crusafont-Pairó and Golpe-Posse (1973a); *Progenetta crassa* (forms A and B) in Crusafont Pairó and Petter (1969); *Protictitherium crassum* in Agustí et al. (1997), Alba et al. (2006, 2009, 2011a,b) and Casanovas-Vilar et al. (2008, 2011a); Ictitheriinae indet. in Alba et al. (2007).

***Protictitherium gaillardi* (Major, 1903).** Range: early Aragonian to late Vallesian (MN4–MN10). Sites: ACM/C3-Ak, CB, CLL1, CM1, CP1, CS, HPI, SA, TNA and TSA. Bibliographic citations and synonyms: *Progenetta gaillardi* in Crusafont-Pairó and Golpe-Posse (1973a) and de Beaumont and Crusafont-Pairó (1982); *Protictitherium gaillardi* in Golpe-Posse (1974), Petter (1976), Golpe-Posse et al. (1979) and Alba et al. (2011b); *Herpestes dissimilis* in Villalta Comella and Crusafont Pairó (1943a), Crusafont and Truyols (1954) and Villalta and Crusafont (1946b); *Progenetta crassa* in Crusafont and Truyols (1954), Crusafont Pairó and Truyols Santoja (1954) and Crusafont (1964); *Progenetta gaillardi*, shape A and shape B, in Crusafont Pairó and Petter (1969) and Crusafont Pairó and Kurtén (1976); *Progenetta crassa* in Crusafont and Truyols (1954), Crusafont Pairó and Truyols Santoja (1954), Crusafont Pairó (1964) and de Beaumont and Crusafont-Pairó (1982); cf. *Protictitherium* sp. in Alba et al. (2006, 2009, 2011a,b) and Casanovas-Vilar et al. (2008); *Protictitherium* sp. in Casanovas-Vilar et al. (2011b); cf. *Ictitherium* sp. in Alba et al. (2007); *Progenetta* sp. in Crusafont-Pairó and Golpe-Posse (1973a); *Protictitherium crassum* in Agustí et al. (1997).

?*Protictitherium llopisi* (Crusafont Pairó and Petter, 1969). Range: late Vallesian (MN10). Sites: CBA [type locality]. Bibliographic citations and synonyms: *Progenetta crassa llopisi* in Crusafont Pairó and Petter (1969).

Three species of *Protictitherium* are currently recorded in the Vallès-Penedès Basin: ?*Pr. llopisi*, *Pr. crassum* and *Pr. gaillardi*. *Protictitherium llopisi* was originally described by Crusafont Pairó and Petter (1969) as *Protictitherium crassa llopisi*, based on remains from CBA, and subsequently elevated to species rank by Werdelin and Solounias (1991). The latter authors noted similarities in the lower carnassial of ?*Pr. llopisi* with the m1 of *Plioviverrops*. Given the lack of new material, *Pr. llopisi* has been here provisionally included in the genus *Protictitherium*, but future studies would be necessary to further decipher its taxonomic affinities. Regarding the other two species of this genus recorded in the Vallès-Penedès, *Pr. crassum* was previously known from the Vallesian (Crusafont Pairó and Kurtén 1976; Crusafont Pairó and Petter 1969), but here it is also reported from the late Aragonian based on unpublished remains from various ACM localities. In turn, *Pr.*

gaillardi is reported from the MN4 (based on unpublished remains from CS) to the MN10 of TNA and TSA (based on a p3 and a humerus and ulna; Golpe-Posse et al. 1979). These two species of *Protictitherium* have long been considered distinct (Viret 1951; Schmidt-Kittler 1976; Werdelin and Solounias 1991), with *Pr. gaillardi* being smaller than *Pr. crassum*, and both being recorded from multiple Miocene sites (Viret 1951; Werdelin and Solounias 1991; Turner et al. 2008). The range of *Pr. crassum* in the Vallès-Penedès Basin agrees with that elsewhere in Europe, being recorded at La Grive Saint-Albain (France; MN7+8), Los Valles de Fuentidueña (Spain, MN9) and Dorn-Dürkheim (Germany; MN10), among other localities (Viret 1951; Ginsburg et al. 1981; Ginsburg 1999; Werdelin and Solounias 1991). With regard to *Pr. gaillardi*, it is record in the early Aragonian of the Vallès-Penedès Basin, thus also in agreement with previous reports from French localities of the MN4 (such as Bézian and Pontlevoy; Werdelin and Solounias 1991). Although the presence of *Pr. crassum* during the Vallesian (MN9-MN10) in other localities from Western Eurasia is very doubtful (Werdelin and Solounias 1991), in the Vallès-Penedès this species would be also recorded until the MN10, further coexisting with *P. crassum* during the MN7+8 in various ACM localities. However, more detailed studies would be required to better substantitate the presence of both species during this the late Aragonian.

Family **Herpestidae** Bonaparte, 1845

Subfamily **Herpestinae** (Veron 2004)

Genus ***Leptoplesictis*** Major, 1903

***Leptoplesictis aurelianensis* (Schlosser, 1888).** Range: early Aragonian (MN4). Sites: CBL, CC, CS and EC. Bibliographic citations and synonyms: *Palaeogale minuta* in Golpe-Posse (1974).

***Leptoplesictis filholi* (Gaillard, 1899).** Range: late Aragonian to early Vallesian (MN7+8–MN9). Sites: ACM/BCV1, CM1 and HP. Bibliographic citations and synonyms: as *Herpestes aurelianense* in Bataller (1941), Villalta Comella and Crusafont Pairó (1941, 1943a), Villalta and Crusafont (1946b) and Crusafont and Truyols (1954); *Herpestes* (*Leptoplesictis*) sp. in Petter (1976); *Leptoplesictis filholi* in Roth (1987, 1988); cf. *Leptoplesictis* sp. in Alba et al. (2006); *Leptoplesictis* cf. *aurelianense* in Alba et al. (2006, 2009, 2011a,b), Casanovas-Vilar et al. (2008).

The genus *Leptoplesictis*, formerly considered a subgenus of *Herpestes* Illiger, 1811, was elevated to genus rank by Roth (1988), who further established *L. filholi* as a valid species distinct from *L. aurelianensis*. Both species are recorded in the Vallès-Penedès Basin, *L. filholi* being distinguished from *L. aurelianensis* by the sharper and more pointed cusps in the p3, the smaller accessory distal cuspulid in the p4, the smaller and shorter m1 talonid relative to the trigonid, and the larger m2 roots (Roth 1988). In the Vallès-Penedès Basin, *L. aurelianensis* was reported from the late Aragonian of the area of els Hostalets de Pierola (Bataller 1941; Villalta Comella and Crusafont Pairó 1941, 1943a), but Roth (1988) reassigned it to *L. filholi*, in agreement with the chronostratigraphic record of the latter species in other similarly-aged European localities, such as Anwil and La Grive (Viret 1951; Roth 1988). Based on the same criteria, the isolated deciduous upper premolars from the same area, assigned by Petter (1976) to *Leptoplesictis* sp., and not mentioned by Roth (1988), are here also attributed to *L. filholi*. The unpublished material from ACM/BCV1 is here also attributed to the same taxon. In contrast, the presence of *L. aurelianensis* in the Vallès-Penedès is restricted to the early Aragonian, based on the remains from various localities (CS, CC and CB1) that had been previously attributed to *Palaeogale minuta* by Golpe-Posse (1974).

Suborder **Caniformia** Kretzoi, 1943

Family **Amphicyonidae** Haeckel, 1866

Subfamily **Amphicyoninae** Haeckel, 1866

Genus ***Amphicyon*** Lartet, 1836

***Amphicyon* sp.** Range: Ramblian to early Aragonian (MN3-MN4). Sites: CBL, CJ, CS, EC, LCV and MC. Bibliographic citations and synonyms: *Amphicyon* sp. in Golpe-Posse (1974) and Casanovas-Vilar et al. (2011b,c); cf. *Amphicyon* sp. in Agustí et al. (1985); *Amphicyon* cf. *helbingi* in Crusafont and Truyols (1954), Crusafont et al. (1955) and Vicente-Castell (1987); *Cynelos* cf. *helbingi* in Golpe-Posse (1974); cf. *Amphicyon steinheimensis* in Crusafont and Truyols (1954), Crusafont-Pairó (1963) and Agustí et al. (1985); *Amphicyon steinheimensis* in Crusafont et al. (1955), Golpe-Posse (1974) and Agustí et al. (1984).

***Amphicyon major* Blainville, 1841.** Range: early Vallesian (MN9). Sites: CB and CP1. Bibliographic citations and synonyms: *Amphicyon major* in Crusafont-Pairó and Golpe-Posse (1973a), Crusafont Pairó and Kurtén (1976), Golpe-Posse (1974) and Agustí et al. (1997).

***Amphicyon olisiponensis* Antunes and Ginsburg, 1977.** (Fig. 1A–B) Range: early Aragonian (MN4). Sites: CS. Bibliographic citations and synonyms: *Amphicyon giganteus* in Casanovas-Vilar et al. (2011b).

At least two different species of *Amphicyon* are recorded in the Vallès-Penedès Basin: *A. olisiponensis*, from the early Aragonian locality of CS; and *A. major*, from early Vallesian localities. The former species, originally erected by Antunes and Ginsburg (1977) on the basis of a mandible from the early Aragonian (MN5) of Lisbon (Portugal), is a large-bodied amphicyonid (larger than a brown bear) that displays a meso-carnivorous dental morphology (with both trenchant and bunodont features). The unpublished remains from CS constitute the most complete sample of this species (and indeed of genus *Amphicyon* as a whole) from the Iberian record, consisting in several complete and partial skeletons, including skulls, mandibles and abundant postcranial material. This sample was preliminarily attributed to *Amphicyon giganteus* Blainville, 1841 and *Amphicyon* sp. by Casanovas-Vilar et al. 2011b; although this species displays a similar dental size and morphology to *A. olisiponensis*, it can be distinguished from the CS remains of the latter species by the lack of a marked parastyle in the P4. The remains of *A. major* from CB and CP1 were described by Crusafont Pairó and Kurtén (1976), although subsequent revision will be needed in the future to better substantiate the species attribution. The material from the remaining Vallès-Penedès localities is provisionally left unassigned to species here, because it mostly consists in fragmentary dentognathic material, isolated teeth and postcranial remains. Although some tentative species attributions were provided for these remains in the past (see above), these attributions remain unclear due to the nature of the available material. However, subsequent revision of the material might ultimately enable a more precise taxonomic attribution.

Genus ***Ictiocyon*** Crusafont et al., 1955

***Ictiocyon socialis* (Schlosser, 1904).** (Fig. 2A–B) Range: early Aragonian (MN4). Sites: EC. Bibliographic citations and synonyms: *Ictiocyon* sp. in Crusafont (1955); *Amphicyon* (*Ictiocyon*) *dehmi* in Crusafont-Pairó et al. (1955); *Ictiocyon dehmi* in Golpe-Posse (1974), Ginsburg (1992) and Galindo (2000).

Ictiocyon was originally erected as a subgenus by Crusafont et al. (1955), who further described, based on the material from EC, *Amphicyon* (*Ictiocyon*) *dehmi* and designated it as the type species of the new subgenus. Ginsburg (1992) formally elevated *Ictiocyon* to genus rank, and further considered that its type species is a junior synonym of *Amphicyon socialis* Schlosser, 1904, thereby proposing the new combination *Ic. socialis*. This view is followed here. *Ictiocyon* is closer to *Pseudarctos* Schlosser, 1899, although it differs from the latter by its larger size, presence of p1, well-developed m1 and m2 talonid, absence of mandibular diastema, and presence of well-developed upper molars (M1–M3), with a mesiodistally subequeal paracone and metacone in the M1 and M2 (Ginsburg 1992). The chronostratigraphic range of *Ic. socialis* in the Vallès-Penedès Basin is comparable to that elsewhere in Europe (MN3–MN4; Ginsburg 1992).

Genus ***Magericyon*** Peigné et al., 2008

***Magericyon castellanus* (Ginsburg et al., 1981).** Range: early Vallesian (MN9). Sites: CLL1.

This genus and its type species, *Magericyon anceps* Peigné et al., 2008, were originally described based on abundant material from Batallones-1 (MN10), corresponding to at least twelve individuals, and including skulls, mandibles and postcranial remains (Peigné et al. 2008; Siliceo et al. 2012). *Magericyon anceps* is a large-bodied amphicyonid (similar in size to a female lion) very derived towards a hypercarnivorous diet (with slender and trenchant carnassials and a cursorial postcranial adaptations). Although its dentition is somewhat convergent with the Thaumastocyoninae (see below), the attribution of *Magericyon* to the Amphicyoninae seems clear (Peigné et al. 2008). The citation from CLL1 provided here, based on two unpublished lower molars, represents the first report of *Magericyon* from the Vallès-Penedès Basin. In spite of the scarcity of the available material, it indicates an attribution to *Ma. castellanus*, originally described from the similarly-aged (MN9) locality of Los Valles de Fuentidueña (Ginsburg et al. 1981), which differs from the type species of the genus by the less derived dental morphology (Peigné et al. 2008).

Subfamily **Thaumastocyoninae** Hurzeller, 1940

Genus ***Thaumastocyon*** Stehlin and Helbing, 1925

***Thaumastocyon dirus* Ginsburg et al., 1981.** Range: early Vallesian (MN9). Sites: CLL1. Bibliographic citations and synonyms: *Agriotherium* sp. in Crusafont-Pairó (1955); *Amphicyon* sp. in Crusafont Pairó (1959a), Crusafont Pairó and Truyols Santoja (1960), Crusafont (1964), Golpe-Posse (1974), Agustí et al. (1997) and Alba et al. (2011b); Hyaenidae indet. sp. 1 in Crusafont-Pairó and Golpe-Posse (1973a); *Amphicyon major* in Golpe-Posse (1974), Crusafont-Pairó and Golpe-Posse (1973a) and Alba et al. (2011b); *Amphicyon* cf. *major* in Crusafont Pairó and Kurtén (1976); *Agnotherium antiquus* and *Pseudarctos* sp. in Alba et al. (2011b).

Remarks. The genus *Thaumastocyon* was originally erected by Stehlin and Helbing (1925) for *Thaumastocyon bourgeoisi* Stehlin and Helbing, 1925 from the Middle Miocene (MN5), whereas the species reported here was described by Ginsburg et al. (1981) based on material from the Late Miocene (MN9) of Los Valles de Fuentidueña. This genus is a large-sized amphicyonid, similar to *Agnotherium* Kaup, 1932, and characterized by an extremely hypercarnivorous dentition and a rather robust postcranial skeleton. These two genera are similar in many traits, but *Agnotherium* differs from *Thaumastocyon* by its less derived dental features (such as the presence of metaconid in the m1 and m2, and the presence of m3; Peigné et al. 2008). The known record of these genera in Iberia might imply the local extinction of *Thaumastocyon* and subsequent replacement by *Agnotherium* during the Middle Miocene, followed by a second immigration of *Thaumastocyon* by the Late Miocene. Alternatively, the Early and Late Miocene species might belong to different genera, having independently converged in dental morphology due to adaptation to a hypercarnivorous diet. In any case, *Th. dirus* is here first reported from the Vallès-Penedès Basin, based on a few teeth from CLL1, which had been previously referred to *Amphicyon* cf. *major* by Crusafont Pairó and Kurtén (1976). Although the available remains are scarce, both the m2 and P4 show close resemblances to those of *Th. dirus* from Los Valles de Fuentidueña (Ginsburg et al. 1981), thereby justifying their attribution to the same species.

Family **Hemicyonidae** Frick, 1926

Subfamily **Hemicyoninae** Ginsburg and Morales, 1995

Genus ***Plithocyon*** Ginsburg, 1955

***Plithocyon conquense* Ginsburg and Morales, 1998.** Range: Early Aragonian (MN4). Sites: CS. Bibliographic citations and synonyms: *Hemicyon* sp. in Casanovas-Vilar et al. (2011c); *Hemicyon stehlini* in Casavanovas-Vilar et al. (2011b).

Hemicyonids (dog-bears) share many morphological features with ursids (true bears) and were until recently included into the same family (McLellan and Reiner 1994; Ginsburg and Morales 1998; Ginsburg 1999), although most recent authors tend to distinguish them at the family rank (McKenna and Bell 1997; Abella et al. 2014). Two subfamilies (Phoberocyoninae and Hemicyoninae), mainly distinguished by their different degree of hypercarnivorism, are distinguished (Ginsburg and Morales 1998). In the Vallès-Penedès, only a single hemicyonid from the nominotypical subfamily is recorded. This taxon is here attributed to the quite hypercarnivorous *Pli. conquense*, originally described from the early Miocene (MN4) locality of La Retama in Spain, thereby representing its first citation from the Vallès-Penedès Basin. This species is intermediate in size between *Plithocyon bruneti* Ginsburg, 1980 and *Plithocyon armagnacensis* Ginsburg, 1955, being characterized by a slightly higher m1 protoconid and a less marked constriction in the labial wall at the level of the trigonid-talonid notch. The unpublished sample of *Pli. conquense* from CS, previously attributed to *Hemicyon stehlini* Hürzeler, 1944 or *Hemicyon* sp. by Casanovas-Vilar et al. (2011b,c), includes abundant material (skulls, mandibles and postcranials), which in the future will enable a better description of the morphology of this species.

***Hemicyon goeriachensis* (Toula, 1884).** Range: late Aragonian (MN7+8). Sites: CMA (=CPA, HP and HPI). Bibliographic citations and synonyms: *Pseudocyon sansaniensis* in Villalta Comella and Crusafont Pairó (1944, 1946b), Crusafont Pairó (1953) and Crusafont and Truyols 1954; *Hemicyon sansaniensis* in Golpe-Posse (1974); *Hemicyon goeriachensis* in Ginsburg and Morales (1998) and Abella et al. (2014); *Plithocyon armagnacensis* in Abella et al. (2014).

An isolated M2 from CMA was attributed to *Pseudocyon sansaniensis* Lartet, 1851 by Villalta Comella and Crusafont Pairó (1944). Subsequently, in their revision of early and Middle Miocene hemicyonids, Ginsburg and Morales (1998) attributed the former to *He. goeriachensis*, on the basis of its occlusal morphology (paracone higher than the metacone, and presence of a mesiodistally-oriented lingual crest without clear cups and encompassing the protocone and a metaconule). The genus *Hemicyon* includes other species, such as *Hemicyon gargan* (MN3; France), *Hemicyon stehlini* (MN4-MN5; France) and *Hemicyon sansaniensis* (MN5-MN6; France and Lisbon), the latter with several subspecies (Ginsburg and Morales 1998). *Hemicyon goeriachensis* can be distinguised on the basis of dental size (intermediate between *He. gargan* and *He. sansaniensis*), as well as by the presence of the above-mentioned mesiodistally-alined and lingually-situated crest in the M2 (which is lacking in the other species of the genus). The chronostratigraphic range of *He. goeriachensis* known from elsewhere in Europe (France, Germany and Austria), which ranges from MN6 to MN7+8, fits well with the age of the Vallès-Penedès remains. Unfortunally, we have been unable to locate this material among the ICP collections, so that it is not possible to confirm this taxonomic attribution.

Family **Ursidae** Fischer Von Waldheim, 1817

Genus ***Ursavus*** Schlosser, 1899

Ursavus brevirhinus **Hoffman, 1887.** Range: late Vallesian (MN9). Sites: CCN20 and CLL1. Bibliographic citations and synonyms: *Ursavus primaevus* in Crusafont Pairó (1959a), Crusafont Pairó and Truyols Santoja (1960), Crusafont (1964), Golpe-Posse (1974), Crusafont-Pairó and Golpe-Posse (1973a), Crusafont Pairó and Kurtén (1976), Alba et al. (2011b) and Abella et al. (2014); *Ursavus brevirhinus* in Crusafont Pairó and Truyols Santoja (1960), Crusafont Pairó (1964), Golpe-Posse (1974), Alba et al. (2011b) and Abella et al. (2014); Canidae indet. in Crusafont-Pairó and Golpe-Posse (1973a) and Crusafont Pairó and Kurtén (1976); *Ursavus* sp. in Agustí et al. (1997).

Ursavus is one of of the basal-most genera of ursids, although being more derived than *Ballusia* Ginsburg and Morales, 1998. Although this genus is recorded from the Early Miocene to the Late Miocene elsewhere in Europe, in the Iberian Peninsula it is only recorded from the MN9 of CLL1. The morphological heterogeneity among the species of this genus might indicate that the Turolian (MN11–MN12) species belong to a different genus, but this is not the case for the Early to Middle Miocene ones. The latter also applies to the specimens from CLL1, which show the typical features of *Ursavus*, such as the wide upper molars and the relatively primitive carnassials (e.g., cutting P4 with relatively small protocone and m1 with high trigonid). Crusafont Pairó and Kurtén (1976) included the relatively abundant material from CLL1 to two species, *Ursavus primaevus* (Gaillard, 1899) and *U. brevirhinus* (Hoffmann, 1887), due to differences in size among the available dental sample. However, these differences are here merely attributed to sexual size dimorphism, as it is frequent in ursids. Here all the *Ursavus* material from CLL1 is thus attributed to *Ur. brevirhinus*, known from the early and middle Aragonian (MN4–MN6) of Europe (Ginsburg and Morales 1998). Given that the CLL1 material represents the youngest record of *Ur. brevirhinus*, more detailed comparisons would be required to further confirm the attribution of the CLL1 remains to this species.

Subfamily **Ailuropodinae** Grevé, 1894

Ailuropodinae indet. Range: early Vallesian (MN9). Sites: CP1. Bibliographic citations and synonyms: *Ursavus brevirhinus* in Crusafont-Pairó and Golpe-Posse (1973a) and *Ursavus primaevus* in Crusafont Pairó and Kurtén (1976) and Abella et al. (2014).

A mandibular fragment with m1-m3 and several unpublished canines and m3 from CP1, belonging to an ailuropodine, are here left unassigned to genus. The mandible was attributed to *U. primaevus* and compared with *U. brevirhinus* by Crusafont Pairó and Kurtén (1976). However, based on some of the preserved features (more eloganted and clearly lower crowned m1 with a longer paraconid and larger m2 and m3), it is more likely to belong to *Kretzoiarctos* or maybe *Agriarctos*. Until more specimens become available, these remains are best merely assigned to Ailuropodinae indet.

Kretzoiarctos Abella et al., 2012

***Kretzoiarctos beatrix* (Abella et al., 2011).** (Fig. 2K–L) Range: late Aragonian (MN7+8). Sites: ACM/C6-Camí. Bibliographic citations and synonyms: Amphicyonidae indet. in Alba et al. (2007); *Kretzoiarctos beatrix* in Abella et al. (2012, 2014).

The small-sized genus *Kretzoiarctos* shares many morphological features with other Middle to Late Miocene Eurasian ursids (such as *Ursavus*, *Indarctos* Pilgrim, 1913, *Agriarctos* Kretzoi, 1942 and *Ailurarctos* Qiu and Qi, 1989), from which it differs by a unique combination of features. Its type and only species, described on the basis of material from Nombrevilla 2 (MN7+8; Abella et al. 2011), was originally attributed to *Agriarctos*. Subsequently, however, a new genus was erected based on additional remains from a single ACM locality (Abella et al 2012). A cladistic analysis indicated that *Kretzoiarctos* is more closely related to other ursids from the tribe Ailuropodini Grevé, 1894 (further including the extinct *Agriarctos* and *Ailurarctos*, and the extant giant panda *Ailuropoda* Milne-Edwards, 1870), than to ailuropodines from the genus *Indarctos* (tribe Indarctini Abella et al., 2012). In any case, *Kretzoiarctos* represents the oldest known record of the giant panda lineage, which (given its Iberian records) has profound paleobiogeographic implications for the evolution of this group of ursids (Abella et al. 2012). Some ursid remains from the late Vallesian of CP1, including a mandibular fragment with m1–m3, and originally attributed to *Ursavus primaevus* Crusafont Pairó and Kurten (1976), show closer resemblances to *Kretzoiarctos*. Without additional material, however, it cannot be currently excluded an alternative attribution to *Agriarctos* for this material, which is thus left unassigned to genus.

Genus *Indarctos* Pilgrim, 1913

***Indarctos punjabiensis* (Weithofer, 1888).** Range: late Vallesian (MN10). Sites: LTR1 and TF. Bibliographic citations and synonyms: *Felis* sp. (partim) in Villalta Comella and Crusafont Pairó (1948); *Indarctos atticus* in Pons-Moyà (1990), Agustí et al. (1997) and *Indarctos punjabiensis* in Abella et al. (2014).

***Indarctos vireti* Villalta Comella and Crusafont Pairó, 1943.** Range: late Vallesian (MN9–MN10). Sites: CLL1, CP1, CPL [type locality] and VL. Bibliographic citations and synonyms: *Indarctos vireti* in Villalta Comella and Crusafont Pairó (1943c), Villalta and Crusafont (1946a), Villalta Comella and Crusafont Pairó (1948), Crusafont and Truyols (1954), Crusafont-Pairó (1955), Crusafont Pairó and Truyols Santoja (1954, 1960), Crusafont (1964), Crusafont-Pairó and Golpe-Posse (1973a), Golpe-Posse (1974), Crusafont Pairó and Kurtén (1976), Agustí et al. (1984, 1997), Alba et al. (2011b) and Abella et al. (2014); *Agriotherium* (*Hyaenarctos*) sp. in Villalta and Crusafont (1946a); *Agriotherium* sp. in Villalta Comella and Crusafont Pairó (1948); *Hyaenarctos insignis* var. *pontiensis* in Crusafont and Truyols (1954) and Crusafont Pairó (1959a).

The large-sized ursid genus *Indarctos,* recorded from the early Vallesian (MN9) to the late Turolian (MN13) of Europe (Abella et al. 2012), is considered to represent the sister-taxon (tribe Indarctini) of the giant panda lineage in a strict sense (Ailuropodini). Two species are recorded in the Vallès-Penedès Basin: *In. vireti* and *In. punjabiensis*. The former was originally described by Villalta Comella and Crusafont Pairó (1943c) based on a partial mandible from CPL in the area of Viladecavalls, although it is best represented by the sample from CLL1, which includes an almost complete skull, several mandibles and abundant postcranials (Crusafont Pairó and Kurtén 1976). This species, only secured recorded in the Vallès-Penedès Basin (although specimens from Central Europe might be also tentatively attributed to it), shows a combination of primitive and derived dental features, with long and relatively slender molars that contrast with those of more basal ursids (*Ballusia* and *Ursavus*), coupled with relatively well-developed diastemata between the premolars and no trace of P4 parastyle. In the Turolian, a different species, *In. punjabiensis*, is recorded at TF in the area of Terrassa (Pons-Moyà 1990). *Indarctos punjabiensis* differs from *In. vireti* by its larger overall size, shorter muzzle and relatively wider teeth; moreover, the premolars of the former are reduced in both size and morphology (showing a high degree of imbrication), while the molars are relatively wide and the P4 has a well-developed parastyle. In spite of the scarcity of records in the Vallès-

Penedès Basin (probably due to the lack of Turolian macromammal localities), *In. punjabiensis* is also recorded from other Iberian basins since the MN10 onwards (Alcalá et al. 2005), further being the more widespresed species of the genus (being recorded in North and Central America, most of Eurasia and North Africa).

Family **Ailuridae** Gray, 1843

Genus ***Protursus*** Crusafont Pairó and Kurtén, 1976

***Protursus simpsoni* Crusafont Pairó and Kurtén, 1976 (nomen dubium).** Range: late Vallesian (MN9). Sites: CLL1 [type locality]. Bibliographic citations and synonyms: *Metarctos batalleri* in Crusafont-Pairó and Golpe-Posse (1973a) and Crusafont Pairó and Kurtén (1976); *Protursus simpsoni* in Crusafont-Pairó and Golpe-Posse (1973a), Crusafont Pairó and Kurtén, 1976 and Peigné et al. (2005a); *Simocyon simpsoni* in Golpe-Posse (1974) and Alba et al. (2011b).

The monotypic genus *Protursus* was erected by Crusafont Pairó and Kurtén (1976) based on an m2 from CLL1, which is the only known locality of this taxon (both in the Vallès-Penedès Basin and elsewhere). These authors considered this species to be an ursid, but Thenius (1977) showed it to be an ailurid and synonymized it with *Simocyon*. More recently, Peigné et al. (2005a) resurrected the genus *Protursus*, given the distinctive features of its m2 compared with those of *Simocyon* (such as smaller size, less elongated proportions, presence of paraconid, and more structured talonid). The taxonomic validity of this genus and species, and particularly its distinct status compared to similarly-aged ailurids from Europe, is currently uncertain, and therefore we consider it a nomen dubium here.

Subfamily **Simocyoninae** Dawkins, 1868

Genus ***Simocyon*** Wagner, 1858

***Simocyon batalleri* (Viret, 1929).** Range: late Aragonian to late Vallesian (MN9–MN10). Sites: BS and SBL [type locality]. Bibliographic citations and synonyms: *Metarctos batalleri* in Villalta Comella and Crusafont Pairó (1941, 1943a), Villalta and Crusafont (1946a), Villalta Comella and Crusafont Pairó (1948), Crusafont and Truyols (1954), Crusafont Pairó and Truyols Santoja (1960), Golpe-Posse (1974) and *Simocyon batalleri* in Peigné et al. (2005a).

Ailurids, currently represented by a single extant species (the red or lesser panda, *Ailurus fulgens* F. Cuvier, 1825, are neither very abundant in the fossil record. *Simocyon* is a well-known extinct ailurid, customarily included in a distinct subfamily Simocyoninae Dawkins, 1868 (McKenna and Bell 1997; Wang 1997; Baskin 1998; Ginsburg 1999). At least three different valid species, of European distribution and differing in dentognathic morphology, are recognized (Peigné et al. 2005a): *Simocyon diaphorus* (Kaup, 1832), from the early Vallesian (MN9); *Si. Batalleri*, from the Vallesian (mostly MN10); and the type species, *Simocyon primigenius* (Roth and Wagner, 1854), from the Turolian. In the Vallès-Penedès Basin, only *Si. batalleri* is recorded, based on a single specimen (a maxillary fragment with P4–M2) from SBL and fragmentary dental material from a few other localities. The specimen from SBL constitutes the holotype of the species, which is best known based on the more complete craniodental material from the MN10 of Batallones-1 (Peigné et al. 2005a).

Family **Mephitidae** Bonaparte, 1845

Genus ***Plesiomeles*** Viret and Crusafont Pairó, 1955

***Plesiomeles* sp.** Range: early Vallesian (MN9). Sites: CB. Bibliographic citations and synonyms: Melinae indet. in Petter (1976); ?*Plesiomeles* sp. and ?*Plesiomeles pusilla* in Golpe-Posse (1984).

***Plesiomeles cajali* Viret and Crusafont Pairó, 1955.** Range: late Vallesian (MN10). Sites: CT. Bibliographic citations and synonyms: *Plesiomeles cajali* in Viret and Crusafont (1955), Crusafont and Truyols (1954), Crusafont-Pairó (1955), Crusafont Pairó and Truyols Santoja (1960), Golpe-Posse (1984).

***Plesiomeles* aff. *cajali* Viret and Crusafont Pairó, 1955**. Range: early Vallesian (MN9). Sites: CP1. Bibliographic citations and synonyms: Melinae indet. in Petter (1976).

The monotypic genus *Plesiomeles* was described by Viret and Crusafont Pairó (1955) based on a right partial mandible with m1 from CT, which is the type and only known locality of this species. It is characterized by a combination of derived features (absence of p1 and great length of the m1) with other primitive characters (m1 with high protoconid and mesially-situated metaconid). *Plesiomeles cajali* displays similarities with some melines recorded in the Vallès-Penedès Basin, such as *Palaeomeles*, but the mandibular bone of the former is narrower than that of the latter; moreover, the lower carnassial of *Ple. cajali* is mesiodistally shorter and buccolingually wider, and displays a longer talonid relative to the trigonid (Crusafont Pairó and Golpe-Posse 1982; Golpe-Posse 1984). Petter (1976) and Golpe-Posse (1984) further reported the presence of three 'melines' (currently mephitids) unassigned to genus from the early Vallesian localities of CB and CP1, based on an isolated M1 as well as an isolated M1 and m1, respectively. The upper molars resemble those of mephitids in the lingual expansion and overall occlusal morphology, and would fit well with the lower dentition of *Ple. cajali* from CT (Petter 1976). However, the lower carnassial from CP1, in spite of similarities with *Ple. cajali* in talonid length and ornamentation (Petter 1976; Golpe-Posse 1984), is mesiodistally longer (Petter 1976, Golpe-Posse 1984). Accordingly, until additional remains become available, the mephitids from CB and CP1 are attributed to *Plesiomeles* sp. and *Plesiomeles* aff. *cajali*, respectively.

Genus ***Promephitis*** Gaudry, 1862

***Promephitis pristinidens* Petter, 1963.** (Fig. 3K) Range: early to late Vallesian (MN9–MN10). Sites: CLL1, CP1, CPL [type locality]. Bibliographic citations and synonyms: *Promephitis* sp. in Villalta and Crusafont (1946a), Crusafont and Truyols (1954) and Crusafont Pairó and Truyols Santoja (1960); *Promephitis pristinidens* in Petter (1963), Crusafont-Pairó and Golpe-Posse (1973a), Golpe-Posse (1974), Crusafont Pairó and Kurtén (1976), Agustí et al. (1984), Alba et al. (2011b).

The genus *Promephitis* is recorded from the Late Miocene to the Early Pliocene (MN9–MN15) of Eurasia (Wang and Qiu 2004), with multiple species being recorded in the Vallesian of Europe. In the Vallès-Penedès, only *Prom. pristinidens* is recorded from both the early and late Vallesian. This species was erected by Petter (1963) based on material from the type locality (CPL), being not recorded outside the Vallès-Penedès Basin. It is characterized by the presence in the P4 of a rounded and non-individualized protocone (unlike in *Martes*) and a basal cingulum surrounding the crown. It differs from other species of this genus, such as *Promephitis larteti* Gaudry, 1861 from Pikermi, by the presence of the P4 cingulum as well as the lower M1 protocone (Petter 1963). Wang and Qiu (2004) revised all the species of genus *Promephitis*, and concluded that *Prom. pristinidens* is the most primitive known species of this genus.

Genus ***Mesomephitis*** Petter, 1967

***Mesomephitis medius* (Petter, 1963).** (Fig. 3H–J) Range: late Aragonian to early Vallesian (MN7+8–MN9). Sites: ACM/C6-C1, CCN20, CLL1 [type locality], CP1, HP and SA. Bibliographic citations and synonyms: *Proputorius* sp. nov. in Crusafont-Pairó (1953); *Martes pusilla* in Crusafont and Truyols (1954); *Proputorius medius* in Petter (1963); *Mesomephitis medius* in Petter (1967, 1976), Crusafont-Pairó and Golpe-Posse (1973a), Golpe-Posse (1974), Crusafont Pairó and Kurtén (1976), Alba et al. (2011b); ?*Martes pusillus* in Petter (1976).

Crusafont-Pairó (1953) already noted the presence of an undescribed species of *Proputorius* Filhol, 1890 at Sansan and La Grive-Saint-Alban (MN7+8), although the species was not erected until Petter (1963) as *Proputorius medius*, based on material from CLL1 (MN9). This species was subsequently reported from other MN7+8 to MN9 localities from the Vallès-Penedès, such as CP1 and HP (Petter 1967, 1976). Subsequently, however, Petter (1967) erected a new genus on the basis of this species, based on differences in the morphology of the P4 (smaller and with a protocone not aligned with the metacone), M1 (more buccolingually compressed paracone and metacone, aligned in a crest; continuous basal cingulum; lack of metaconule) and m1 (long talonid; unfused protoconid and metaconid; lack of entoconid). In occlusal morphology, *Mesomephitis* is in fact similar to both *Proputorius* and *Promephitis* Gaudry, 1862 (see below), present in other Europea Middle to Late Miocene sites (Ginsburg 1961; Petter 1963), as well as to *Plesiomeles* (see above). In the Vallès-Penedès Basin, *Me. medius* is recorded from the late Aragonian (area of els Hostalets de Pierola, including a citation first reported here for an ACM locality) to the early Vallesian. However, it is not restricted to this basin, having been also reported from the ealy Vallesian in a few other MN9 localities from Europe, such as Buzhor 1 in Moldova and Götzendord in Austria (Rögl et al. 1003).

Family **Mustelidae** Fischer von Waldheim

Mustelidae indet. Range: MN4–MN9. Sites: ACM/C2-A3, ACM/C2-B, ACM/C3-Ak, ACM/C4-A1, ACM/C4-C, ACM/C4-C2, ACM/C5-A, ACM/C5-A8, ACM/C5-C3, ACM/C5-C4, ACM/C5-Ce, ACM/C5-D1, ACM/C5-D3, ACM/C5-D6, ACM/C5-Dd, ACM/C6-A, ACM/C6-C1, ACM/C6-C2, ACM/C6-C3, CJ and ECM. Bibliographic citations and synonyms: Mustelidae indet. in Golpe-Posse (1974) and Alba et al (2012).

The presence of mustelids unassigned to genus has been previously reported from the MN4 (CJ; Golpe-Posse 1974) and the MN9 (ECM; Alba et al. 2012). Additional remains housed at the ICP further show the presence of mustelids unassigned to genus in MN7+8 localities of ACM. The fragmentary nature of many of the available remains hinders a taxonomic attribution below family rank, although this cannot be discounted in all instances, once these remains are studied in further detail.

Subfamily **Mustelinae** Fischer von Waldheim, 1817

Mustelinae indet. Range: MN4–MN9. Sites: CC and SA. Bibliographic citations and synonyms: Mustelinae indet. in Petter (1976).

Unpublished fragmentary remains from the MN4 of CC housed at the ICP, together with those published by Petter (1976) from SA are attributed to the Mustelinae but cannot be assigned to genus without further study.

Genus ***Martes*** Pinel, 1792

***Martes* sp.** Range: late Aragonian to late Vallesian (MN4-MN10). Sites: ACM/C1-ET, ACM/C3-A7, ACM/C6-A, ACM/C8-A, ACM/C8-Bj, ACM/C8-B3, ACM/C8-B, ACM/C8-Bw, ACM/C8-C, B40OV, CB, and CS. Bibliographic citations and synonyms: *Martes* sp. in Casanovas-Vilar et al. (2011b) and Alba et al. (2006, 2010).

***Martes delphinensis* Depéret, 1892.** Range: late Aragonian (MN7+8). Sites: BG (=HPI). Bibliographic citations and synonyms: *Martes delphinensis* in Bataller (1941), Villalta Comella and Crusafont Pairó (1941, 1943a), Villalta and Crusafont (1946b), Crusafont and Truyols (1954), Golpe-Posse (1974), and Agustí et al. (1984).

***Martes munki* Roger, 1900.** (Fig. 4D–E) Range: early to late Aragonian (MN4–MN7+8). Sites: ACM/C3-Ak, ACM/C4-A1, ACM/C5-C3, ACM/C6-Ad, ACM/C6-C1, EC, SM, and SQ. Bibliographic citations and synonyms: *Martes munki* in Villalta Comella and Crusafont Pairó (1941, 1943a), Villalta and Crusafont (1946c), Crusafont-Pairó (1953), Crusafont and Truyols (1954), Petter (1963), Golpe-Posse (1974), Agustí et al. (1984), Galindo (2000), Alba et al. (2006, 2009, 2011a,b) and Casanovas-Vilar et al. (2008); *Martes* cf. *munki* in Petter (1963) and Golpe-Posse (1974); *Martes laevidens* in Golpe-Posse (1974) and Agustí et al. (1984, 1985); *Martes* or “*Mustela*” *larteti* in Villalta Comella and Crusafont Pairó (1944), Villalta and Crusafont (1946c), Crusafont-Pairó (1953), Golpe-Posse (1974) and Agustí et al. (1984, 1985).

***Martes* cf. *andersoni* Schlosser, 1924.** Range: early Vallesian (MN9). Sites: CP1. Bibliographic citations and synonyms: *Martes* cf. *andersoni* in Petter (1967), Golpe-Posse (1974) and Crusafont Pairó and Kurtén (1976).

***Martes melibulla* Petter, 1963.** Range: early to late Vallesian (MN9–MN10). Sites: CLL1 [type locality], TNA. Bibliographic citations and synonyms: *Martes melibulla* in Petter (1963), Crusafont-Pairó and Golpe-Posse (1973a), Golpe-Posse (1974, 1984), Crusafont Pairó and Kurtén (1976) and Alba et al. (2011b); *Martes* sp. in Petter (1963) Crusafont-Pairó and Golpe-Posse (1973a) and Golpe-Posse et al. (1979); *Martes munki* in Crusafont Pairó and Truyols Santoja (1960), Crusafont Pairó (1964), Golpe-Posse (1974), Crusafont Pairó and Kurtén (1976) and Alba et al. (2011b); *Martes* cf. *melibulla* in Pons-Moyà (1990); *Martes delphinensis* in Crusafont Pairó (1959a), Crusafont Pairó and Truyols Santoja (1960), Crusafont Pairó (1964), Golpe-Posse (1974) and Alba et al. (2011b).

***Martes basilii* Petter, 1964.** Range: early Vallesian (MN9). Sites: CP1. Bibliographic citations and synonyms: *Martes* cf. *basilii* in Petter (1976).

The genus *Martes* is widely distributted across the whole Miocene of the Vallès-Penedès Basin, with at least four different species recorded. In the early Aragonian, only *Ma. munki* is recorded. This species is recorded until the late Aragonian, where it coexists with *Ma. delphinensis*. The coexistence of these two species is not rare, having been previously documented in other European localities, such as Vieux-Collonges (MN5; Mein 1958) or La Grive (MN7+8; Viret 1951). An additional species, *Martes laevidens* Dehm, 1950, was reported from the early Aragonian of SM (Golpe-Posse 1974), where *Ma. munki* had been already reported (Peter 1963). However, given that *Ma. laevidens* is smaller than *Ma. munki* (Petter 1963; Ginsburg et al. 2000), our assessment of the material from this locality indicates that only *Ma. munki* is present at this locality. Some of the remains attributed here to *Ma. munki* were in the past attributed to *Martes larteti* (Villalta Comella and Crusafont Pairó 1944). In the early Vallesian, *Ma.* cf. *andersoni* coexists with *Ma. basilii* and *Ma. melibulla*, the latter species being last recorded in the basin during the late Vallesian. These three species can be distinguished based on several details of dental morphology. Thus, *Ma. melibulla* can be distiguished from *Ma.* cf. *andersoni* in having a shorter lower carnassial with a longer trigonid, as well as a p4 with a more distally-situated main cuspid and without a distal accessory cuspid (Petter 1963, 1967). In turn, *Ma. melibulla* differs from *Ma. basilii* in having a shorter and lower m1 talonid with a basal buccal cingulum (Petter 1963, 1976). Finally, *Ma.* cf. *andersoni* can be distinguished from *Ma. basilii in* having a longer m1 as well as lower and more robust premolars (Petter

1967). The two latter species were only tentatively identified from CP1 (Petter 1976; Crusafont Pairó and Kurtén 1976). Our revision of the material confirms that two species are present at this locality, and allow us to confirm the identification of *Ma. basilii*, whereas that of *Ma.* cf. *andersoni* (displaying a smaller dental size, with relatively longer lower cheek teeth) must remain tentative given the scarcity of the available material. Based on previous publications and unpublished material housed at the IPS, *Martes* remains not attributable to species are also recorded at some additional Vallès-Penedès localities (see above), although further study in the future might enable the attribution of some of these remains to species.

Genus ***Stromeriella*** Dehm, 1950

***Stromeriella franconica* Dehm, 1950.** Range: Ramblian (MN3). Sites: MC. Bibliographic citations and synonyms: *Stromeriella franconica* in Crusafont and Truyols (1954), Crusafont et al. (1955), Crusafont-Pairó (1963), Golpe-Posse (1974) and Agustí et al. (1984, 1985).

In the Vallès-Penedès, this species is only recorded by a maxillary fragment with partial P4, complete M1 and M2 roots from the MN3 of MC (Crusafont et al. 1955), further being recorded in other similarly-aged localities from France (Morlo, 1996). The *genus Stromeriella* includes two additional species (Morlo, 1996): *Stromeriella depressa* Morlo, 1996 from Wiesbaden-Amöneburg (MN2; Germany) and *Stromeriella aginensis* de Bonis, 1973 from Laugnac (MN2; France). The attribution of the Vallès-Penedès material to *Str. franconica* is based on diagnostic dental features, such as the non-reduced M1 without parastyle and with a well-developed talonid (Crusafont et al. 1955; Morlo 1996). *Stromeriella franconica* differs from *Str. depressa* by displaying an M1 with a weakly-developed lingual cingulum and a more asymmetric profile in occusal view (Morlo 1996). No upper dentition of *Str. aginensis* is known, so that a direct comparison with the Vallès-Penedès material is not possible, although an alternative attribution of the latter to *Str. aginensis* is not supported by differences in their chronostratigraphic ranges (Morlo, 1996).

Genus ***Circamustela*** Petter, 1967

***Circamustela dechaseauxi* Petter, 1967.** (Fig. 3D–F) Range: early Vallesian (MN9). Sites: CLL1 [type locality]. Bibliographic citations and synonyms: *Martes* sp. in Petter

(1963);?*Circamustela dechaseauxi* in Petter (1976); *Circamustela dechaseauxi* in Petter (1967), Crusafont-Pairó and Golpe-Posse (1973a), Golpe-Posse (1974), Crusafont Pairó and Kurtén (1976) and Alba et al. (2011b).

This monotypic genus was originally erected by Petter (1967) based on material from CLL1. It is characterized by a completely reduced m1 metaconid and a short and rectangular m1 talonid, with the hypoconulid being the main talonid cusp (situated distobuccally on the cingulid that surrounds the whole talonid). *Circamustela* displays similarities in the m1 talonid with *Sinictis dolichognathus* Zdansky, 1924, which is present in the late Miocene of several basin of Linxia Basin in Gansu (China; Deng 2005; Deng et al. 2011). The presence of a distintive hypoconulid in the buccal side of the talonid is a common feature among these genera, but *Circamustela* displays a lower carnassial with a more reduced metaconid than *Sinictis* Zdansky, 1924, and the lower profile of the mandible is more convex in the former (Petter 1967). Currently, the record of *C. dechaseauxi* is restricted to the Late Miocene (MN9) of the Vallès-Penedès Basin, although the genus has been also reported from the MN9 of Dorn-Dürheim 1 (Germany; Costeur et al. 2013).

Genus *Marcetia* Petter, 1967

***Marcetia santigae* Petter, 1967.** Range: early Vallesian (MN9). Sites: CLL1 [type locality]. Bibliographic citations and synonyms: *Paralutra* sp. in Crusafont Pairó and Truyols Santoja (1960), Crusafont (1964), Crusafont-Pairó and Golpe-Posse (1973a), Golpe-Posse (1974), Crusafont Pairó and Kurtén (1976) and Alba et al. (2011a,b); *Marcetia santigae* in Petter (1967), Crusafont-Pairó and Golpe-Posse (1973a), Golpe-Posse (1974), Crusafont Pairó and Kurtén (1976) and Alba et al. (2011b).

This monotypic genus, like *Circamustela*, was originally by Petter (1967) based on material from CLL1. It is characterized by its M1 morphology, similar to that of an archaic Lutrinae (with an oblique and crest-like protocone and a trapezoidal occlusal contour), which would explain its probably attribution to *Paralutra* sp. in earlier publications (Crusafont Pairó and Truyols Santoja 1960; Crusafont 1964; Golpe-Posse 1974). Given that no lutrine material has been found among the collections of this locality, it is most likely that these citatiosn correspond to *Marcetia*. The M1 of *Mar. santigae* resembles that of *Paralutra jaegeri* Fraas, 1862, although the P4 of the former is more primitive in displaying a more developed protocone, which is more mesially situated than in lutrines

(Petter, 1967). Although the taxonomic validity of this taxon is widely accepted, its record is currently restricted to its type locality.

Subfamily **Gulolinae** Gray, 1825

Genus ***Ischyrictis*** Helbing, 1830

***Ischyrictis mustelinus* (Viret, 1933).** (Fig. 4A–C) Range: late Aragonian (MN7+8). Sites: ACM/C1-E9, ACM/C4-A1, ACM/C4-C2, ACM/C6-C2, ACM/C8-A, CM1, HP, HPI and SQ. Bibliographic citations and synonyms: *Laphyctis mustelinus* in Baltaller (1941), Villalta Comella and Crusafont Pairó (1941, 1943a, 1944), Villalta and Crusafont (1946b,c), Crusafont-Pairó (1953); *Laphictis mustelinus* in Crusafont Pairó and Truyols Santoja (1954) and Crusafont-Pairó and Golpe-Posse (1973a); *Laphictis* sp. in Crusafont-Pairó (1963); *Ischyrictis mustelinus* in Petter (1963), Crusafont-Pairó (1979a), Casasnovas-Vilar et al. (2008) and Alba et al. (2006, 2009, 2011a,b); *Ischyrictis* (*Laphyctis*) *mustelinus* in Golpe-Posse (1974) and Agustí et al. (1984, 1985); *Ischyrictis* cf. *mustelinus* in Alba et al. (2007).

***Ischyrictis* cf. *bezianensis* Ginsburg and Bulot, 1982.** Range: early Aragonian (MN4); Sites: TV. Bibliographic citations and synonyms: *Ischyrictis zibethoides* in Crusafont and Truyols (1954), Crusafont et al. (1955), Crusafont-Pairó (1963) and Galindo (2000).

Two species of *Ischyrictis* are here reported from the Vallès-Penedès Basin, although most of the material corresponds to *I. mustelinus*. The earliest record in this basin corresponds to a talus from the early Aragonian locality of TV, previously attributed to *Ischyrictis zibethoides* (Blainville, 1842) by (Crusafont et al. 1955). Among the three recognized species of the genus, size seems to be a good taxonomic criterion, with *I. bezianensis*, from the MN4–MN5 of France (Ginsburg and Bulot 1982; Peigné 2012), being smaller than both *I. mustelinus* and *I. zibethoides*, from the MN5 to the MN9 of Europe (Helbing 1930; Viret 1951; Ginsburg 1961; Crusafont-Pairó 1972; Ginsburg 1999; Peigné, 2012). Given that the talus from TV is smaller than another talus attributed to *I. zibethoides* (Ginsburg 1961; Peigné 2012), here we attribute the former to *I. bezianensis*, in further agreement with its MN4 age. However, we consider such attribution as tentative, given that no dental remains conclusively confirming the presence of this species in the Vallès-Penedès have been recovered. With regard to the late Aragonian remains of this genus, those from CM1 and SQ were previously attributed to *I. mustelinus* (Villalta Comella and Crusafont Pairó 1941, 1943a; Petter 1963; Crusafont-Pairó 1979a). In fact, the first known skull of this species was reported from CM1 (Villalta Comella and Crusafont Pairó 1943a), being subsequently employed by Petter (1963) to describe in greater detail the craniodental features of this taxon. *Ischyrictis mustelinus* has a longer and lower m1 talonid, with a less developed metaconid, than *I. zibethoides*, from which it also differs by the presence of a basal lingual crest in the P4 paracone (Viret 1951; Ginsburg 1961; Peigné 2012). Based on this criteria, here we confirm the attribution of the previously-known late Aragonian material to *I. mustelinus*, and further report this taxon from several ACM localities.

Genus ***Trochictis*** von Meyer, 1842

***Trochictis narcisoi* Petter, 1976.** (Fig. 3A–C). Range: early Vallesian (MN9). Sites: CLL1 [type locality]. Bibliographic citations and synonyms: *Trochictis narcisoi* in Petter (1976), Golpe-Posse (1974, 1984) and Alba et al. (2011b); *Taxodon sansaniensis* in Crusafont-Pairó (1955) and Alba et al. (2011b); *Taxodon* cf. *sansaniensis* in Petter (1963), Crusafont-Pairó and Golpe-Posse (1973a), Golpe-Posse (1974) and Crusafont Pairó and Kurtén (1976).

The genus *Trochictis* is present from the Early Miocene of France (MN4) to the Late Miocene (MN9) of the Iberian Peninsula, being restricted to the Vallès-Penedès locality of CLL1 (Petter 1976; Golpe-Posse 1974, 1984; Alba et al. 2011b). It resembles *Proputorius* Filhol, 1890 and *Taxodon* Lartet, 1851, the CLL1 material having been attributed to the latter in the past, until Petter (1976) erected *Trochictis narcisoi* based on these remains. It can be distinguished from both *Proputorius* and *Taxodon* by the presence of p1, the sharper premolars, and the presence of a distal accessory cusp in p4 (Petter 1976). Regarding other mustelid genera recorded at the basin, *Trochictis* is similar in size to *Plesiomeles* Viret and Crusafont Pairó, 1955, from which it can be readily distinguished by the presence of p1, the longer m1 relative to p3 and p4, and the lack of crenulations in the m1 talonid (Petter 1976).

Genus ***Hoplictis*** Ginsburg, 1961

***Hoplictis helbingi* (Viret, 1951).** (Fig. 3P–R) Range: early Vallesian (MN9). Sites: CB. Bibliographic citations and synonyms: *Ischyrictis* (*Hoplictis*) *helbingi* in Crusafont-Pairó (1972).

***Hoplictis petteri* (Crusafont-Pairó, 1972).** (Fig. 3L–N) Range: early Vallesian (MN9). Sites: CLL1 [type locality]. Bibliographic citations and synonyms: probably *Plesiogulo* sp. or *Plesiogulo* sp. nov. in Crusafont Pairó and Truyols Santoja (1960), Crusafont (1964), Golpe-Posse (1974), Crusafont Pairó and Kurtén (1976) and Alba et al. (2011b); *Ischyrictis* sp. in Petter (1963, 1967) and Crusafont-Pairó and Golpe-Posse (1973a); *Ischyrictis* (*Ischyrictis*) *petteri* in Crusafont-Pairó (1972), Golpe-Posse (1974) and Crusafont Pairó and Kurtén (1976); *Hoplictis petteri* in Alba et al. (2011b).

The genus *Hoplictis* differs from *Ischyrictis* by the larger size and more carnivorous dental morphology of the former, including a somewhat higher m1 with a residual (even absent) metaconid, as well as a talonid reduced in length (Ginsburg 1961, 1999; Crusafont-Pairó 1972). However, a better developed and more individualized P4 protocone (as it is common in mustelids) enables the distinction of *Hoplictis* from felids (Crusafont-Pairó 1972). Two species are recorded in the Vallès-Penedès Basin, being restricted to the MN9: *H. helbingi*, otherwise recorded in the MN7+8 of La Grive (Viret 1951), from the earliest Vallesian of CB (Crusafont-Pairó 1972); and *H. petteri*, from the slightly younger locality of CLL1. These two species differ in the more reduced m1 talonid and better developed P4 protocone in *H. helbingi* (Crusafont-Pairó 1972). Petter (1963, 1967) reported from CLL1 the presence of *Ischyrictis* sp., whereas Crusafont (1964) reported that of *Plesiogulo*, but our assessment of the material available from this locality indicates that none of these genera is recorded at CLL1, their citations probably corresponding to *H. petteri*. This species was originally described by Crusafont-Pairó 1972, based on an isolated P4 from CLL1, as *Ischyrictis petteri*, being subsequently assigned to *Hoplictis* by Ginsburg (1999). Although this species is restricted to the type locality, the genus *Hoplictis* is present in various French localities from the MN5 to the MN7+8 (Viret 1951; Ginsburg 1961, 2002).

Genus ***Iberictis*** Ginsburg and Morales, 1992

***Iberictis buloti* Ginsburg and Morales, 1992.** Range: early Aragonian (MN4); Sites: CS. Bibliographic citations and synonyms: *Iberictis buloti* in Casanovas et al. (2011b).

This species was originally erected by Ginsburg and Morales (1992) based on material from the MN4 locality of La Romieu (France). In the Vallès-Penedès Basin, its record is restricted to CS, from where it was first reported by Casanovas et al. (2011b). The presence of a less individualized protocone and less developed lingual cingulum in the P4 enables the distinction of this species from both *Iberictis azanzae* Ginsburg and Morales, 1992 and

Ischyrictis spp., further being distinguishable from the latter by the more elongated m2 (Ginsburg and Morales 1992).

Subfamily **Melinae** Bonaparte, 1838

Genus ***Palaeomeles*** Villalta Comella and Crusafont Pairó, 1943a

***Palaeomeles pachecoi* Villalta Comella and Crusafont Pairó, 1943a.** (Fig. 3O) Range: late Aragonian to early Vallesian (MN7+8-MN9). Sites: ACM/C5-A9, ACM/C5-Ce, ACM/C5-C4, ACM/C8-A2, CB, CM1, CV and HPI [type locality]. Bibliographic citations and synonyms: probably as Lutrinae nov. in Bataller (1941); Melidae indet. in Villalta Comella and Crusafont Pairó (1941); *Palaeomeles pachecoi* in Villalta Comella and Crusafont Pairó (1943a); Villalta Comella and Crusafont Pairó (1944), Villalta and Crusafont (1946b), Crusafont-Pairó (1953, 1955), Crusafont and Truyols (1954), Crusafont-Pairó and Golpe-Posse (1973a, 1982), Golpe-Posse (1974, 1984), Agustí et al. (1984, 1985).

This monotypic genus species was originally erected by Villalta Comella and Crusafont Pairó (1943a) based on the late Aragonian material from HP. Subsequently, additional remains of this taxon were reported from similarly-aged localities of the same basin (Villalta Comella and Crusafont Pairó 1944; Crusafont-Pairó and Golpe-Posse 1982), being also cited from the Iberian locality of Escobosa de Calatañazor (MN6; Sesé Benito 1980). It is characterized by the following features (Villalta Comella and Crusafont Pairó 1943a and Crusafont Pairó and Golpe-Posse 1982): a low-crowned m1, with a low and robust trigonid with a well-developed metaconid, and an extremely elongated talonid with a well distinct hypoconulid; a basal cingulum surrounding the whole crown on the upper cheek teeth; P4 with a small protocone aligned with the larger and higher paracone; and quadrangular M1 with two buccally-aligned and two centrally-aligned cusps that constitute two parallel mesiodistal crests, and an oblique crest running from the mesiolingual to the distal portions of the crown. The dentition of *Pal. pachecoi* shows similarities with other mustelid genera (*Trocharion*, *Mesomephitis* and *Promephitis*) present in the late Aragonian and early Vallesian (MN7+8-MN9) of the Vallès-Penedès Basin. Similarities include the occlusal morphology of the M1, in which the cusps are mesiodistally aligned in two main crests, as well as the buccal profile of the upper premolars (Villalta Comella and Crusafont Pairó 1943a). However, *Pal. pachecoi* differs from the above-mentioned genera in the more reduced upper premolars relative to the M1, the less developed P4 protocone, and the lack of a distolingual secondary cuspule in the upper carnassial.

Genus ***Sabadellictis*** Petter, 1963

***Sabadellictis crusafonti* Petter, 1963.** (Fig. 3G). Range: early Vallesian (MN9). Sites: CLL1 [type locality]. Bibliographic citations and synonyms: *Sabadellictis crusafonti* in Petter (1963), Crusafont-Pairó and Golpe-Posse (1973a), Crusafont Pairó and Kurtén (1976), Golpe-Posse (1974, 1984) and Alba et al. (2011b).

This monotypic genus was originally reported by Petter (1963) from CLL1 and has not been subsequently reported from any other Vallès-Penedès locality, although the presence of the genus has been subsequently reported from Cerro de los Batallones (MN10) and Los Casiones (MN12) (Pesquero 2003; Morales et al. 2008; Salesa et al. 2012). This taxon is characterized by a mesiodistally elongated M1 with a well-developed metacone and paracone, an elongated protocone, and an well-developed metaconule (Petter 1963, Golpe-Posse 1984). Petter (1963) noted the similarity of its M1 with that of the extant meline *Melogale* I. Geoffroy Saint-Hilaire, 1831 from Indonesia, including the presence of a small and mesiolabially-situated parastyle relative to the paracone, a distinct and clearly individualized metacone, and an elongated protocone. Due to these similarities, the genus *Sabadellictis*, although somewhat more primitive, is likely to be related to the extant meline *Melogale* (Petter 1963, Golpe-Posse 1984), although more detailed comparisons would be required to further substantiate their phylogenetic relationships.

Subfamily **Lutrinae** Bonaparte, 1838

Genus ***Limnonyx*** Crusafont Pairó, 1950

***Limnonyx sinerizi* Crusafont Pairó, 1950.** Range: early Vallesian (MN9). Sites: CP1 [type locality]. Bibliographic citations and synonyms: *Limnonyx sinerizi* in Crusafont Pairó (1950), Crusafont and Truyols (1954), Crusafont-Pairó (1955), Crusafont Pairó and Truyols Santoja (1960), Crusafont-Pairó and Golpe-Posse (1973a), Golpe-Posse (1974) and Crusafont Pairó and Kurtén (1976).

This species, originally described by Crusafont Pairó (1950) based on a partial right mandible with p4-m1 from CP1, is restricted to its type locality. It is characterized by morphology of the m1, with a wide talonid and a well-developed paraconid (relative to the protoconid and the metaconid). The length of the lower carnassial, being lower than the width of the mandibular ramus, constitutes a diagnostic character among the lutrid tribe Aonychini (Crusafont Pairó 1950; Raghavan et al. 2007). This feature, together with the similar disposition of the lower carnassial cusps compared to other members of this tribe (such as *Amblonyx indicus* Raghavan et al., 2007), confirms the attribution of *Li. sinerizi* to the Aonychini (Raghavan et al. 2007).

Subfamily **Leptarctinae** Gazin, 1936

Genus ***Trocharion*** Major, 1903

***Trocharion albanense* Major, 1903.** (Figs. 3V–X, 4I–K,) Range: late Aragonian to early Vallesian (MN7+8–MN9). Sites: ACM/BDA, ACM/C4-A1, ACM/C5-D, ACM/C5-D1, ACM/C6-A2, ACM/C6-Cb, CB, CLL1 and SQ. Bibliographic citations and synonyms: *Trocharion albanense* in Villalta Comella and Crusafont Pairó (1944), Villalta and Crusafont (1946c), Crusafont-Pairó (1953), Crusafont and Truyols (1954), Petter (1967, 1976), Crusafont-Pairó and Golpe-Posse (1973a), Golpe-Posse (1974), Crusafont Pairó and Kurtén (1976), Agustí et al. (1984), Alba et al. (2006, 2007, 2009, 2011a,b), Casanovas-Vilar et al. (2008, 2011a), Robles et al. (2009, 2010a).

This monotypic genus, widely recorded from the Middle to Late Miocene of Eurasia (Robles et al. 2010a), is the only leptarctine mustelid from the Vallès-Penedès Basin. Although its presence in the late Aragonian and early Vallesian of the Vallès-Penedès Basin has been long recorded in the localities of SQ, CB and CLL1 (Villalta Comella and Crusafont Pairó 1944; Petter 1967, 1976; Robles et al. 2009, 2010a), most recently Robles et al. (2010a) reported new material from ACM localities, which for the first time included relatively complete cranial remains. On their basis, these authors provided an emended diagnosis of this taxon, which is characterized by the presence of two temporal crests, strong, broad and deep zygomatic arches, strong postorbital processes, small orbits, a mandible with strong subangular lobe and a deep masseteric fossa, and a biradiculated m2 among other dental features. A cladistic analysis performed based on the Vallès-Penedès remains indicates that *Trocharion* is a basal-most member of the Leptarctinae, further suggesting that the carnassial notch was independently lost in this family and in other mustelids (Robles et al. 2009, 2010a).

Discussion and Conclusions

According to the results of this study, a total of 11 families, 17 subfamilies, 41 genera and 55 species of carnivorans are recorded from the Early to the Late Miocene in the Vallès-Penedès Basin. The taxonomic revision provided here, which shows a considerable diversity of carnivorans during the whole Miocene in this basin, represents an important update compared to the previous synthesis by Pons-Moyà (1990), even when taking into account other subsequent publications that further reported carnivoran records in the form of faunals lists (Moyà-Solà & Rius Font 1993; Agustí et al. 1997; Agustí & Galobart 1998; Garcés et al. 1997; Gómez-Alba 1997; Checa Soler & Rius Font 2000; Alba et al. 2006, 2007, 2009, 2010, 2011a,b; Casanovas-Vilar et al. 2006, 2008, 2011a,b,c,d; Casanovas-Vilar 2007; Carmona et al. 2011).

An updated faunal list of carnivorans from the Vallès-penedès Basin, after the revision undertaken in this work, is reported in Figs. 5 to 7, thus showing their chronostratigraphic distribution from the Ramblian (MN3) to the Turolian (MN11–MN12). It can be seen that the number of carnivoran families increases from the MN3 (in which only isolated and fragmentary remains attributed to Viverridae, Felidae, Amphicyonidae and Mustelidae are recored) to the MN4 (in which these families become more diverse at both the genus and species ranks). Moreover, by the MN4 other carnivoran families (Hyaenidae, Herpestidae and Hemicyonidae) are recorded in the Vallès-Penedès Basin. During the MN5–MN6, the record of carnivorans in the Vallès-Penedès Basin is restricted to several isolated and fragmentary remains from CAL, the absence of many taxons from this time interval being merely attributable to the lack of continental sites (due to the marine transgressions that occured during this time span; Casanovas-Vilar et al. 2011a).

During the MN7+8, carnivoran paleobiodiversity in the Vallès-Penedès Basin increases again, with several families already recorded in the MN3 or MN4 (Mustelidae, Felidae and Hyaenidae) reaching their maximum diversity, and other families being first recorded in the basin (Ursidae and Barbourofelidae). In contrast, other families (Hemicyonidae and Amphicyonidae) show a diversity decrease during this time interval. The great diversity of Vallès-Penedès carnivorans during the MN7+8 is best reflected in the abundant (more than a hundred) carnivoran-bearing localitites from the stratigraphic series of ACM, and to a lesser extent in other localities such as SQ. An even higher diversity of carnivorans is recorded during early Vallesian (MN9), which, with 11 carnivoran-bearing localities, shows the maximum diversity of Vallès-Penedès carnivorans at the genus level. This peak of diversity of Vallès-Penedès carnivorans during the MN9 is best reflected in CLL1 and CB.

In contrast, carnivoran paleobiodiversity is considerably impoverished during the MN10 and, especially, the MN11 and MN12. The drastic decrease in carnivoran diversity by the MN10 reflects a more general phenomenon referred to as the 'Vallesian crisis', which has been related to a progressive trend of climatic cooling (Domingo et al., 2014). Various carnivoran families previously recorded at the Vallès-Penedès Basin (Barbourofelidae, Herpestidae, Amphicyonidae, and Hemicyonidae) are no longer recorded after the MN9. Several other carnivoran families are last recorded in the MN10 (Viverridae, Ursidae, Ailuridae, Mephitidae and Mustelidae), further displaying a decreased diversity at the genus and species levels compared to previous intervals. Carnivoran paleobiodiversity is lowest in the MN11 and MN12, during which this group is only recorded by Felidae and Hyaenidae. Although the diversity drop from the MN9 to the MN10 might be partially attributable to a sampling bias, the subsequent reduction in carnivoran paleobiodiversity during the Turolian is most clearly attributable to the restricted number of available localities from this time interval.

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References

Abella, J., Montoya, P., & Morales, J. (2011). A New species of Agriarctos (Ailuropodinae, Ursidae, Carnivora) in the locality of Nombrevilla 2 (Zaragoza, Spain). *Estudios Geológicos, 67,* 187–191.

Abella, J., Alba, D.M., Robles, J.M., Valenciano, A., Rotgers, C., Carmona, R., et al. (2012). *Kretzoiarctos* gen. nov., the oldest member of the panda clade. *PLoS ONE, 7,* e48985.

Abella, J., Montoya, P., & Morales, J. (2014). Paleodiversity of the Superfamily Ursoidea (Carnivora, Mammalia) in the Spanish Neogene, related to environmental changes. *Journal of Iberian Geology, 40,* 11–18.

Agustí, J., Moyà-Solà, A., & Gibert, J. (1984). Mammal distribution dynamics in the Eastern Margin of the Iberian Peninsula during the Miocene. *Paléobiologie continentale*, *14,* 33–46.

Agustí, J., Cabrera, L., & Moyà-Solà, S. (1985). Sinopsis estratigráfica del Neógeno de la fosa del Vallès-Penedès. *Paleontologia i Evolució, 18,* 57–81.

Agustí, J. & Galobart, A. (1998). Noves localitats amb mamífers fòssils en el miocè de la Conca del Vallès-Penedès. *Tribuna d'Arqueologia, 1996–1997,* 9–22.

Agustí, J., Cabrera, L., Garcés, M., & Parés, J.M. (1997). The Vallesian mammal succession in the Vallès-Penedès Basin (Northeast Spain): Paleomagnetic calibration and correlation with global events. *Palaoegeography, Palaeoclimatology, Palaeoecology, 133,* 149–180.

Alba, D.M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Rotgers, C., et al. (2006). Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l'Anoia, Cataluña), una sucesión de localidades del Aragoniense superior (MN6 y MN7+8) de la cuenca del Vallès-Penedès. Campañas 2002-2003, 2004 y 2005. *Estudios Geológicos, 62,* 295–312.

Alba, D.M., Galindo, J., Casanovas-Vilar, I., Robles, J.M., Moyà-Solà, S., Köhler, M., et al. (2007). La intervenció paleontològica a la nova fase del dipòsit controlat de Can Mata (Els Hostalets de Pierola, Anoia): campanyes 2002-2003, 2004 i 2005. *Tribuna d'Arqueologia*, *2006,* 7–33.

Alba, D.M., Robles, J.M., Rotgers, C., Casanovas-Vilar, I., Galindo, J., Moyà-Solà, S., et al. (2009). Middle Miocene vertebrate localities from Abocador de Can Mata (els Hostalets de Pierola, Vallès-Penedès Basin, Catalonia, Spain): An update after the 2006-2008 field campaigns. *Paleolusitana, 1,* 59–73.

Alba, D.M., Carmona, R., Bolet, A., Robles, J.M., Casanovas-Vilar, I., Furió, M., et al. 2010. Intervención paleontológica en la Autovía Orbital de Barcelona B-40, tramo Olesa de Montserrat-Viladecavalls: Resultados preliminares. *Cidaris, 30,* 51–59.

Alba, D.M., Casanovas-Vilar, I., Robles, J.M., & Moyà-Solà, S. (2011a). Parada 3. El Aragoniense superior y la transición con el Vallesiense: Can Mata y la exposición paleontológica de els Hostalets de Pierola. *Paleontologia i Evolució, memòria especial núm. 6,* 95–109.

Alba, D.M., Casanovas-Vilar, I., Moyà-Solà, S., & Robles, J.M. (2011b). Parada 4. El Vallesiense inferior y su transición con el Vallesiense superior: Can Llobateres. *Paleontologia i Evolució, memòria especial núm. 6,* 111–123.

Alba, D. M., Carmona, R., Bertó Mengual, J. V., Casanovas-Vilar, I., Furió, M., Garcés, M., et al. (2012). Intervenció paleontológica a l'Ecoparc de Can Mata (els Hostalets de Pierola, conca del Vallès-Penedès). *Tribuna d'Arqueologia, 2012*, 115–130.

Alcalá, L. (1994). *Macromamíferos neógenos de la fosa de Alfambra-Teruel.* Teruel: Instituto de Estudios Turolenses / Museo Nacional de Ciencias Naturales.

Alcalà, L. & Montoya, P. (1990). Las faunas de macromamíferos del Turoliense inferior español. *Paleontologia i Evolució, 23,* 111–119

Alcalá, L., Van Dam, J., Luque, L., Montoya, P., & Abella, J. (2005). Nuevos mamíferos vallesienses en Masía de La Roma (Cuenca de Teruel). *Geogaceta, 37,* 199–202.

Antón, M., Salesa, M.J., Morales, J., & Turner, A. (2004). First known complete skulls of the scimitar-toothed cat *Machairodus aphanistus* (Felidae, Carnivora) from the Spanish Late Miocene site of Cerro Batallones-1. *Journal of Vertebrate Paleontology, 24,* 957–969.

Antunes, M.T. & Ginsburg, L. (1977). Notes sur la Géologie et al Paléontologie du Miocène de Lisbonne. XIX. Sur un *Amphicyon* (Mammalia, Ursidae) du Burdigalien. *Comunicaçoes Serviços Geológicos de Portugal, 6,* 335–342.

Baskin, J.A. (1998). Procyonidae. In: C.M. Janis, K.M. Scotte & L.L. Jacobs (Eds.), *Evolution of Tertiary mammals of North America* (pp. 144–151). Cambridge: Cambridge University Press.

Bataller, J.R. (1921). Mamífers fòssils de Catalunya. Nota paleontològica. *Butlletí de la Institució Catalana d'Història Natural, 21,* 81–86.

Bataller, J.R. (1924). Contribució a l'estudi de nous mamífers fòssils de Catalunya. *Arxius de l'Institut de Ciències, 12,* 1–53.

Bataller, J.R. (1941). Los yacimiento paleontológicos de Piera (Barcelona). *Boletim da Sociedade Geológica de Portugal, 1,* 1–10.

Bernor, R.L., Kovar-Eder, J., Lipscomb, D., Rögl, F., Sen, S., & Tobien, H. (1988). Systematic, stratigraphic and palaeoenvironmental contexts of first-appearing *Hipparion* in the Vienna basin, Austria. *Journal of Vertebrate Palaeontology, 8,* 427–452.

Casanovas-Vilar, I., Furió, M., Agustí, J. 2006. Rodents, insectivores and paleoenvironment associated to the first-appearing hipparionine horses in the Vallès-

Penedès Basin (Northeastern Spain). *Beiträge zur Paläontologie,* 30, 89–107.

Casanovas-Vilar, I., Alba, D. M., Moyà-Solà, S., Galindo, J., Cabrera, L., Garcès, M. et al. (2008). Biochronological, taphonomical and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae). *Journal of Human Evolution, 55,* 589–603.

Casanovas-Vilar, I., Alba, D.M., Robles, J.M., & Moyà-Solà, S. (2011a). Registro palentológico continental de la cuenca del Vallès-Penedès. *Paleontologia i Evolució, memòria especial núm. 6,* 55–80.

Casanovas-Vilar, I., Alba, D.M., & Moyà-Solà, S. (2011b). Parada 1. Panoràmica general de la cuenca y yacimientos de Els Casots (Subirats): una fauna de vertebrados del Aragoniense inferior. *Paleontologia i Evolució, memòria especial núm. 6,* 95–109.

Casanovas-Vilar, I., DeMiguel, D., Galindo, J., Robles, J.M., Garcés, M. & Cabrera, L. (2011c). The continental Burdigalian (Early Miocene) of the Vallès-Penedès Basin (Catalonia, Spain). In: A. Pérez-García, F. Gascó, J.M. Gasulla & F. Escaso (Eds.), V*iajando a mundos pretéritos* (pp. 93–100). Morella: Ayuntamiento de Morella.

Checa Soler, L. & Rius Font, L. 2000. Intervenció paleontològica a l'EDAR Sabadell-Riu Ripoll (Can Llobateres, Sabadell, Vallès Occidental). *Tribuna d'Arqueologia, 1999-2000*, 1–7.

Costeur, L., Maridet, O., Montuire, S., Legendre, S. (2013). Evidence of northern Turolian savanna-woodland from the Dorn-Dürkheim 1 fauna (Germany). *Palaeobiology and Palaeoenvironments*, *9,* 259–275.

Crusafont Pairó, M. (1950). *Limnonyx* un nuevo lútrido del mioceno español. *Notas y Comunicaciones del Instituto Geológico y Minero de España, 20,* 129–142.

Crusafont Pairó, M. (1952). La presencia del félido *Pseudaelurus tournauensis* (Hoernes) en el Mioceno de Hostalets de Pierola y Sabadell. *Notas y Comunicaciones del Instituto Geológico y Minero de España, 28,* 95–109.

Crusafont-Pairó, M. (1953). El sistema miocénico en la depresión española del Vallés-Penedés. *Memorias y Comunicaciones del Insituto Geológico Provincial, 10,* 13–23.

Crusafont-Pairó, M. (1955). Données biogéographiques relevées par la paléomammalogie du Miocène espagnol. In: *Colloque International sur "Problèmes Actuels de Paléontologie" C. N. R. C. Paris, avril 1955* (pp. 101–108).

Crusafont Pairó, M. (1959a). Primer hallazgo en España del género *Ursavus* (Carnivora, Ursidae). *Notas y Comunicaciones del Instituto Geológico y Minero de España, 55,* 137–144.

Crusafont Pairó, M. (1959b). Biometría y evolución. *Revista Universidad Madrid, 8,* 29–31.

Crusafont, M. (1959c). Trouvaille en Espagne du plus ancien Procyonidé d'Eurasie. *Annales du Paléontologie, 45,* 127–140.

Crusafont Pairó, M. (1962). Algunos principios teóricos derivados del cálculo masterométrico. *Boletín de la Real Sociedad Española de Historia Natural, 60,* 167–176.

Crusafont-Pairó, M. (1963). Perspectivas de la biocenótica en paleontología. *Boletín de la Real Sociedad Española de Historia Natural (Biología), 61,* 149–159.

Crusafont Pairó, M. (1964). La biota de Can Llobateres (Sabadell) y su significación biológica. *Cursillos y Conferencias del Instituto "Lucas Mallada", 9,* 177–179.

Crusafont-Pairó, M. (1972). Les *Ischyrictis* de la transition Vindobonien-Vallésien. *Paleovertebrata, 5,* 253–260.

Crusafont-Pairó, M. (1979a). Nova troballa de l'*Ischyrictis mustelinus* (Viret, 1933). *Butlletí Informatiu de l'Institut de Paleontologia de Sabadell, 11,* 17–23.

Crusafont-Pairó, M. (1979b). Novetats paleomastològiques del Vallès-Penedès. Nota preliminar. *Acta Geológica Hispánica. Homenatge a Lluís Solé i Sabarís*, 14, 354–355.

Crusafont-Pairó, M. & Aguirre, E. (1972). *Stenailurus*, Félidé nouveau du Turolien d'Espagne. *Annales de Paléontologie, 58,* 211–225.

Crusafont-Pairó, M. & Ginsburg, L. (1973). Les Carnassiers fossiles de Los Vallès de Fuentiduena (Ségovie, Espagne). *Bulletin du Muséum Nationale d'Histoire Naturelle, 131,* 29–45.

Crusafont Pairó, M. & Golpe-Posse, J.M. (1972). Los yacimientos de mamíferos fósiles del Vallès. *Boletín Informativo del Instituto de Paleontología de Sabadell, 4,* 20–24.

Crusafont-Pairó, M. & Golpe-Posse, J.M. (1973a). New Pongids from the Miocene of the Vallès Penedes Basin (Catalonia, Spain). *Journal of Human Evolution, 2,* 17–23.

Crusafont Pairó, M. & Golpe Posse, J. M. (1973b). Nuevos hallagos de *Progeneta montadai* en el Mioceno de Cataluña. *Boletín Geológico y Minero, 84,* 105–113.

Crusafont-Pairó, M. & Golpe-Posse, J.M. (1981). Hallazgo de una nueva especie del género *Semigenetta* (*S. grandis*) del Vindoboniense terminal de Castell de Barberà (Depresión Prelitoral Catalana, España). *Boletín de la Real Sociedad Española de Historia Natural (Geol.), 79,* 67–76.

Crusafont Pairó, M. & Golpe-Posse, J.M. (1982). Hallazgo de *Palaeomeles pachecoi* Vill. et Crus., 1943, en Castell de Barberà (Vallès-Penedès). *Acta Geològica Hispànica, 17,* 27–37.

Crusafont Pairó, M. & Kurtén, B. (1976). Bears and bear-dogs from the Vallesian of the Vallès-Penedès Basin, Spain. *Acta Zoologica Fennica, 144,* 1–29.

Crusafont Pairó, M. & Petter, G. (1969). Contribution a l'étude des Hyaenidae. La sous-familie des *Ictitheriinae*. *Annales de Paléontologie, 55,* 89–127.

Crusafont, M. & Truyols, J. (1953). Un ensayo goniométrico sobre la carnicera inferior de los Fisípedos. *Estudios Geológicos, 18,* 225–256.

Crusafont, M. & Truyols, J. (1954). *Catálogo paleomastológico del Mioceno del Vallés-Penedés y de Calatayud-Teruel. Segundo Cursillo Internacional de Paleontología.* Sabadell: Museu de la Ciudad de Sabadell.

Crusafont Pairó, M. & Truyols Santoja, J. (1954). Sinopsis estratigrafico-paleontológica del Vallés-Penedés. *Arrahona, 1954,* 1–15.

Crusafont-Pairó, M. & Truyols-Santoja, J. (1956). A biometric study of the evolution of fissped carnivores. *Evolution, 10,* 314–332

Crusafont Pairó, M. & Trujols Santoja, J. (1957a). Un estudio de la evolución de los Carnívoros por métodos numéricos. *Estudios Geológicos, 34,* 177–202.

Crusafont Pairó, M. & Truyols Santoja, J. (1957b). Estudios masterométricos en el Evolución de los Fisípidos: I: Los módulos angulares "alfa" y "beta". II: Los Parámetros lineales P, C y T. *Boletín del Instituto Geológico y Minero de España, 68,* 85–224.

Crusafont Pairó, M. & Truyols Santoja, J. (1958). Masterometría, sintetotipo y Evolución. *Boletín de la Real Sociedad Española de Historia Natural, 68,* 85–225.

Crusafont Pairó, M. & Truyols Santoja, J. (1960). Sobre la caracterización del Vallesiense. *Notas y Comunicaciones del Instituto Geológico y Minero de España, 60,* 109–126.

Crusafont, M. & Truyols Santoja, J. (1966a). A quantitative study of stasigenesis in Fissipede Carnivores. *Nature, 181,* 289–290.

Crusafont-Pairó, M. & Truyols Santoja, J. (1966b). Masterometry and evolution, again. *Evolution, 20,* 204–210.

Crusafont Pairó, M. & Villalta Comella, J. (1952). Una nueva localidad con mamíferos fósiles del Burdigaliense continental del Penedés (nota previa). *Notas y Comunicaciones del Instituto Geológico y Minero de España, 27,* 151–158.

Crusafont, M., Villalta, J. F. & Truyols, J. (1955). El Burdigaliense continental de la cuenca del Vallés-Penedés. *Memorias y Comunicaciones del Instituto Geológico, 12*, 102–153.

Crusafont Pairó, M., Aguirre, E., & García, J. (1968). Un nuevo yacimiento de vertebrados en el Burdigaliense de Martorell (Provincia de Barcelona). *Acta Geológica Hispánica, 3,* 44–47.

de Beaumont, G. (1961). Recherches sur *Felis attica* Wagner du Pontien eurasiatique avec quelques observations sur les genres *Pseudaelurus* Gervais et *Proailurus* Filhol. *Nouvelles Archives du Museum d'Histoire Naturelle de Lyon, 6,* 17–45.

de Beaumont, G. (1975). Recherches sur les Félidés (Mammifères, Carnivores) du Pliocène inférieur des sables à *Dinotherium* des environs d'Eppelsheim. *Archives des Sciencies de Genève, 28,* 369–405.

de Beaumont, G. (1978). Notes complementaires sur quelques Félidés (Carnivores). *Archives des Sciences Physiques et Naturelles, Géneve, 31,* 219–227.

de Beaumont de, G. & Crusafont-Pairó, M. (1982). Les Félidés (Mammifères, Carnivores) du Vallésien du Vallès, Catalogne, Espagne. *Archives des Sciences Physiques et Naturelles, Géneve, 35,* 41–64.

Deng, T. (2005). New discovery of Iranotherium morgani (Perissodactyla, Rhinocetoridae) from the late Miocene of the Linxia Basin in Gansu, China, and its sexual dimorphism. *Journal of Vertebrate Paleontology*, *25,* 442–450.

Deng, T., Hou, S., Shi, Q., Chen, S., He, W. & Chen, S. (2011). Terrestrial Mio-Pliocene Boundary in the Linxia Basin, Gansu, China. *Acta Geologica Sinica, 85*, 452–464.

Domingo, M. S., Badgley, C., Azanza, B., DeMiguel, D., Alberdi, M. T. (2014). Diversification of mammals from the Miocene of Spain. *Paleobiology 40*, 196–220.

Fraile, S., Pérez, B., De Miguel, I. & Morales, J. (1997). Revisión de los carnívoros presentes en los yacimientos del Neógeno español. In: J.P. Calvo & J. Morales (Eds.), *Avances en el conocimiento del Terciario ibérico* (pp. 77–80).

Galindo, J. (2000). *Castellbisbal, un viatge a través del temps.* Castellbisbal: Publicacions del Museu de la Pagesia.

Ginsburg, L. (1961). La faune des Carnivores miocènes de Sansan (Gers). *Mémoires du Muséum National d'Histoire naturelle, 9,* 1–190.

Ginsburg, L. (1992). Les genres *Pseudarctos* et *Ictiocyon*, Amphicyonidae (Carnivora, Mammalia). *Bulletin du Muséum d'Histoire Naturelle, 14,* 301–317.

Ginsburg L. (1999). Order Carnivora. In: G.E. Rössner & K. Heissig (Eds), *The Miocene land mammals of Europe* (pp. 109–148). München: Verlag Dr. Friedrich Pfeil.

Ginsburg, L. & Bulot, C. (1982). Les Carnivores du Miocène de Bézian près de la Romieu (Gers, France). *Proceedings of the Koninklije Nederlandse Akademie van Wetenschappen B, 85,* 53–76.

Ginsburg. L. & Morales, J. (1992). Contribution à la connaissance des Mustélidés (Carnivora, Mammalia) du Miocène européen *Trochictis* et *Ischyrictis*, genres affines et genres nouveaux. *Comptes Rendus de l'Académie des Sciences de Paris, 315,* 111–116.

Ginsburg, L. & Morales, J. (1998). Les Hemicyoninae (Ursidae, Carnivora, Mammalia) et les formes apparentées du Miocène inférieur et moyen d'Europe occidentale. *Annales de Paléontologie, 84,* 71–123.

Ginsburg, L., Morales, J., & Soria, D. (1981). Nuevos datos sobre los carnívoros de Los Valles de Fuentidueña (Segovia). *Estudios Geológicos*, *37,* 383–415.

Ginsburg, L., Cheneval, J., Janvier, P., Pouit, D., & Sen, S. (2000). Les Vertébrés des sables continentaux d'âge Orléanien inférieur (MN3) de Mauvières à Marcilly-sur-Maulne (Indre-et-Loire), La Brosse à Meigné-le-Vicomte (Maine-et-Loire) et Chitenay (loir-et-Cher). *Geodiversitas, 22,* 597–631.

Ginsburg, L. (2002). Les carnivores fossiles des sables de l'Orléanais. *Annales de Paléontologie, 88,* 115–146.

Golpe-Posse, J.M. (1974). Faunas y yacimientos con suiformes del Terciario español. *Paleontologia i Evolució, 8,* 1–87.

Golpe-Posse, J.M., Santafé Llopis, J.V., & Casanovas-Cladellas, M.L. (1979). Datos sobre el Vallesiense medio-superior de los alrededores de Terrassa. *Acta Geológica Hispánica, 14,* 356–361.

Golpe-Posse, J.M. (1981a). Datos comparativos de tres formas viverrinas del Vindoboniense superior y Vallesiense medio del Vallès-Penedès (depresión prelitoral catalana, España). *Acta Geològica Hispànica, 16,* 191–194.

Golpe-Posse, J.M. (1981b). Estudios comparativo entre la mandíbula de *Semigenetta grandis* del Vindoboniense de Castell de Barberà (Depresión Prelitoral Catalana, España) y otros ejemplares europeos de *Semigenetta*. *Paleontologia i Evolució, 16, 15*–24.

Golpe-Posse, J.M. (1984). Las formas melinoideas de la transición Vindoboniense superior – Vallesiense medio del Vallès-Penedès (Depresión Prelitoral Catalana, España). *Acta Geològica Hispànica, 19,* 11–18.

Gómez-Alba, J. 1997. Catálogo razonado de los vertebrados fósiles de España del Museo de Geología de Barcelona (1882-1982). *Treballs del Museu de Geologia de Barcelona, 6,* 1–289.

Heizmann, E.P.J. (1973). Die Carnivoren des Steinheimer Beckens. B. Ursidae, Felidae, Viverridae sowie Ergänzungen und Nachträge zu den Mustelidae. *Palaeontographica, Suppl. 8,* 1–95.

Helbing, H. (1930). Zur Kenntnis der miocänen *"Mustela" zibethoides* Blainville. *Eclogae geologicae Helvetiae, 23,* 637–644.

International Commission on Zoological Nomeclature (ICZN) (1999). *International code of Zoological Nomenclature. Fourth Edition*. London: The International Trust for Zoological Nomenclature.

Kretzoi, M. (1929). Feliden-Studien. *A magyar Királyi Földtani Intézet Hazinyomdaja, 24,* 1–22.

Kretzoi, M. (1938). Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauna. *Annales Musei Nationalis Hungarici, 31,* 88–157.

Koufos, G.D. (2011). The Miocene carnivore assemblage of Greece. *Estudios Geológicos*, 67, 291–320.

Koufos, G.D. (2012). New material of Carnivora (Mammalia) from the Late Miocene of Axios Valley, Macedonia, Greece. *Comptes Rendus Paleovol, 11,* 49–64.

Madurell-Malapeira, J., Robles, J. M., Casanovas-Vilar, I., Abella, J., Obradó, P., & Alba, D.M. (under review). The scimitar-toothed cat *Machairodus aphanistus* (Carnivora: Felidae) in the Vallès-Penedès Basin (NE Iberian Peninsula). *Comptes Rendus Palevol.*

McKenna, M.C. & Bell, S.K. (1997). *Classification of mammals above the species level.* New York: Columbia University Press.

McLellan, B & Reiner, D.C. (1994). A review of bear evolution. *International Conference of Bear Research and Management, 9,* 85–96

Mein, P. (1958). Les Mammifères de la faune sidérolithique de Vieux-Collonges. *Nouvelles Archives du Muséum Naturelle de Lyon, 5,* 1–122.

Montoya, P., Alcalá, L. & Morales, J. (2001). Primer hallazgo de un vivérrido (Carnivora, Mammalia) en el Mioceno superior de la Fosa de Teruel (España). *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica), 96,* 101–109.

Morales, J. & Soria, D. (1979). Nuevos datos sobre los carnívoros del área de Teruel. Síntesi y biostratigrafía. *Estudios Geológicos, 35,* 497–504.

Morales, J., Pozo, M., Silvia, P. G., Domingo, M. S., López-Antoñanzas, R., Álvarez Sierra, M. A., et al. (2008). El sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid: estado actual y perspectivas. *Paleontologica Nova SEPAZ, 8,* 41–117.

Morlo, M. (1996). Carnivoren aus dem Unter-Miozän des Mainzer Beckens (2. Mustelida, Pinnipedia, Feliformia, *Palaeogale*). *Senckenbergiana lethaea, 76,* 193–249.

Morlo, M. (1997). Die Raubtiere (Mammalia, Carnivora) aus dem Turolium von Dorn-Dürkheim 1 (Rheinhessen). Teil 1: Mustelida, Hyaenidae, Percrocutidae, Felidae. *Courier Forschungs-Institut Senckenberg, 197,* 11–47.

Moyà-Solà, S. & Rius Font, L. 1993. El jaciment paleontològic dels Casots (Subirats, Alt Penedès). *Tribuna d'Arqueologia, 1991-1992*, 7–12.

Nagel, D. (2003). Carnivores from the Middle Miocene deposits of Grund (Lower Austria). *Annalen des Naturhistorischen Museum in Wien, 104A,* 297–305.

Peigné, S., Salesa, M.J., Antón, M., & Morales, J. (2005a). Ailurid carnivoran mammal *Simocyon* from the late Miocene of Spain and the systematics of the genus. *Acta Palaeontologica Polonica, 50,* 219–238.

Peigné, S., de Bonis, L., Likius, A., Mackaye, H.T., Vignaud, P., & Brunet, M. (2005b). A new machairodontine (Carnivora, Felidae) from the Late Miocene hominid locality of TM 266, Toros-Menalla, Chad. *Comptes Rendus Palevol, 4,* 243–253.

Peigné, S., Salesa, M.J., Antón, M., & Morales, J. (2008). A new amphicyonine (Canivora: Amphicyonidae) from the Upper Miocene of Batallones-1, Madrid, Spain. *Palaeontology, 51,* 943–965.

Peigné, S. (2012). Les Carnivora de Sansan. In: S. Peigné & S. Sen (Eds.), *Mammifères de Sansan. Mémoires du Muséum national d'Histoire naturelle, 203,* 559–660.

Pesquero, M.J. (2003). *Hipparion* from the Late Turolian of Las Casiones (Teruel Basin). *, Vol. Ext. 1,* 511–548.

Petter, G. (1963). Contribution a l'étude des Mustélidés des bassins Néogènes du Vallès-Penedès et de Calatayud-Teruel (Espagne Orientale). *Mémoires de la Société Géologique de France, 43,* 1–44.

Petter, G. (1964). Deux Mustélidés nouveaux du pontien d'Espagne Orientale. *Bulletin du Muséum National d'Histoire Naturelle, 36,* 270–278.

Petter, G. (1967). Mustélidés nouveaux du Vallesian de Catalogne. *Annales de Paléontologie, 53,* 19–23.

Petter, G. (1976). Étude d'un nouvel ensemble de petits Carnivores du Miocène d'Espagne. *Géologie Méditerranéenne, 3,* 135–154.

Pons-Moyà, J. (1990). Presencia de carnívoros turolienses en el Vallesiense terminal (MN10) de Terrassa (Catalunya). *Paleontologia i Evolució, 23,* 199–203.

Raghavan, P., Pickford, M., Patnaik, P., & Gayathri, P. (2007). First fossil small-clawed otter, *Amblonyx*, with a note on some specimens of *Lutra*, from the Upper Siwaliks, India. *Estudios Geológicos, 63,* 135–146.

Robles, J.M., Alba, D.M., & Moyà-Solà, S. (2009). The morphology of the upper fourth premolar in *Trocharion albanense* Major, 1903 (Mustelidae: Leptarctinae) and the independent loss of the carnassial notch in leptarctines and other mustelids. *Paleolusitana, 1,* 403–409.

Robles, J.M., Alba, D.M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Rotgers, C., et al. (2010a). New craniodental remains of *Trocharion albanense* Major, 1903 (Carnivora, Mustelidae), from the Vallès-Penedès Basin (Middle to Late Miocene, Barcelona, Spain). *Journal of Vertebrate Paleontology, 30,* 547–562.

Robles, J.M., Alba, D.M., Carmona, R., Rotgers, C., Galindo, J., Balaguer, J., et al. (2010b). Nuevos hallazgos de *Sansanosmilus jourdani* (Filhol 1883) (Carnivora: Barbourofelidae) del Mioceno Medio de la serie estratigráfica del Abocador de Can Mata (cuenca del Vallès-Penedès, Barcelona, España). *Cidaris, 30,* 265–271.

Robles, J.M., Madurell-Malapeira, J., Abella, J., Rotgers, C., Carmona, R., Almécija, S., et al. (2013a). New *Pseudaelurus* and *Styriofelis* remains (Carnivora: Felidae) from the Middle Miocene of Abocador de Can Mata (Vallès-Penedès Basin). *Comptes Rendus Palevol, 12,* 101–113.

Robles, J.M., Alba, D.M., Fortuny, J., De Esteban-Trivigno, S., Rotgers, C., Balaguer, J., et al. (2013b). New craniodental remains of the barbourofelid *Albanosmilus jourdani* (Filhol, 1883) from the miocene of the Vallès-Penedès Basin (NE Iberian Peninsula) and the phylogeny of the Barbourofelini. *Journal of Systematic Palaeontology, 11,* 993–1022.

Robles, J. M., Madurell-Malapeira, J., Casanovas-Vilar, I., Abella, J., Alba, D. M. (2013c). The scimitar-toothed cat *Machairodus aphanistus* (Carnivora, Felidae) in the Vallès-

Penedès Basin (NE Iberian Peninsula): new remains and taxonomic revision [Abstract]. *Journal of Vertebrate Paleontology 33 Suppl. 1*, 200.

Rögl, F., Zapfe, H., Bernor, R., Brzobohaty, R., Daxner-Höck, G., Draxler, I., et al. (1993). Die Primatenfundstelle Götzendorf an der Leitha (Obermiozän des Wiener Beckens, Niederösterreich). *Jarbuch der Geologischen Bundesanstalt, 136,* 503–526.

Roman, R. & Viret, J. (1934). La faune de Mammifères du Burdigalien de La Romieu (Gers). *Mémoires de la Société Géologique de France, 21,* 1–78.

Roth, C. (1987). Die Raubtierfauna aus den miozänen Spaltenfüllungen Petersbusch 2 und Erketshofen 2. Taxonomie-Stratigraphie-Ökologie. Ph.D. Dissertation, Institute für Geowissenschaften (Paläontologie), Johannes Gutenberg-Universität Mainz.

Roth, C. (1988). *Leptoplesictis* Major, 1903 (Mammalia, Carnivora, Viverridae) aus dem Orleanium und Astaracium/Miozän von Frankreich und Deutschland. *Paläontologische Zeitschrift, 62,* 333–343.

Rothwell, T. (2003). Phylogenetic Systematics of North American Pseudaelurus (Carnivora, Felidae). *American Museum Novitates, 3403*, 1–64.

Salesa, M.J., Montoya, P., Alcalá, L., & Morales, J. (2003). El género *Paramachairodus* Pilgrim, 1913 (Felidae, Machairodontinae) en el Mioceno superior español. *Coloquios de Paleontología, Vol. Ext. 1,* 603–615.

Salesa, M.J., Antón, M., & Morales, J. (2005). Inferred behaviour and ecology of the primitive sabre-toothed cat *Paramachairodus ogygia* (Felidae, Machairodontinae) from the Late Miocene of Spain. *Journal of Zoology, 268,* 243–254.

Salesa, M. J., Antón, M., Turner, A., Alcalá, L., Montoya, P., & Morales, J. (2010). Systematic revision of the Late Miocene sabre-toothed felid *Paramachaerodus* in Spain. *Palaeontology, 53,* 1369–1391.

Salesa, M.J., Antón, M., Morales, J., & Peigné, S. (2011). Functional anatomy of the postcranial skeleton of *Styriofelis lorteti* (Carnivora, Felidae, Felinae) from the Middle Miocene (MN6) locality of Sansan (Gers, France). *Estudios Geológicos, 67,* 223–243.

Salesa, M.J., Pesquero, M.D., Siliceo, G., Antón, M., Alcalá, L., & Morales, J. (2012). A rich community of Felidae (Mammalia, Carnivora) from the Late Miocene (Turolian, MN13) site of Las Casiones (Villalba Baja, Teruel, Spain). *Journal of Vertebrate Paleontology, 32,* 658–676.

Schmidt-Kittler, N. (1976). Raubtiere aus dem Jungtertiär kleinasiens. *Palaeontographica A, 155,* 1–131.

Sesé Benito, C. (1980). Mamíferos del Mioceno Medio de Escobosa de Calatañazor (Soria). Ph.D. Dissertation, Universidad Complutense de Madrid.

Siliceo, G., Salesa, M.J., Antón, M., & Morales, J. (2012). Aspects of the shoulder anatomy of the Late Miocene amphicyonid *Magericyon anceps*. *Fundamental!, 20,* 239–242.

Spassov, N., Tzankov, T., & Geraads, D. (2006). Late Neogene stratigraphy, biochronology, faunal diversity and environments of South-Western Bulgaria (Struma River Valley). *Geodiversitas, 28,* 477–498.

Stehlin, H.G. & Helbing, H. (1925). Catalogue des ossements de Mammifères tertiaires de la collection Bourgeois. *Bulletin de la Societé d'Histoire Naturelle du Loire-et-Cher, 18,* 1–202.

Thenius, E. (1977). Zur systematischen Stellung von Protursus (Carnivora, Mammalia). *Anzeiger der Österreichischen Akademie der Wissenchaften, mathematisch-naturwissenschaflichen Klasse, 3,* 37–41.

Turner, A., Antón, M., & Werdelin, L. (2008). Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. *Geobios, 41,* 677–687.

Turner, A., Antón, M., Salesa, M.J., & Morales, J. (2011). Changing ideas about the evolution and functional morphology of machairodontine felids. *Estudios Geológicos, 67,* 255–276.

Vicente i Castells, J. (1987). Noves troballes al jaciment de mamífers de Cases de la Valenciana (Gelida, Alt Penedès). *Butlletí del Centre d'Estudis de la Natura del Barcelonès Nord, 3,* 130–131.

Villalta Comella, J.F. & Crusafont Pairó, M. (1941). Noticia preliminar sobre la fauna de carnívoros del Mioceno continental del Vallés-Penedés. *Boletín de la Real Sociedad Española de Historia Natural, 39,* 201–208.

Villalta Comella, J.F. de & Crusafont Pairó, M. (1943a). Los vertebrados del Mioceno continental de la cuenca del Vallés-Panadés (provincia de Barcelona. I. Insectívoros. II. Carnívoros. *Boletín del Instituto Geológico y Minero de España, 56,* 145–331.

Villalta Comella, J.F. & Crusafont Pairó, M. (1943b). *Contribución al conocimiento de* Albanosmilus jourdani *Filhol.* Madrid: Consejo Superior de Investigaciones Científicas (pp. 1–44).

Villalta Comella, J.F. de & Crusafont Pairó, M. (1943c). *Indarctos vireti*, nova sp. Un nuevo úrsido del grupo de los hemiciónidos del Mioceno superior del Vallés-Panadés. Madrid: Consejo Superior de Investigaciones Científicas (pp. 45–62).

Villalta Comella, J.F. de & Crusafont Pairó, M. (1944). Nuevos carnívoros del Vindoboniense de la cuenca del Vallés-Panadés. *Notas y Comunicaciones del Instituo Geológico y Minero de España, 13,* 53–88.

Villalta Comella, J.F. & Crusafont Pairó, M. (1945). *Enhydriodon lluecai* nova sp. El primer lútrido del pontiense español. *Boletín de la Real Sociedad Española de Historia Natural, 43,* 383–396.

Villalta, J.F. & Crusafont, M. (1946a). Les gisements de Mamifères du Néogène espagnol. III. Bassin du Vallés-Penadés (Catalogne). Pontien. *Comptes Rendus Sommaires de la Société Géologique de France, 1946,* 224–227.

Villalta, J.F. & Crusafont, M. (1946b). Les gisements de Mammifères du Néogène espagnol. II. Bassin de Vallès-Pénadès (Catalogne), Vindobonien, Hostalets de Pierola. *Comptes Rendus Sommaires de la Société Géologique de France, 1946,* 133–134.

Villalta, J.F. & Crusafont, M. (1946c). Les gisements de Mammifères du Néogène espagnol. I. Bassin du Valles-Panaeés [sic] (Catalogne) Vindobonien. Sant Quirze de Galliners. *Comptes Rendus Sommaires de la Société Géologique de France, 1946,* 49–51.

Villalta Comella, J.F. & Crusafont Pairó, M. (1948). Nuevas aportaciones al conocimiento de los carnívoros pontienses del Vallés-Penedés. *Miscelánea Almera. Publicaciones del Instituto Geológico, 7,* 81–121.

Villalta, J.F. & Crusafont, M. (1952). *Grivasmilus* remplaçant *Albanosmilus* (=*Sansanomilus*). *Comptes Rendus Sommaires de la Société Géologique de France, 14,* 308–309.

Viret, J. (1951). Catalogue critique de la faune des Mammifères Miocènes de la Grive Saint-Alban (Isère). Première partie. Chiroptères, Carnivores, Édentés Pholidotes. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon, 3,* 1–104.

Viret, J. & Crusafont-Pairó, M. (1955). *Plesiomeles Cajali* n. gen. n. sp., un Méliné du Vallésien d'Espagne. *Eclogae geologicae Helvetiae, 4,* 447–452.

Wang, X. (1997). New cranial material of *Simocyon* from China, and its implications for phylogenetic relationship to the red panda (Ailurus). *Journal of Vertebrate Paleontology, 17,* 184–198.

Wang, X. & Qiu, Z. (2004). Late Miocene *Promephitis* (Carnivora, Mephitidae) from China. *Journal of Vertebrate Paleontology, 24,* 721–731.

Werdelin, L. (2004). The Carnivora of Rudabánya (MN9, Late Miocene, Hungary). *Palaeontographia Italica, 90,* 163–180.

Werdelin, L. & Solounians, N. (1990). Studies of fossil hyaenids: the genus *Adcrocuta* Kretzoi and the interrelationships of some hyaenid taxa. *Zoological Journal of the Linnena Society, 98,* 363–386.

Werdelin, L. & Solounias, N. (1991). The Hyaenidae: taxonomy, systematics and evolution. *Fossils and Strata, 30,* 1–104.

Werdelin. L. & Peigné, L. (2010). Carnivora. In: L. Werdelin & W.J. Sanders (Eds), *Cenozoic Mammals of Africa* (pp. 603–657). Berkeley: University of California Press.

Werdelin, L., Yamaguchi, N., Johnson, W.E. & O'Brien, S.J. (2010). Phylogeny and evolution of cats (Felidae). In: D. Macdonald & A. Loveridge (Eds), *The biology and conservation of wild felids* (pp. 59–82). Oxford: Oxford University Press.

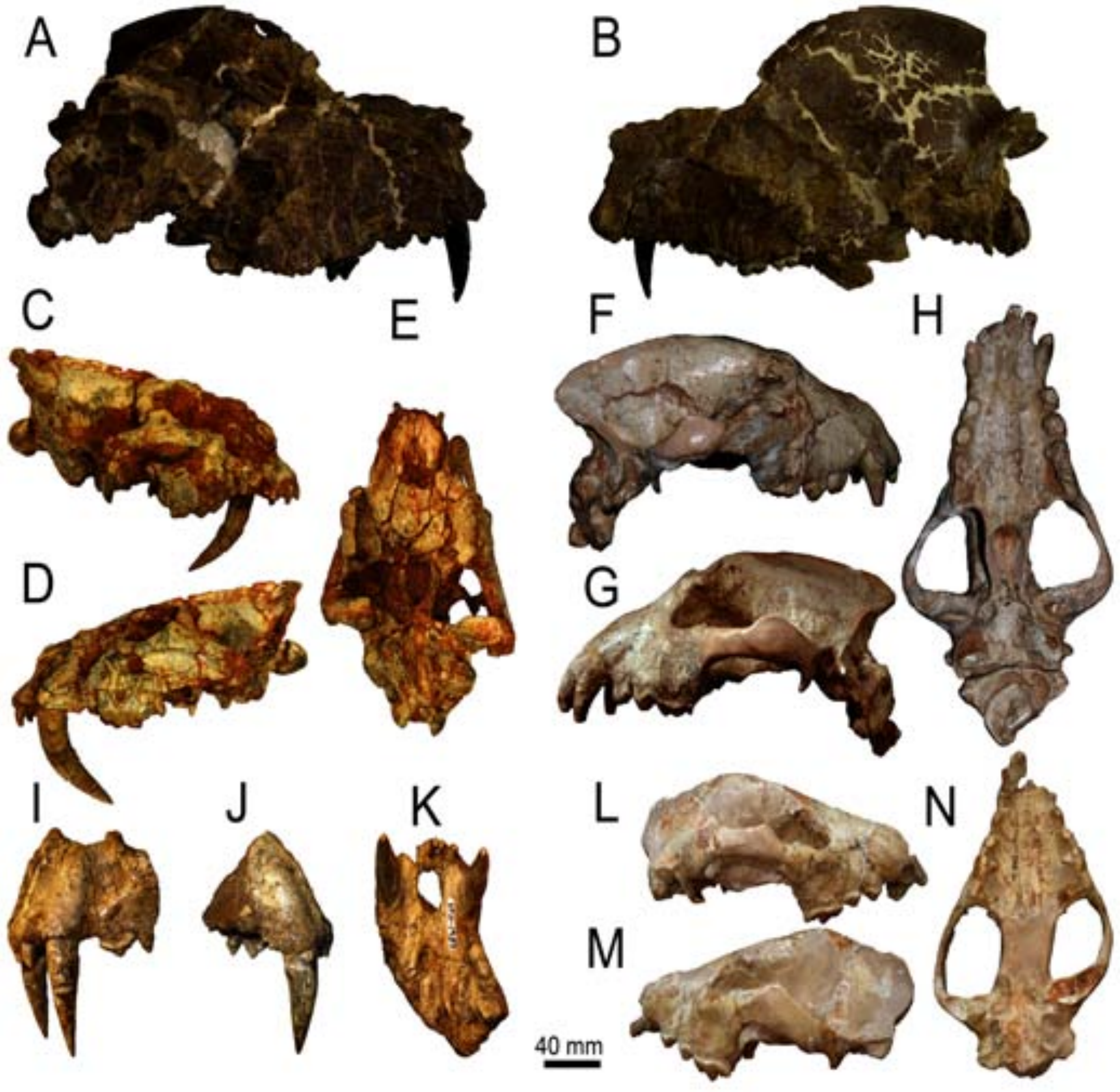

Figure 1. Cranial remains of amphicyonids, felids and hyaenids from of the Vallès-Penedès Basin. (**A–B**) Partial cranium of *Amphicyon olisiponensis* (IPS10156) from CS (MN4), in right lateral (A) and left lateral (B) views. (**C–E**) Cranium of *Albanosmilus jourdani* (IPS49575) from ACM/C8-B/C (MN7+8), in right lateral (C) and left lateral (D) views. (**F–H**) Cranium of *Adcrocuta eximia* (IPS36253) from TT (MN12), in right lateral (F), left lateral (G) and basal (H) views. (**I–K**) Partial cranium of *Stenailurus teilhardi* (IPS1985) from TT (MN12), in right lateral (I), left lateral (J) and basal (K) views. (**L–N**) Cranium of *Thalassictis montadai* (IPS2063) from CM1 (MN7+8), in right lateral (L), left lateral (M) and basal (N) views.

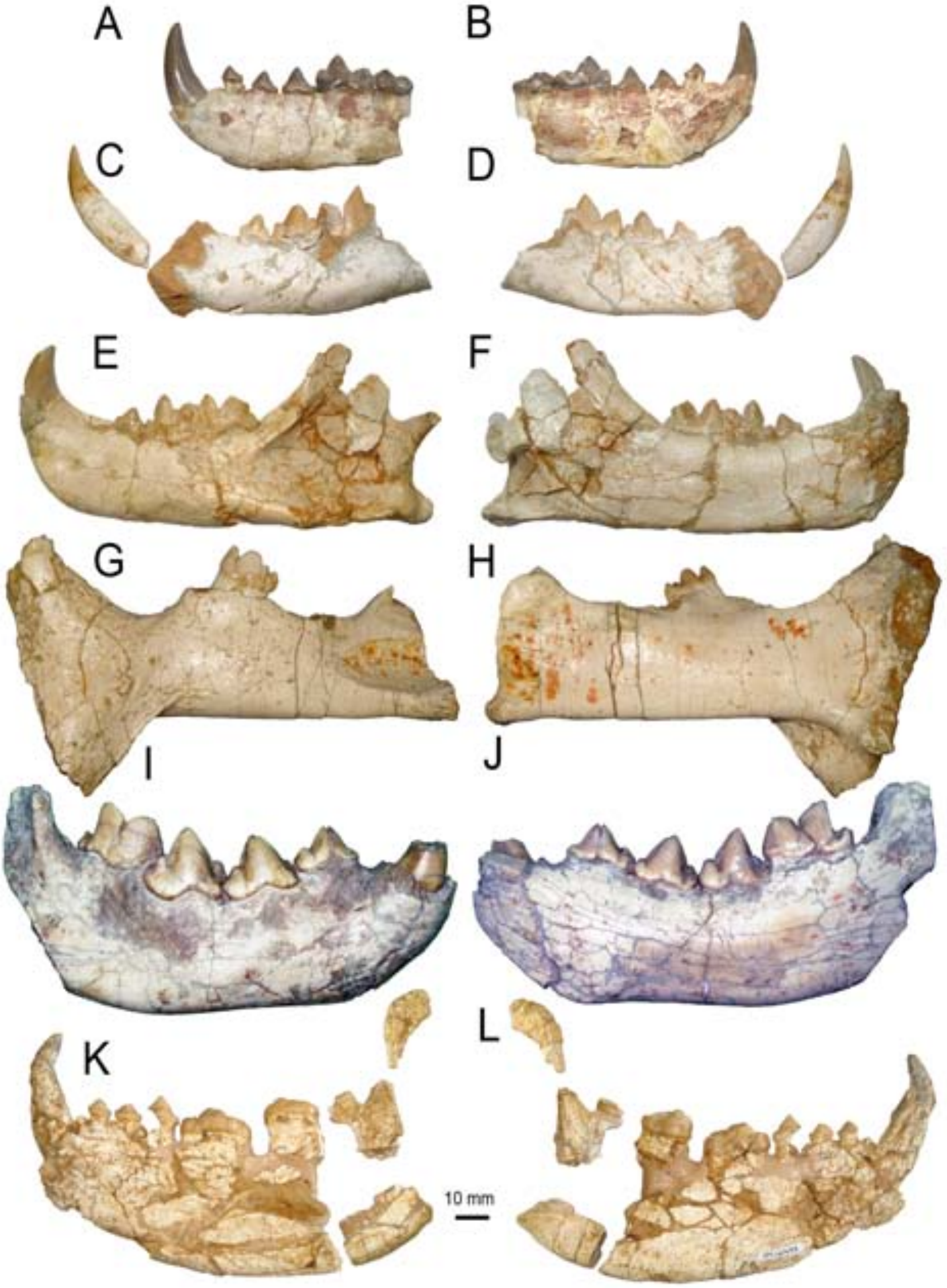

Figure 2. Mandibular remains of carnivorans from the Vallès-Penedès Basin. (**A–B**) Partial left mandible with c1–m1 of *Ictiocyon socialis* (IPS12980) from EC (MN4), in buccal (A) and lingual (B) views. (**C–D**) Partial left mandible with c1–m1 of *Pseudaelurus quadridentatus* (IPS60892c) from ACM/C8-Bd' (MN7+8), in buccal (C) and lingual (D) views. (**E–F**) Partial left mandible with c1–m1 of *Pseudaelurus romieviensis* (IPS42063) from ACM/C5-C (MN7+8), in buccal (E) and lingual (F) view. (**G–H**) Partial left mandible with c1 (partial) and p4 of *Albanosmilus jourdani* (IPS54866) from ACM/C7-A (MN7+8), in buccal (G) and lingual (H) views. (**I–J**) Partial right mandible with c1 (partial) and p2–m1 of *Hyaenictis almerai* (MGSB16501) from SMT (MN10), in buccal (I) and lingual (J) views. (**K–L**) Partial right mandible with c1–m2 of *Kretzoiarctos beatrix* (IPS46473) from ACM/C6-Camí (MN7+8), in buccal (K) and lingual (L) views.

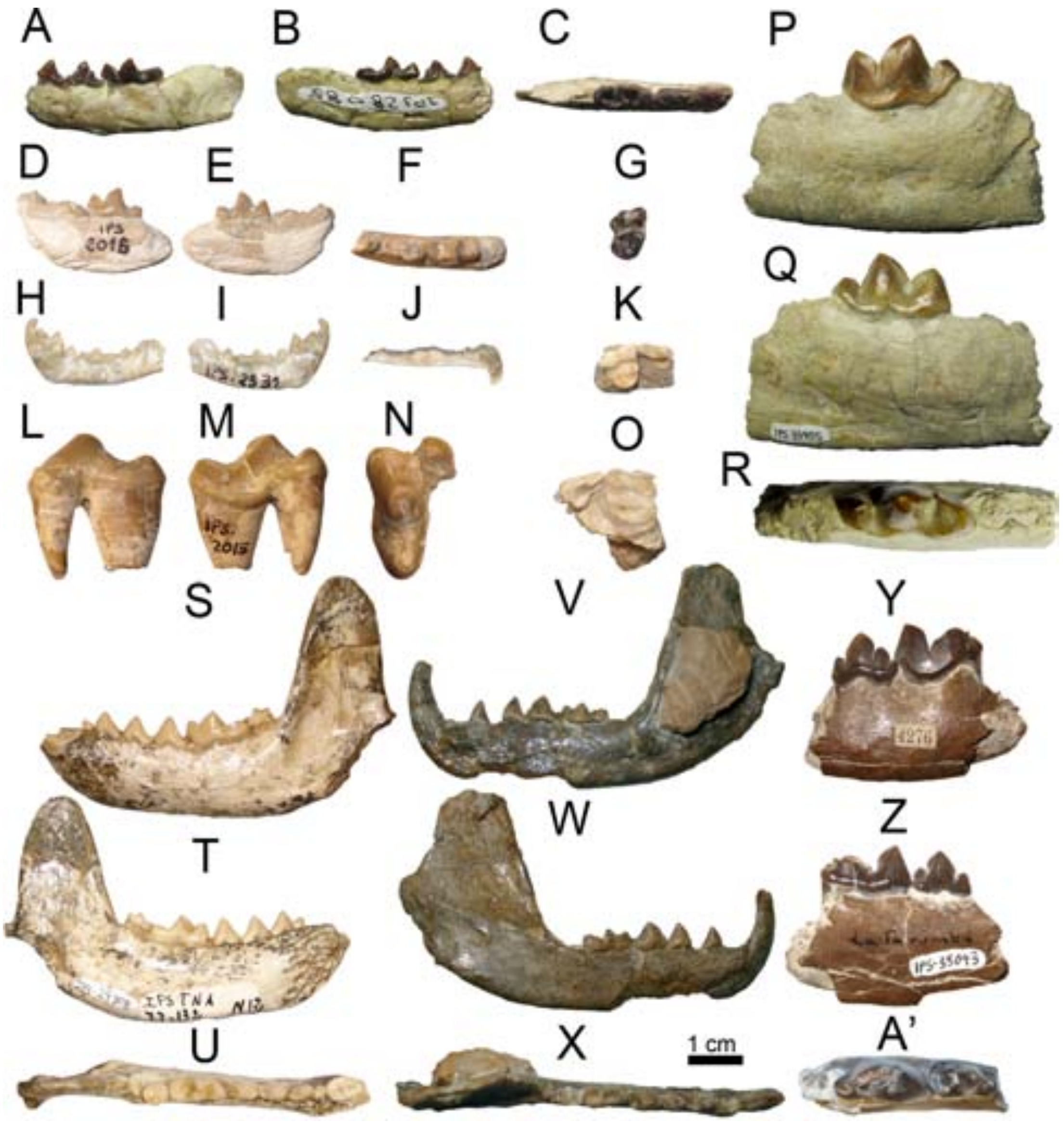

Figure 3. Dentognathic remains of mustelids and felids from the Vallès-Penedès Basin. (**A–C**) Partial left mandible with p3–m1 of *Trochictis narcisoi* (IPS28085) from CLL1 (MN9), in buccal (A), lingual (B) and occlusal (C) views. (**D–F**) Partial mandible with m1 of *Circamustela dechaseauxi* (IPS2016) from CLL1 site (MN9), in buccal (D), lingual (E) and occlusal (F) views. (**G**) M1 of *Sabadellictis crusafonti* (IPS2530) from CLL1 (MN9), in occlusal view. (**H–J**) Partial left mandible with c1–m2 of *Mesomephitis medius* (IPS2531) from CP1 (MN9), in buccal (H), lingual (I) and occlusal (J) views. (**K**) Partial palate with P4–M1 of *Promephitis pristinidens* (IPS1995) from CPL (MN10), in occlusal view. (**L–N**) P4 of *Hoplictis petteri* (IPS2015) from CLL1 (MN9), in buccal (L), lingual (M) and occlusal (N) views. (**O**) Partial palate with P4–M1 of *Palaeomeles pachecoi* (IPS697) from HPI (MN7+8), in occlusal view. (**P–R**) Partial left mandible with m1 of *Hoplictis helbingi* (IPS33185) from CB (MN9), in buccal (P), lingual (Q) and occlusal (R) views. (**S–U**) Left hemimandible with p1–m2 of *Martes melibulla* (IPS29308) from TNA (MN10), in buccal (S), lingual (T) and occlusal (U) views. (**V–X**) Partial left mandible with c1–m1 of *Trocharion albanense* (IPS44170) from ACM/C5-D (MN7+8), in buccal (V), lingual (W) and occlusal (X) views. (**Y–A'**) Partial left mandible with p4–m1 of cf. *Promegantereon ogygia* (IPS35093) from LTR1 (MN10), in buccal (Y), lingual (Z) and occlusal (A') views.

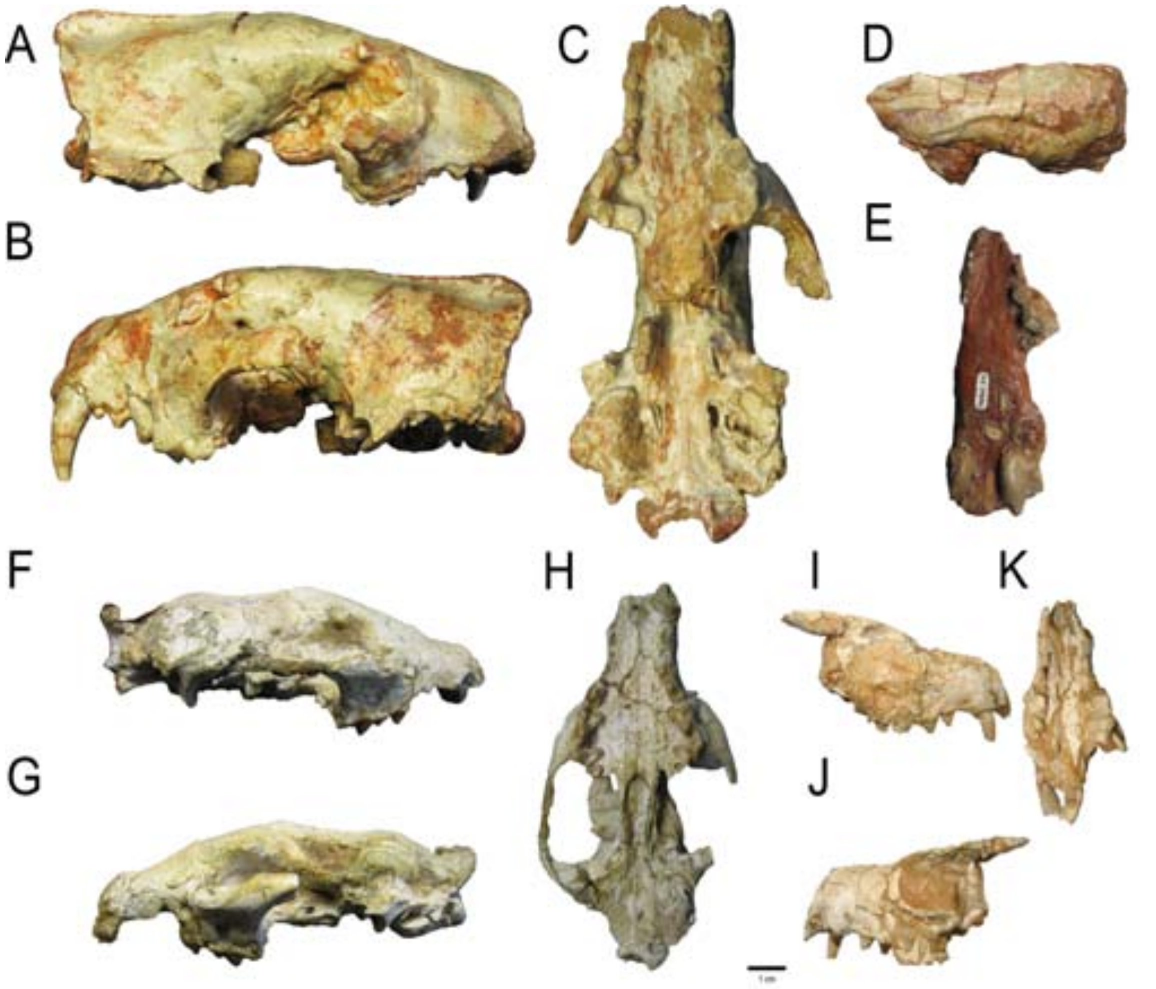

Figure 4. Cranial remains of mustelids and hyaenids from the Vallès-Penedès Basin. (**A–C**) Cranium of *Ischyrictis mustelinus* (IPS36394) from CM1 (MN7+8), in right lateral (A), left lateral (B) and basal (C) views. (**D–E**) Partial cranium of *Martes munki* (IPS31892) from EC (MN4), in dorsal (D) and basal (E) views. (**F–H**) Cranium of *Protictitherium crassum* (IPS20444) from ACM/C1-E9 (MN7+8), in right lateral (F), left lateral (G) and basal (H) views. (**I–K**) Partial cranium of *Trocharion albanense* (IPS44028) from ACM/C6-Cb (MN7+8), in right lateral (I), left lateral (J) and basal (K) views.

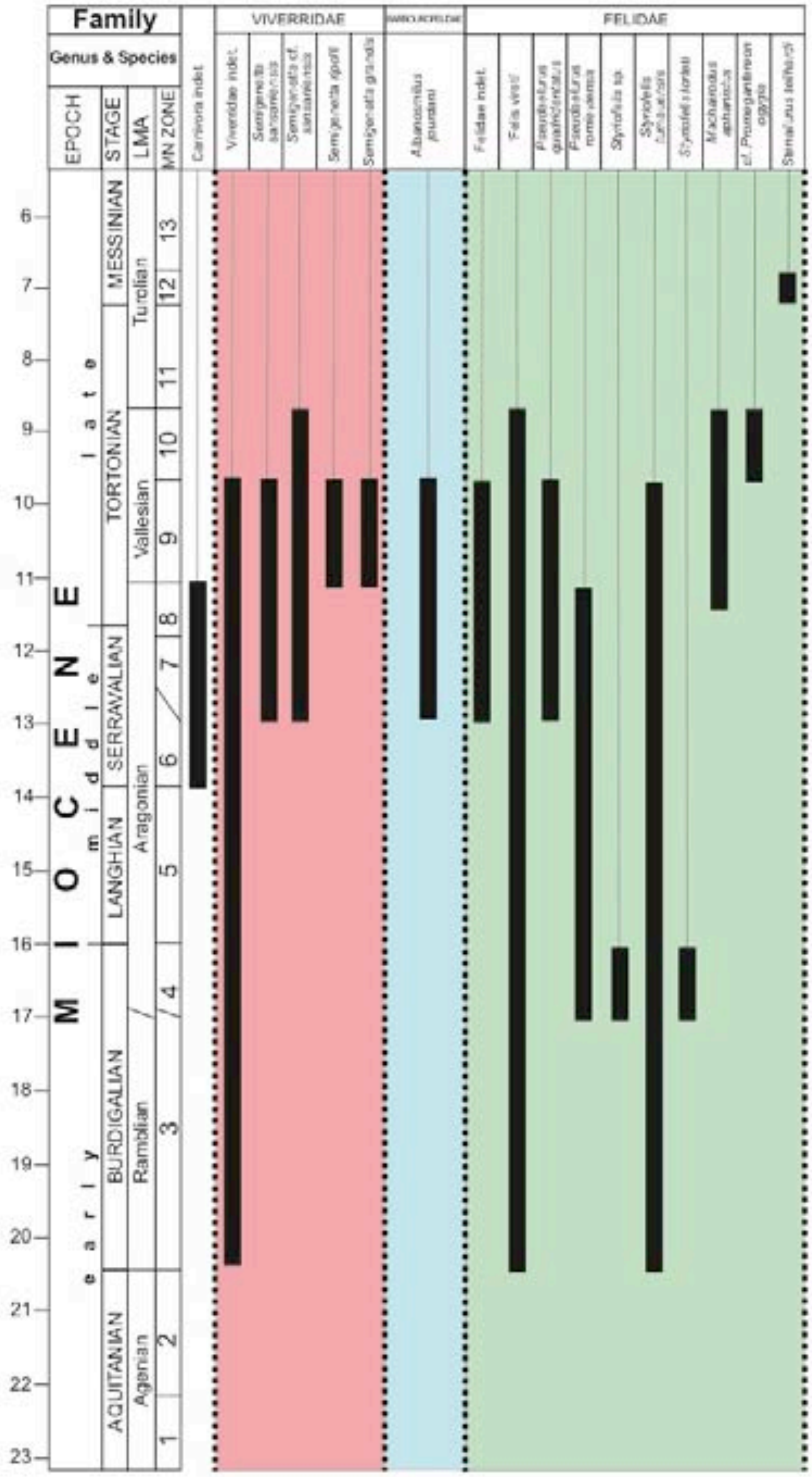

Figure 5. Chronostratigraphic range of the carnivoran families Viverridae, Barbourofelidae and Felidae in the Miocene of the Vallès-Penedès Basin.

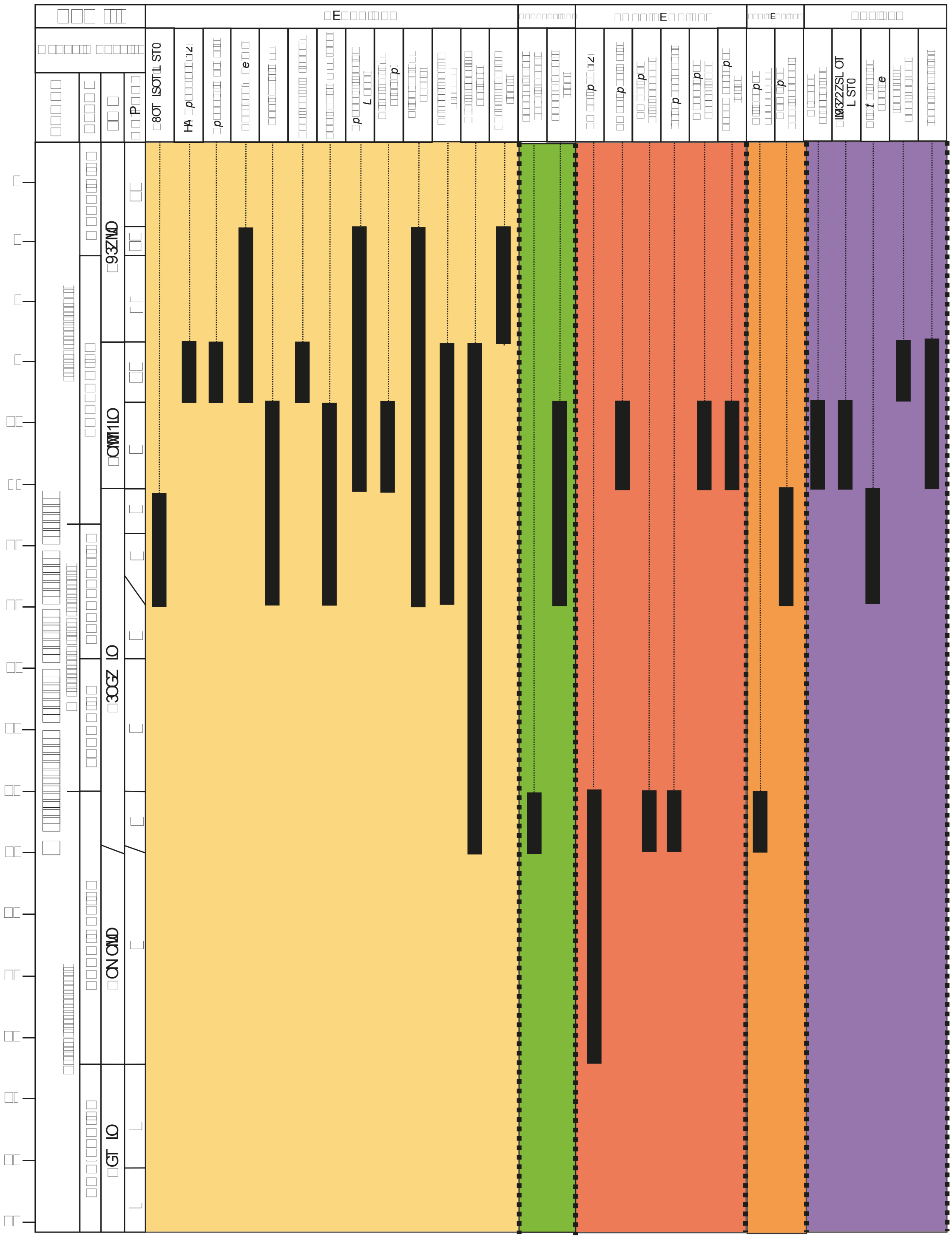

Figure 6. Chronostratigraphic range of the carnivoran families Hyaenidae, Herpestidae, Amphicyonidae, Hemicyonidae and Ursidae in the Miocene of the Vallès-Penedès Basin.

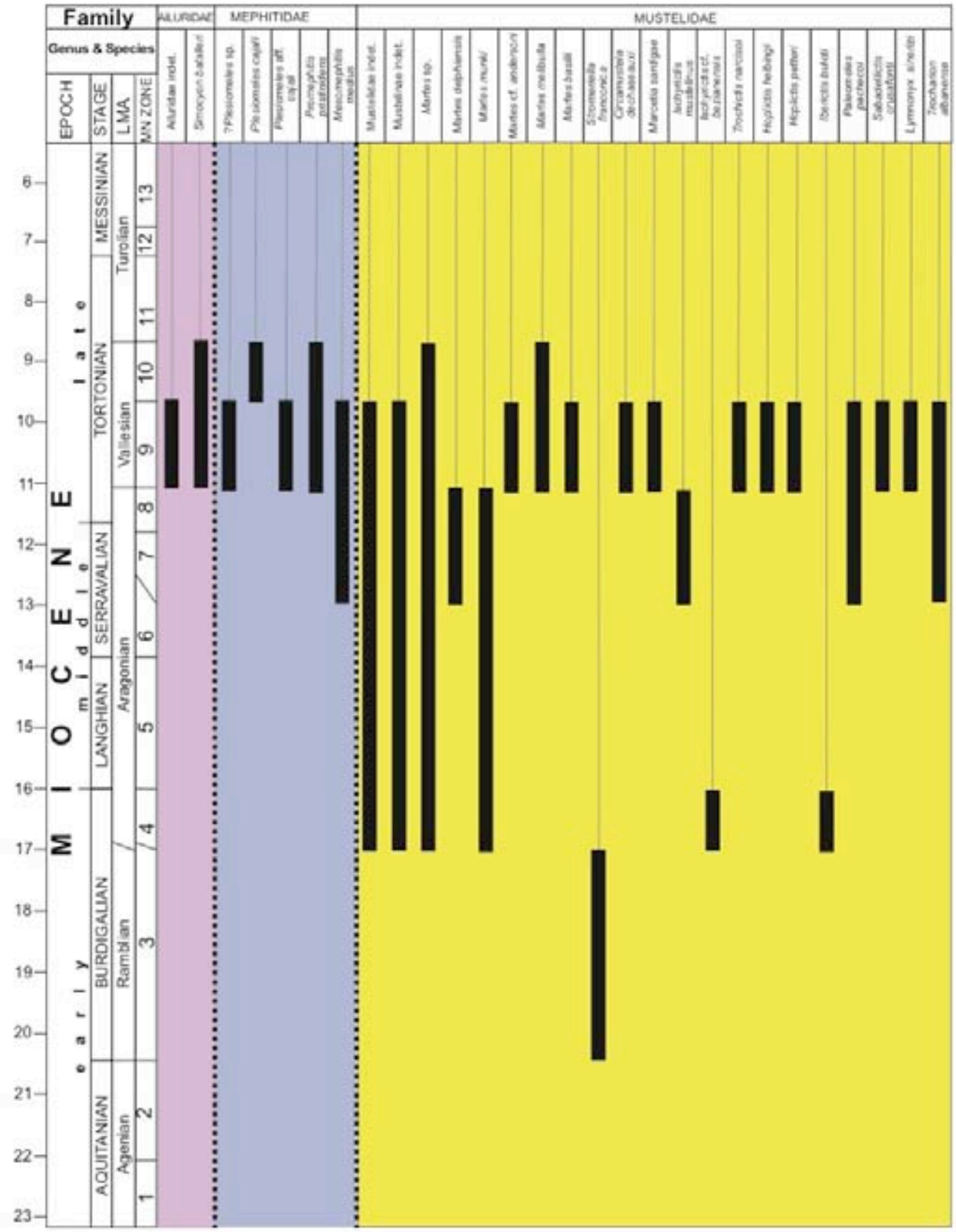

Figure 7. Chronostratigraphic range of the carnivoran families Ailuridae, Mephitidae and Mustelidae in the Miocene of the Vallès-Penedès Basin.