Les Tortugues (Testudines) del

Neogen i Quaternari de Catalunya

(NE de la Península Ibèrica)

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CAPÍTOL 5. AN OVERVIEW OF THE THREATENED PHYLOGENETIC DIVERSITY OF LIVING TESTUDINES BASED O A REVIEW OF THE COMPLEX EVOLUTIONARY HISTORY OF TURTLES

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Chapter 4

AN OVERVIEW OF THE THREATENED PHYLOGENETIC DIVERSITY OF LIVING TESTUDINES BASED ON A REVIEW OF THE COMPLEX EVOLUTIONARY HISTORY OF TURTLES

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ABSTRACT

The history of turtle lineage began around 225 Mya. Since then, this group of reptiles developed diverse ecological strategies and colonized a wide range of environments, from marine to fully terrestrial habitats. In spite of their great ecological diversity, the bauplan of turtles is peculiar and little variable, with a body encased in a rigid shell consisting of a dorsal carapace and a ventral plastron. This fact has made the morphological comparison of turtles with other vertebrates very complicate. Thus, the understanding of the origins and phylogenetic relationships of turtles within the Amniota and the evolution of turtle biology are stimulating challenges for researchers. Several attempts in

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order to resolve these mysteries have been carried out from a multidisciplinary approach, but lacks consensus. The knowledge of the evolutionary history of turtle species and their inclusive groups is relevant for their conservation management, especially taking into account that many species are among moderate and high risk of extinction. In this chapter, we update and review the state of the art of the systematics of turtles from the point of view of several often conflicting disciplines, embryology, morphology, paleontology and molecular systematics. In addition, we sound out the amount of threatened phylogenetic diversity in the turtle tree of life based on fossil evidence, recent phylogenetic hypotheses and data from the red list of the International Union for the Conservation of Nature.

INTRODUCTION

The clade Testudines (= Chelonia *sensu* Gauthier et al., 1988) include about 289 species alive today split up into two primary groups: Pleurodira and Cryptodira (Joyce et al., 2004). Nowadays, cryptodires are more diverse than pleurodires (Figure 1), the latter being more restricted geographically, living only in the southern hemisphere (Gaffney et al., 2006). Cryptodires are also adapted to a wider range of habitats, from open marine to arid environments, whereas pleurodires are restricted to freshwater (Gaffney et al., 2006).

Turtles are mysterious animals for the biologists, especially as far as their obscure evolutionary history is concerned. The origins and phylogenetic relationships of turtles with the remaining amniotes have been explored from different approaches such as paleontology, comparative anatomy, developmental biology, and molecular phylogenetics. However, there is no consensus among different source of data making the position of turtles in the amniote tree of live still rather confusing (see below and Werneburg & Sánchez-Villagra, 2009 and references therein). Uncertain phylogenetic relationships remain unresolved among fossil and extant turtles and even among several living turtle families and higher taxa (Shaffer et al., 1997; Gaffney et al., 2006; Barley et al., 2010). In addition, the evolution of adaptation of turtles to terrestrial and aquatic environments is poorly known because of uncommon preservation of appendicular skeletal elements in extinct turtles and their incomplete fossil record (Scheyer & Sander, 2007). As an example, there has been an intense debate about the terrestrial (e.g. Joyce & Gauthier, 2004;

Scheyer & Sander, 2007) versus semiaquatic (e.g. Gaffney, 1990) origins of turtles.

The knowledge of the evolutionary history of organisms is crucial to characterizing the biological diversity. Phylogeny is a record of how biodiversity has come about and the understanding of the origins of a group of organisms can assist in their conservation by contrasting current versus historical patterns (Harvey et al., 1996; Purvis et al., 2005). Moreover, phylogenies can inform about the risk of lineage extinction and assess the amount of evolutionary history lost if extinction occurs (Purvis et al., 2000). Thus, the extinction of species-poor or monotypic highly divergent lineages containing endangered species would entail the loss of a significant part of the evolutionary history of the inclusive clade. It is also possible to extrapolate from the past and present to the future, in order to predict the state of biodiversity under different scenarios (Rosenzweig, 2001). In addition, well resolved phylogenies are quite important in wildlife management because provide legal basis for conservation programs (O'Brien, 1994).

According to IUCN (2010), near a half of turtle species are threatened. Among them, 59 species are classified as vulnerable, 40 species as endangered and 30 species are critically endangered, representing the 20%, 14% and 10% of the total number of turtle species respectively. Thus, a better understanding of the evolutionary history of turtles is urgently needed in order to estimate the amount of turtle diversity that is at risk of extinction. In this chapter, the evolutionary significance of turtles is discussed by means of a review of the most recent advances in the knowledge of turtle origins, systematics, and the evolution of ecological adaptation. In addition, available data on endangered species is analyzed from a evolutionary point of view in order to obtain a general view of the amount of evolutionary history of turtles that may be lost if no efficient conservation measures are taken.

THE MYSTERIOUS PHYLOGENETIC RELATIONSHIPS OF TURTLES WITHIN AMNIOTA

The origins of turtles and their body plan are one of the great riddles of reptile evolution. Turtles are characterized by a horny beak rather than teeth and a shell composed of an upper carapace and a lower plastron, joined together by a bony bridge. Their shell is like that of no other animal and it is a

composite structure derived from ribs, parts of the shoulder girdle and specialized dermal bones (Reisz & Head, 2008). The peculiar body plan of turtles and their highly derived anatomical features make their phylogenetic position within the amniotes obscure. In fact, there has been an intense debate if turtles evolved from a lineage within Parareptilia —a well supported clade of stem amniotes including pareiasaurs and procolophonoids among others— or belong to Eureptilia which include diapsid reptiles (Tsuji & Müller, 2009).
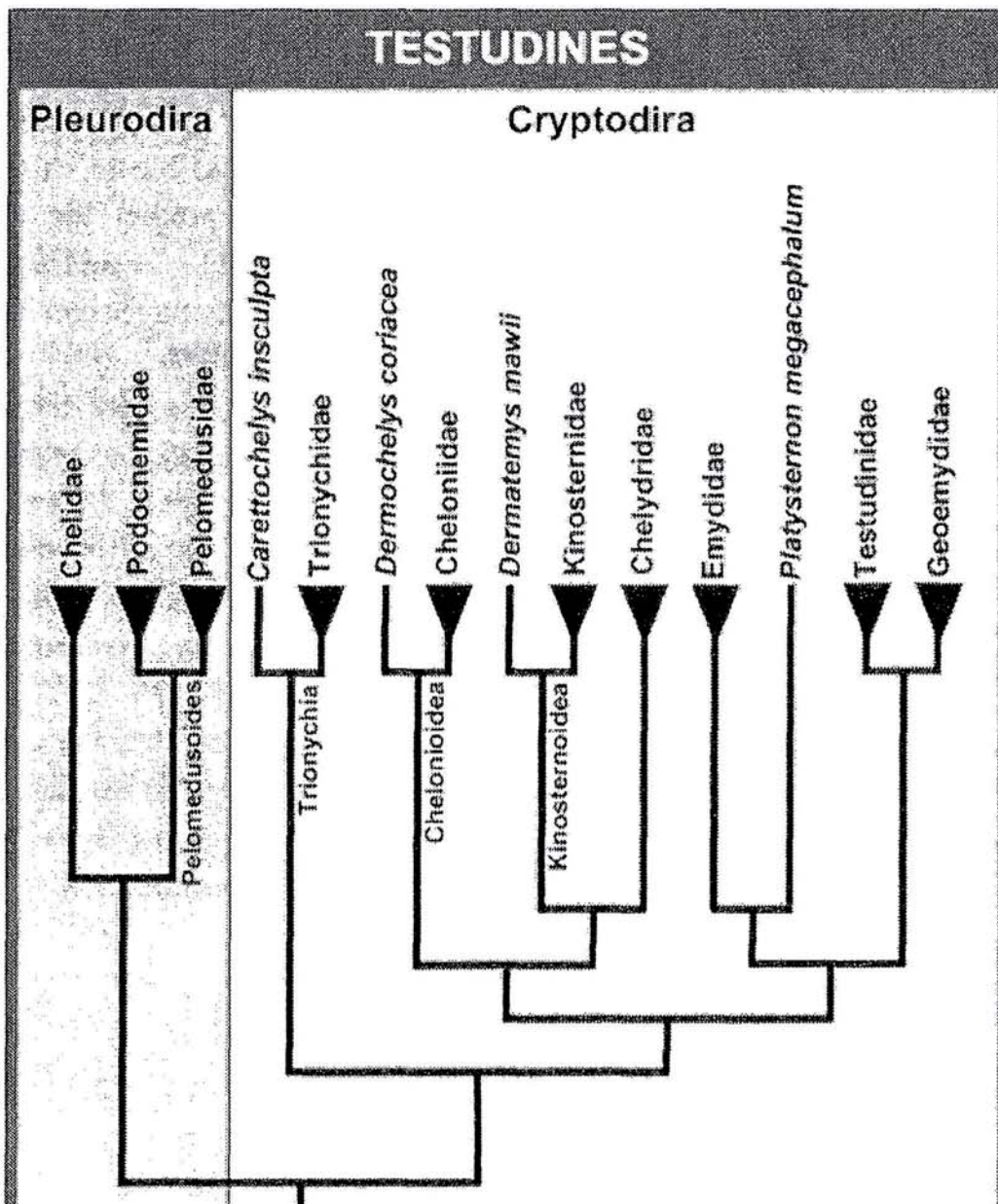
Figure 1. Phylogenetic tree of the main lineages of living turtles based on Joyce et al. (2004) and Barley et al. (2010).

Until today, up to ten phylogenetic hypotheses have been proposed, but none of them has a general acceptance (Figure 2). For instance, it has been

suggested that turtles are sister of Thecodontia (including Mammalia and Archosauria) (Gardiner, 1993), Sauria (crown diapsids) (Caspers et al., 1996), Sphenodontia (Fushitani et al., 1996), Archosauria (Kumazawa & Nishida, 1999), Crocodylia (Hedges & Poling, 1999), Lepidosauria (Zardoya & Meyer, 2000), and Aves (Pollock et al., 2000). However, most of these phylogenetic hypotheses are constructed ignoring extinct taxa. Extensive data including both extinct and extant amniotes suggest that turtles are part of a clade of basal terrestrial "anapsid" reptiles (Gauthier, 1994), are related to procolophonoids (Laurin & Reisz, 1995), or pareiasaurs (Lee, 1997) or they are sister taxa of sauropterygians within Eureptilia (de Braga & Rieppel, 1997). Disagreements among all these hypotheses probably are due to both morphological and molecular data are sensitive to taxon sampling, homology issues, rate heterogeneity and missing data (Lee et al., 2008).
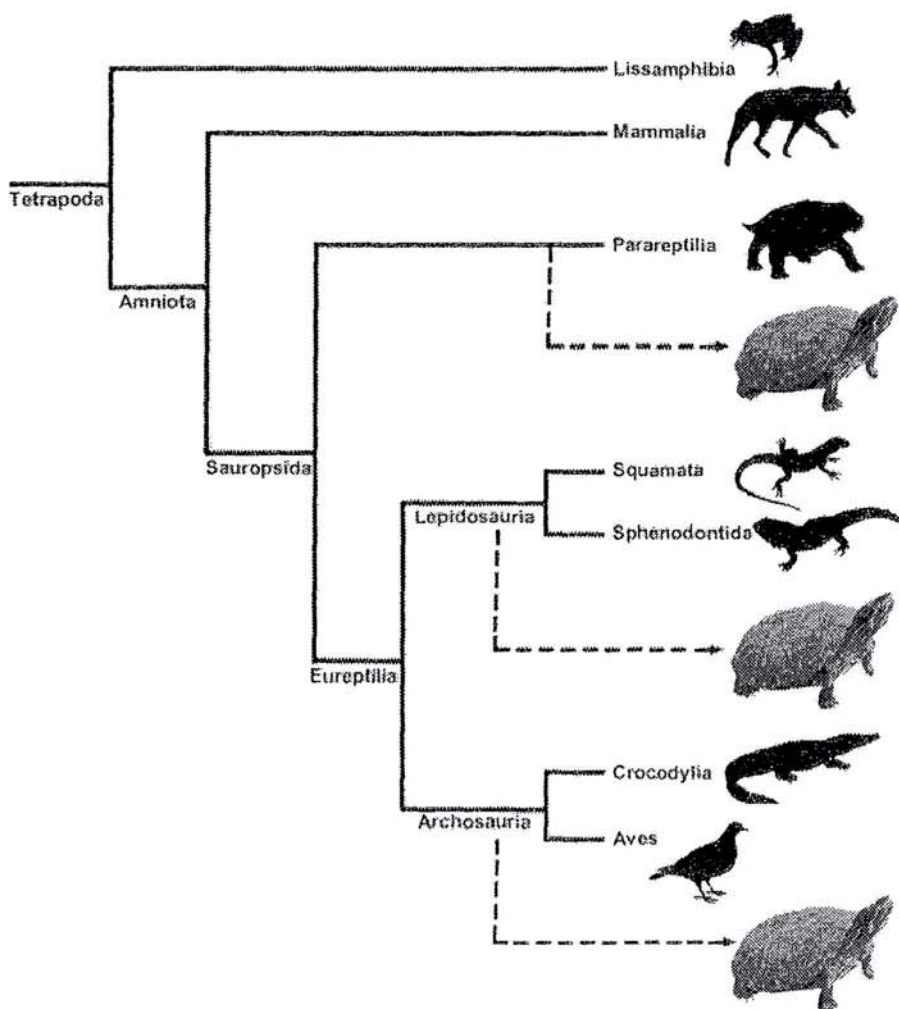

Figure 2. Three (out of ten) main hypotheses for the phylogenetic relationships of turtles with remaining amniotes.

Recent studies have not shed much light to the phylogenetic relationships of turtles within Amniota. New molecular analyses strongly support a turtle + archosaur relationship within Eureptilia (e.g. Hugall et al., 2007; Shedlock et al., 2007). In fact, since the beginnings of 2000s there has been decreasing support to the hypothesis of a turtle-parareptile relationship which is no longer considered valid among the majority of evolutionary biologists (see references in Tsuji & Müller, 2009). However, new embryological data (Werneburg & Sánchez-Villagra, 2009), combined molecular and morphological data (Lee et al., 2008) and fossil evidence (Lyson et al., 2010) place again turtles outside Diapsida. Specifically, in this latter study, turtles nest within parareptiles, forming a well supported clade with the genus *Eunotosaurus*, as the sister group to Diapsida (Figure 3). According to Lyson et al. (2010), basal-most stem turtles *Odontochelys semitestacea* and *Proganochelys quenstedti* have all six unequivocal synapomorphies diagnostic of Parareptilia which were listed by Tsuji & Müller (2009): 1) absence of a lacrimal-nasal contact, 2) absence of a caniniform region, 3) shortened postorbital region, 4) single median embayment of the posterior margin of the skull roof, 5) absence of a supraglenoid foramen and 6) absence of a subtemporal process of the jugal. Thus, the debate about the phylogenetic affinities of turtles with other amniotes seems still open and further analyses are needed to confirm the turtle-parareptile hypothesis as suggest these last studies.

OLDEST KNOWN TURTLES AND THE EVOLUTION OF SHELL

In spite of major controversies on their phylogenetic relationships, the evolutionary history of turtles began in the early Late Triassic, around 220 Mya. Since its discovery in 1884, *Proganochelys quenstedti* from the Late Triassic of Germany was considered the oldest turtle known (Gaffney, 1990). Nevertheless, only two years ago, *Proganochelys* was dethroned as the basal-most Testudinata due to new evidence from China. *Odontochelys semitestacea* is a relatively small turtle, about 40 cm long, approximately five million of years older than *Proganochelys* that was discovered near Guanling, Guizhou Province (southwestern China) (Li et al., 2008). According to these authors, *Odontochelys* is evolutively more primitive than *Proganochelys* in having teeth on premaxilla, maxilla and dentary; absence of fully formed carapace;

absence of acromial process on scapula and presence of long tail, among other characters. *Odontochelys* also shares primitive features with *Proganochelys* (see Li et al., 2008 for details).
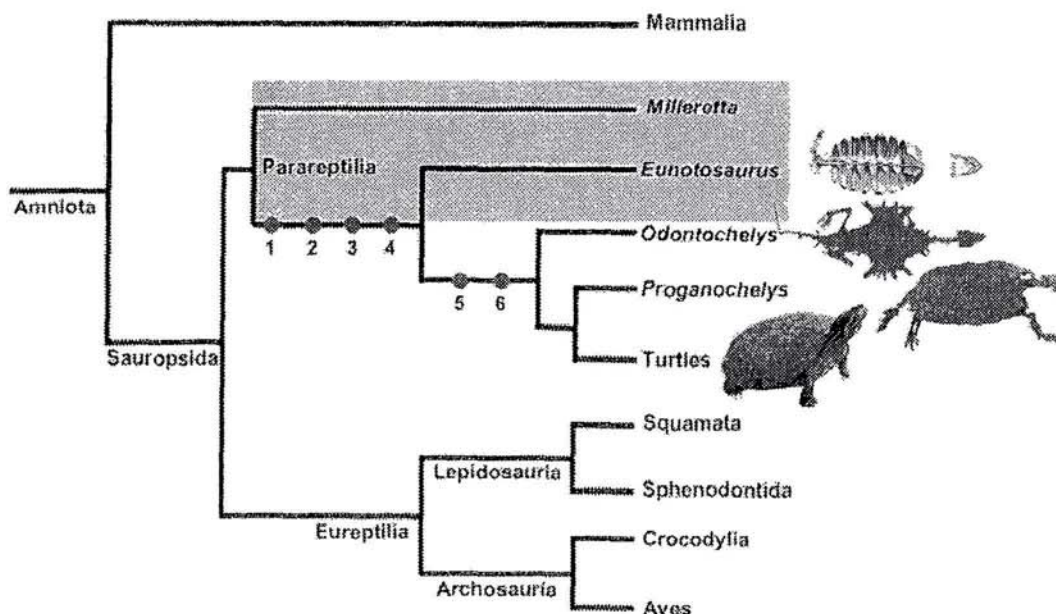

Figure 3. According to new phylogenetic analyses carried out by Lyson et al. (2010) turtles are closely related to the parareptile *Eunotosaurus* based on the following shared characters: 1, broad T-shaped ribs; 2, ten elongate trunk vertebrae; 3, cranial tubercles; 4, wide trunk. Two additional features are shared by *Odontochelys*, *Proganochelys* and extant turtles: 5, presence of plastron and 6, presence of neurals.

Turtle shell represents an evolutionary novelty and some authors propose that turtle evolution might be radical or saltatory instead of a gradual change (Gilbert et al., 2001; Rieppel, 2001). The comparison of rib cage of the parareptile *Eunotosaurus* and the shell of *Odontochelys* and *Proganochelys* provides valuable information about the evolution of turtle shell (Lyson et al., 2010). The dorsal part of turtle shell, or carapace, is derived from the ribs. The scapula is found under the carapace, contrary to the pattern of remaining amniotes in which the scapula is outside the rib cage (Figure 4 and Nagashima et al., 2009). In the Late Permian, *Eunotosaurus* had broadened ribs with apparent metaplastic ossification of the dermis and ribs joined by a second ossification. In the next stage, 44 Myr after, *Odontochelys* developed neural plates and a fully ossified plastron, containing portions of the shoulder girdle and gastralia. The carapace of *Odontochelys* resembles embryonic stages of extant turtles in that there is only some broadening and consequent flattening of the dorsal ribs, which do not expand into costal plates (Li et al., 2008;

Nagashima et al., 2009). Anterior ribs grew posteriorly in *Odontochelys* and the scapula remained anterior to the ribs (Figure 4). The dorsal ribs of *Odontochelys* seem arrested axially and they do not bend ventrally, suggesting that a caparacial-like ridge might be acquired in the flank of their embryos but not persisted and encircled the carapace margin in later development, as in modern turtles (Nagashima et al., 2009). The completion of the shell may have occurred rapidly, approximately in five million of years, which is the timespan that separate *Odontochelys* and *Proganochelys* (Lyson et al., 2010).
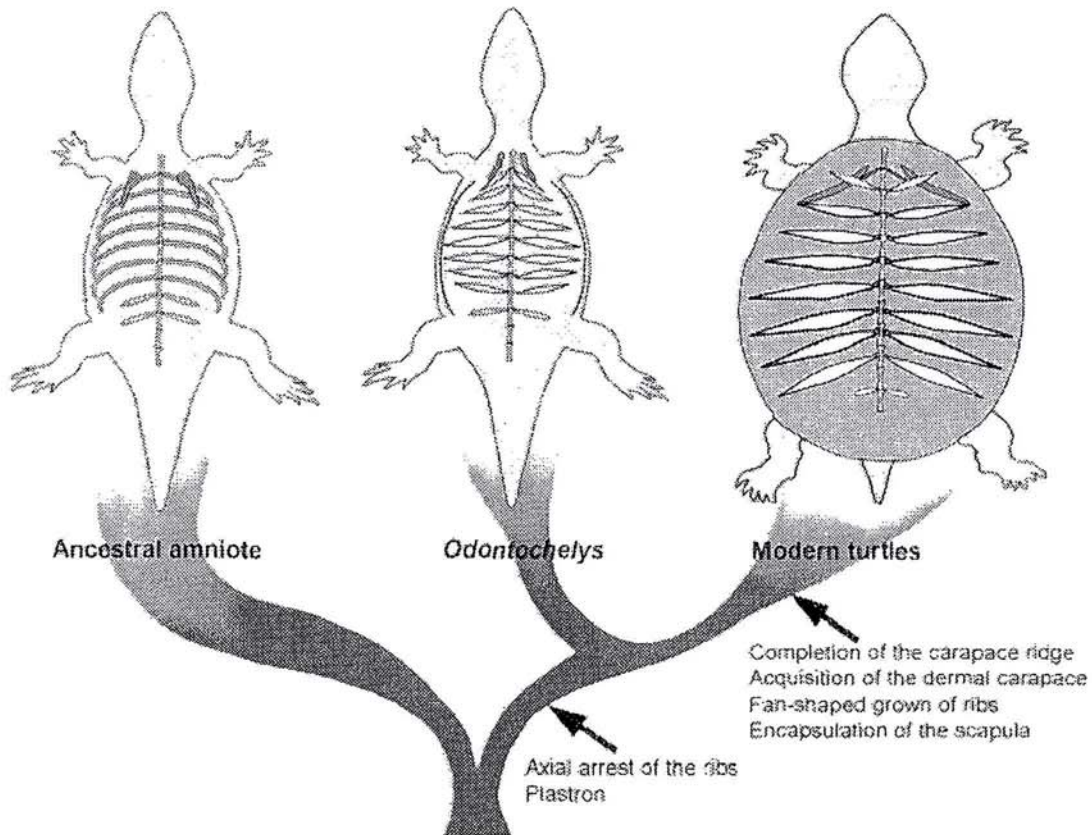
Figure 4. Evolution of turtle body plan. In the general pattern of amniotes (excluding turtles), scapulas (in dark grey) are outside the rib cage. In *Odontochelys*, scapulas are anterior to the ribs whereas in modern turtles they are encapsulated under the carapace. Dorsal ribs are arrested axially in *Odontochelys* and in modern turtles ribs are placed in a fan-like arrangement. The broken black line in *Odontochelys* indicates a carapacial-like ridge that it might be present in their embryos. Modified from Nagashima et al. (2009).

The genus *Proganochelys* is well known from several skeletons. These ancient turtles are characterized by a massive shell and spiked armor on the neck and tail (Reisz & Head, 2008). The shell is fully developed with carapace and plastron enclosing shoulder and pelvic girdles (Gaffney, 1990). The

carapace consists of fused ribs, neural bones with fused thoracic vertebrae and marginal bones. The plastron is formed from interclavicles, clavicle and five paired bones fused together. Other Late Triassic stem turtles are *Proterochersis robusta* from several localities of Germany (Lapparent de Broin, 2001) and *Palaeochersis talampayensis* from northwestern Argentina (Rougier et al., 1995).

TERRESTRIAL VERSUS AQUATIC ORIGINS OF TURTLES

Extant turtles inhabit a wide diversity of terrestrial and fresh- and sea-water environments such as land, ponds, lakes, streams, large rivers, estuaries and ocean. An aquatic origin of turtles has been suggested when they are considered to be closely related to extinct marine sauropterygian reptiles (de Braga & Rieppel, 1997). However, other authors indicate that oldest turtles were clearly terrestrial (Joyce & Gauthier, 2004; Scheyer & Sander, 2007).

The lifestyle of extinct turtles may be inferred from different source of evidence. The gross morphology of shell, shoulder girdle and limbs reveals adaptations to terrestrial or aquatic environments (Depecker et al., 2006). Terrestrial turtles have domed shell and long scapular prong and short coracoid associated with a mode of locomotion in which walking is predominant (Figure 5a). By contrast, in both highly aquatic freshwater and marine turtles the scapular prong is short and the coracoid is long and they are associated with flat shells and swimming locomotion (Figure 5b). However, Joyce & Gauthier (2004) pointed out that some exceptions exist to this general rule. For instance, the aquatic Asian box turtle (*Cuora amboinensis*) has highly domed shell and the terrestrial African pancake tortoise (*Malacochersus tornieri*) has a greatly flattened shell (Ernst & Barbour, 1989). Other commonly used indicator is the depositional environment. Although it is easy to discard marine habitat for turtles discovered in terrestrial sediments, turtles discovered in fluvial or marine sediments may be either aquatic or terrestrial because rivers can bury remains of terrestrial animals or transport them to marine environments (Joyce & Gauthier, 2004). In these cases, detailed taphonomic analysis is needed in order to infer the degree of transport undergone by turtle remains before burying. For instance, isolated plates with evident abrasion marks indicate long distance transport (Figure 6a), whereas articulated shells and lack of abrasion, scavenging and tramping marks suggest short biostratinomic history and little transport (Figure 6b, c) (Brand et al.,

2000; Bertini et al., 2006). In this latter example, the habitat of the fossil turtle can be inferred from the depositional setting (e.g. Marmi et al., 2009).
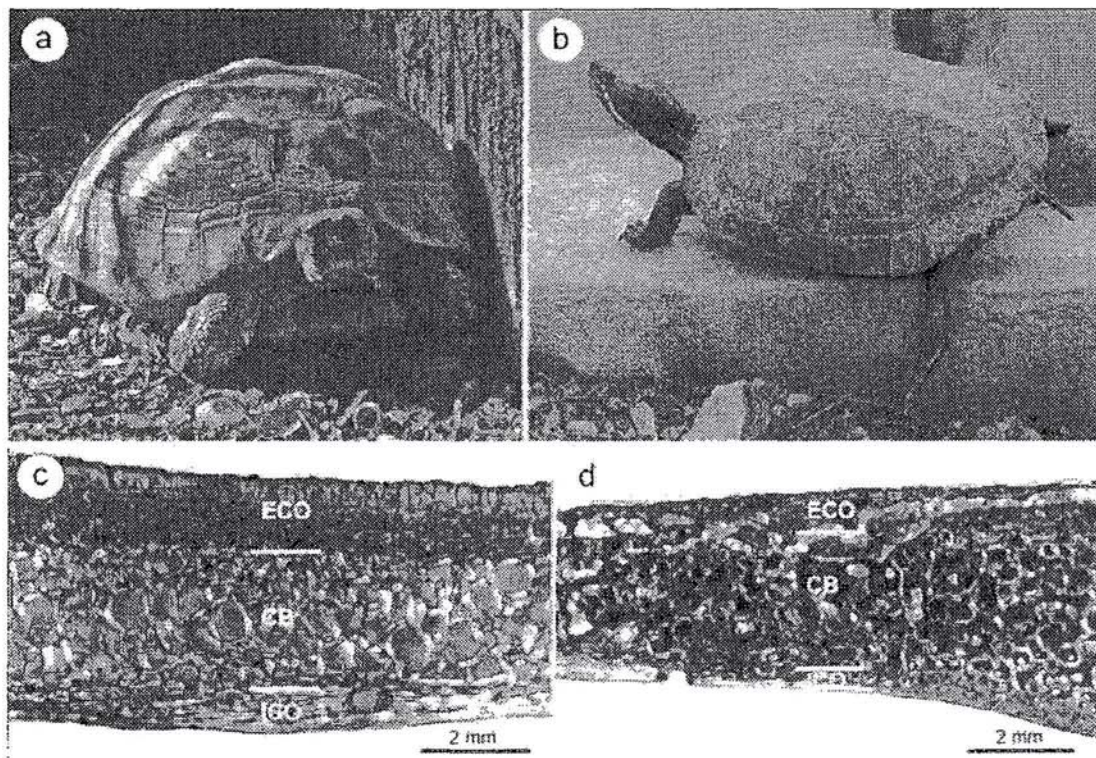

Figure 5. Adaptations to terrestrial and aquatic lifestyles: a, terrestrial *Testudo hermanni* with a moderate domed shaped carapace; b, semiaquatic *Trachemys scripta* with a flat shell; c, thin section of left xiphiplastron of *Testudo hermanni* showing wide and low vascularized external (ECO) and internal (ICO) cortices; d, thin section of a right xiphiplastron of *Trachemys scripta* with thin and highly vascularized external and internal cortices. The cancellous bone (CB) consists of short trabeculae and small to medium sized vascular spaces in both species. The pictures (a) and (b) have been taken at the Centre de Recuperació d'Amfibis i Rèptils de Catalunya (CRARC).

In living turtles, forelimbs usually reflect their lifestyle (Ernst & Barbour, 1989). Morphometric analysis of forelimbs revealed a close relationship between relative hand length and habitat preference (Joyce & Gauthier, 2004). Terrestrial turtles are short-handed to facilitate digital rollover during walking and highly aquatic turtles such as chelonioids are long-handed for swimming (Figure 7). However, after death, skull and limb bones separate from the body early and these elements are generally not preserved in fossil turtles (Brand et al., 2000; 2003). In these cases, histology provides an alternative way for testing the ecology of extinct turtles since the bone structure of the shell of living aquatic and terrestrial turtles reveal histological differences (Scheyer & Sander, 2007). Shell bones of terrestrial turtles exhibit a diploe structure with

well developed external and internal cortices, weak vascularization of the compact bone layers and dense interior cancellous bone with overall short traveculae (Figure 5c). On the contrary, aquatic turtles increase overall vascularization of the bone tissue reducing cortical bone layers and creating medium to large sized vascular spaces in the cancellous bone delimited by long and slender traveculae (Figure 5d). This pattern reported in aquatic turtles may be interpreted as an adaptation to aquatic environments in order to increase buoyancy. However, several exceptions of the general pattern exist, with terrestrial taxa showing moderate levels of vascularization (e.g. *Kinixys homeana* and *Chelonoidis carbonaria*) and aquatic taxa showing terrestrial-like bone microstructures (e.g. *Mauremys mutica* and *Pangshura tentoria*).
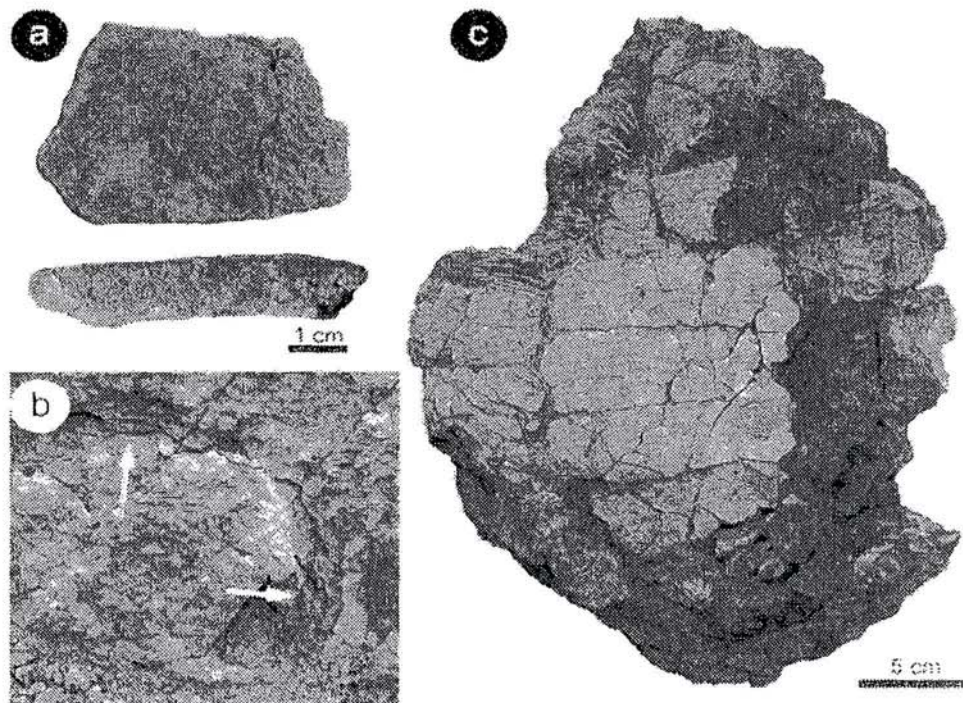
Figure 6. Different examples of preservation of turtle remains from the Late Cretaceous of Pyrenees: a. isolated plate with evident signs of abrasion in the external (top) and articulation (bottom) surfaces suggesting long distance transport (Barranc de Torrebilles site, Isona, southeastern Pyrenees); b. cast of a *Solemys* sp. carapace with remains of peripheral plates (arrowed) from Mina Esquirol site (Vallcebre, southeastern Pyrenees); c. partial shell of a bothremydid with carapace and plastron articulated from Barranc de Torrebilles site. Short transport or autochthony have been inferred for (b) and (c) and the depositional setting suggests that these extinct turtles inhabited lagoonal and fluvial environments, respectively (Marmi et al., 2009 and Marmi et al. under study). The pencil in (b) measures 14.6 cm.
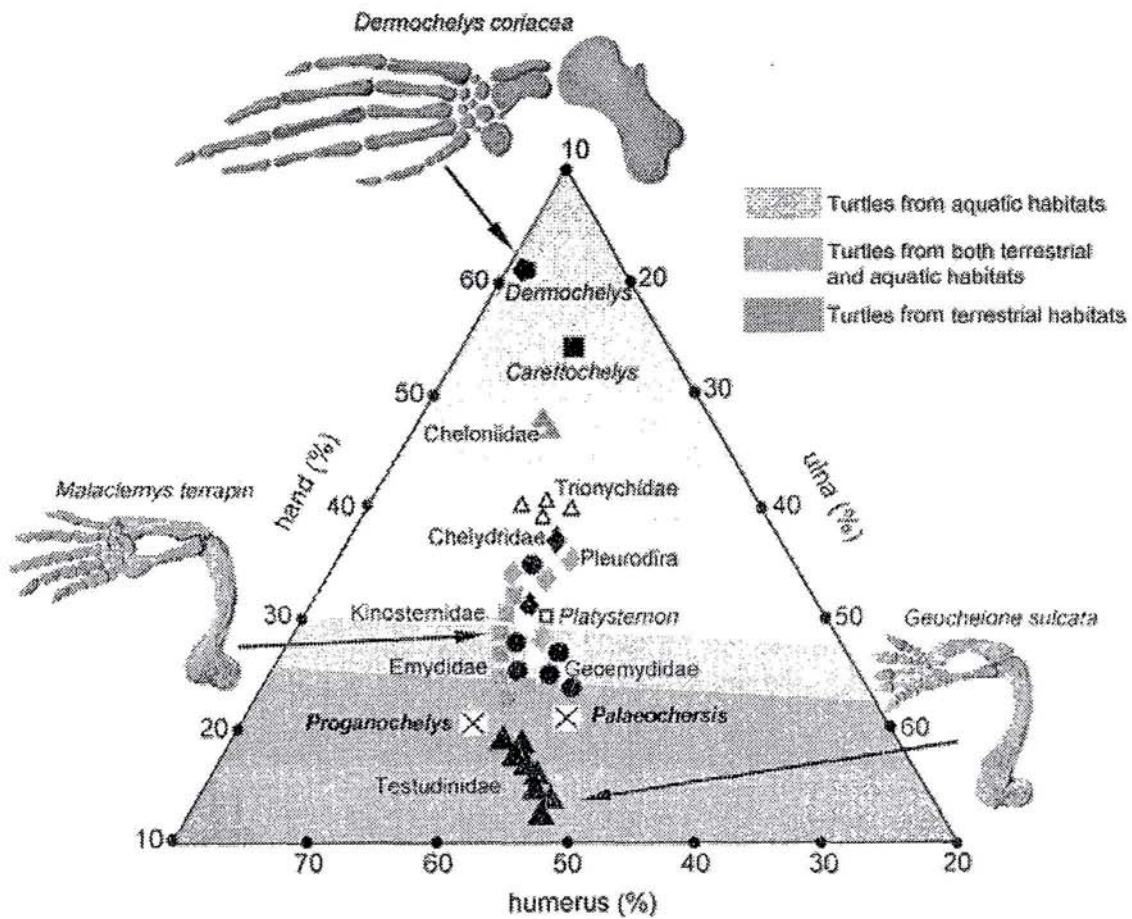
Figure 7. Distribution of taxa and habitat preferences on a ternary plot using forelimb measurements. There is large difference in hand sizes between specialized taxa such as marine *Dermochelys coriacea* and terrestrial *Geochelone sulcata*. Late Triassic turtles *Proganochelys* and *Palaeochersis* are included within the group of terrestrial taxa. Modified from Joyce & Gauthier (2004).

Gaffney (1990) suggested that *Proganochelys* inhabited freshwater as a bottom walker, being not exclusively aquatic or terrestrial, based on interpretations of the depositional environment and features of limb morphology. The analysis of forelimb proportion and depositional environment also indicate aquatic habits for *Odontochelys* and suggest a possible aquatic origin of turtles (Li et al., 2008). According to a recent phylogenetic analysis, stem turtles are closely related to the parareptile *Eunotosaurus* which lacks obvious aquatic adaptations and is only known from terrestrial sediments (Gow 1997; Lyson et al., 2010). In addition, forelimb proportions, shape of shell and histological data provide strong evidence for a terrestrial lifestyle in *Proganochelys* and *Palaeochersis* (Joyce & Gauthier, 2004; Scheyer & Sander, 2007). Thus, the putative marine ecology of *Odontochelys* might be interpreted as independently derived and

not ancestral to the subsequent radiation of turtles, supporting an origin of stem turtles in terrestrial environments (Lyson et al., 2010).

THE SCARCE JURASSIC FOSSIL RECORD AND THE ORIGINS OF CROWN TURTLES

The Jurassic is an outstanding period for understanding the evolution of turtles but their fossil record is fragmentary and sparse from the Late Triassic to the Late Jurassic, with only few known species spread around the world (Sterli, 2008 and references therein). However, as a whole, turtle remains have been collected from almost all continents —southern Africa, southern South America, North America, Europe, India and Central Asia (Sterli, 2008)— suggesting that chelonians were already distributed throughout the world. The Jurassic is also a key period to decipher the timing of the origin of crown groups of turtles (i.e. the clades delimited by living representatives). In this sense, two main hypotheses have been proposed (Figure 8).

The first hypothesis (Figure 8a) suggests that all turtles with the exception of *Proganochelys*, *Palaeochersis* and *Australochelys africanus*, from the Early Jurassic of South Africa, belong to one of the main groups of living turtles, Pleurodira or Cryptodira (Gaffney et al., 2007 and references therein). Based on this hypothesis, the crown turtles originated in the Late Triassic and *Proterochersis* would be interpreted as a stem pleurodire. On the contrary, other authors such as Joyce (2007) and Sterli (2008) interpret Late Triassic to Middle Jurassic turtles as stem groups suggesting that the origins of crown turtles were more recent, during the Middle to Late Jurassic (Figure 8b). According to Sterli & de la Fuente (2010) and references therein, Gaffney's hypothesis was supported by misleading interpretation of some key characters considered as synapomorphies of Pleurodira and Cryptodira. For instance, Gaffney (1975) includes the presence of a processus trochlearis oticum, a vertical flange on the transverse process of the pterygoid, and the presence of an epipterygoid among the synapomorphies that define Cryptodira. However, according to Joyce (2007) and Sterli & Joyce (2007) the former character may be a synapomophy of a more inclusive clade than Cryptodira and the two latter characters should be considered symplesiomorphies of turtles.
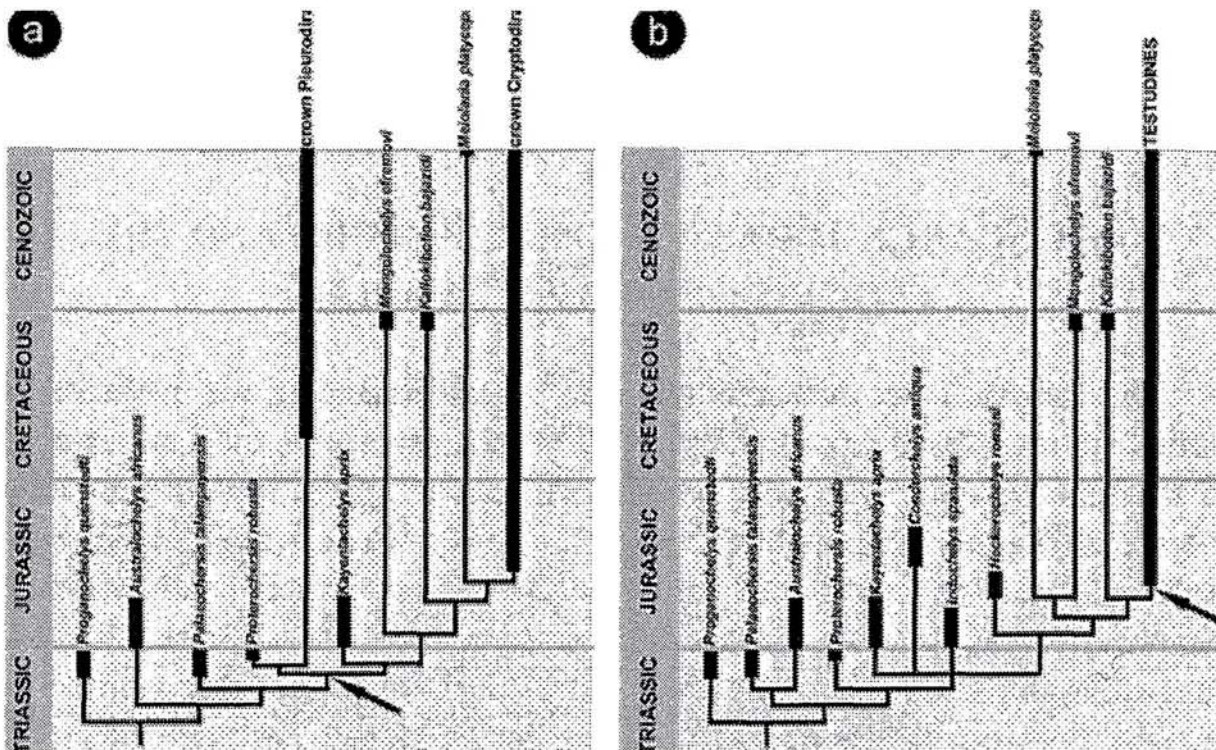
Figure 8. Two phylogenetic hypotheses about the origins of crown turtle taxa: a, lineages leading living turtles originated in the Late Triassic according to Gaffney et al. (2007); b, the origin of living turtle lineages occurred between the Middle and Late Jurassic, according to Joyce (2007) and Sterli (2008). Arrows indicate the crown group. Modified from Sterli & de la Fuente (2010).

ORIGINS AND DIVERSIFICATION OF PLEURODIRA

Extant pleurodires or "side necked turtles" are informally characterized by bending the neck in a horizontal plane (Gaffney et al., 2006). Nowadays, the lineage contains two major crown clades: Chelidae and Pelomedusoides that includes Pelomedusidae and Podocnemidae (Joyce et al., 2004). However, the extensive fossil record has revealed that pleurodires were significantly more complex and diverse in the past (Gaffney et al., 2006). Following Joyce et al. (2004) taxonomic proposal for turtles, only three Late Jurassic fossil species may be situated unambiguously along the phylogenetic stem of pleurodires: *Platychelys oberndoferi* from Europe, *Caribemys oxfordiensis* from Cuba, and *Notoemys laticentralis* from Argentina (de la Fuente & Iturralde-Vinent, 2001; Joyce et al., 2004). The large geographic distances among these three stem taxa indicate that the evolutionary history of the pleurodire lineage started in the Late Jurassic or even before.

The oldest representatives of living clades are reported since the Cretaceous. The clade Chelidae includes around 52 species of freshwater pleurodire turtles living in South America and Australasia that diversified in South Gondwana (Broin, 1988). Classically, the fossil record of this group was considered extremely poor and restricted to Tertiary (Joyce et al., 2004 and references therein). However, findings carried out in South America at the beginnings of 2000s have firmly established the presence of this crown clade in the Late Cretaceous. Thus, the oldest representatives of Chelidae are of Santonian (*Lomalatachelys*), Turonian-Campanian (*Bonapartemys* and *Prochelidella*) and Campanian-Maastrichtian (*Palaeophrynops* and *Yaminuechelys*) ages (De la Fuente et al., 2001; Lapparent de Broin & de la Fuente, 2001). However, Gaffney et al. (2006) recognizes this family since the Early Cretaceous.

Nowadays, Pelomedusidae are less diverse than Chelidae and contains eighteen living species (Joyce et al., 2004). The fossil record attributed to this group is scarce and rather confusing and specimens exhibit few diagnostic features (Joyce et al., 2004; Gaffney et al., 2006). *Teneremys lapparenti*, from the Aptian of Niger, is the only well recognized stem taxa of Pelomedusidae (Lapparent de Broin, 2000a). The crown clade is known at least since the Miocene (Lapparent de Broin, 2000b). According to Gaffney et al. (2006) the Podocnemidinura is sister of the extinct family Bothremydidae. Within the former, Podocnemidae are closely related to *Brasilemys* from the Albian of Brazil and *Hamadachelys* from the Cenomanian of Morocco. The crown taxa of Podocnemidae are recognized since the Late Cretaceous (Joyce et al., 2004). At present, Podocnemidae include eight living species.

ORIGINS AND DIVERSIFICATION OF CRYPTODIRA

Cryptodira is a morphologically diverse clade of turtles that differs from Pleurodira in the manner that retracts their head into the shell, bending their neck in a vertical plane to withdraw the head backwards. Thus, the majority of Cryptodira can put the head straight back into the shell, with some exceptions such as sea turtles or *Platysternon megacephalum*. Nowadays, the Cryptodira is the most extensive and rich group of Testudines that informally includes freshwater turtles, bigheaded turtles, Central American river turtles, pig noise turtles, snapping turtles, mud and musk turtles, box and wood turtles, tortoises, soft shell turtles, and sea turtles. The oldest taxa primitively inhabited

freshwater habitats, but later invaded marine environments at least once and at least four independent lineages diversified in fully terrestrial habitats (Joyce & Gauthier, 2004). Nowadays, the lineage contains eleven clades that can be grouped into four or five major crown clades: Chelonioidea, Trionychoidea, Chelydridae, Kinosternoidea and Cryptoderinea (Joyce et al., 2004; Barley et al., 2010). Although, the fossil record is extensive and fairly complete, the debate about the phylogenetic affinities of extinct Cryptodira with the major crown clades remains still open and further analyses are needed (Gaffney et al., 1987; Gaffney & Meylan, 1988; Joyce et al., 2004; Danilov & Parham, 2006; Anquetin et al., 2009; Joyce et al., 2009).

According to recent hypotheses, the phylogenetic stem of Cryptodira contains a series of common fossil taxa, such as Baenidae, Meiolanidae, Pleurosternidae, Plesiochelydiae, Sinemydidae, and Macrobaenidae (Gaffney, 1996; Gaffney et al., 1998; Parham & Hutchison, 2003; Joyce et al., 2004). However, other analyses suggest that most of these groups diverged before the diversification of Testudines (Sterli, 2010). Following Gaffney et al. (1987), only *Kayentachelys aprix* from the Early Jurassic of North America, may be situated unambiguously along the phylogenetic stem of Cryptodira, taking into account the following characters: presence of the processus trochlearis oticum and processus pterygoideus externus projecting posteriorly with a flat, vertical plate. Nevertheless, other authors propose Sinochelydae, from the Early Cretaceous of China and Mongolia, as the oldest reported Cryptodira based on characteristics of the shell (Hirayama et al., 2000).

Nowadays, the clade Chelonioidea includes seven or eight species of sea turtles belonging to Dermochelyidae and Cheloniidae. All species of this group are characterized by hard-shelled bodies, except for *Dermochelys coriacea* that is covered with horny scutes. The extensive fossil record has revealed that Chelonioidea was more abundant and diverse in the past, including several extinct families, such as Toxochelyidae, Osteopygidae, Thalassemyidae and Protostegidae (e.g. Gaffney et al., 2006). This last family of sea turtles contains the probable oldest representative of the living clade, *Santanachelys gaffneyi* from the Early Cretaceous of Brazil (Hirayama, 1998). This species had a primitive flipper that still possessed movable digits and a specialized skull with large interorbital foramina (Hirayama, 1998). As no other turtles are known from the phylogenetic stem, *Santanachelys gaffneyi* may also represent the oldest Chelonioidea (Joyce et al., 2004). However, it is important to note that new phylogenetic analyses place *Santanacheys* out of the Testudine clade (Sterli, 2010). The oldest remains of dermochelyids are

reported from the Campanian of North America and Japan (Joyce et al., 2004 and references therein) and *Toxochelys latiremys*, from the Late Cretaceous of North America, may be among the oldest stem cheloniids (Hirayama, 1998).

Trionychia is the sister taxa of different basal forms from the Early Cretaceous such as Adocidae and Nanhsiungchelyidae (Danilov & Parham, 2006). According to these authors, *Yehguia tatsunensis*, from the Late Jurassic of China, is placed on the stem of Trionychia, near the clades Adocidae and Nanhsiungchelyidae. Among the list of potential trionychians, *Sandownia harrisi* from the Early Cretaceous (Aptian) of Europe may be the oldest (Meylan et al., 2000). The crown clade Trionychia comprises the families Trionychidae and Carettochelyidae, informally called softshell and pig nosed turtles. The fossil record of the Carettochelyidae was well represented in the Tertiary period but actually only persists a single species, *Carettochelys insculptata*. The oldest representative of Carettochelyidae is *Kizylkumemys schultzi* from the middle Cretaceous (Albian and Cenomanian) of Central Asia (Nessov, 1977; Meylan, 1988). Trionychidae contains 23 especies of living softh-shelled turtles but has a poor fossil record. Despite this, the oldest hypothesized representatives of the trionychid clade are *Trionyx riabinin* and *"Trionyx" kansaiensis*, both reported from the Late Cretaceous (Santonian-early Campanian) of Asia and Kazakhstan (Vitek & Danilov, 2010), and *Aspideretoides allani, A. foveatus, A. splendidus* and *Apalone latus* from the Late Cretaceous (middle Campanian) of North America (Gardner et al., 1995).

Phylogenetic relationships among Kinosternoidea and other clades of cryptodires are unclear. Joyce et al. (2004) places Kinosternoidea within Trionychoidea, following Gaffney (1975). On the contrary, new molecular data supports a deep sister group relationship between Kinosternoidea and Chelydridae (Barley et al., 2010). The sister group relationship between *Dermatemys mawii* and Kinosternidae was only proposed within the last two decades, but currently it is strongly supported by morphological and molecular data (e.g., Gaffney & Meylan, 1988; Hutchison, 1991; Shaffer et al., 1997; Sterli, 2010). The oldest representatives along the stem lineage of *Dermatemys mawii* are *Haplochelys clark* and *Agomphus pectoralis* both from the Late Cretaceous (Maastrichtian) of North America (Knauss et al., 2010). This phylogenetic placement breaks with the tradition started by Hutchison & Bramble (1981), which suggest that *Agomphus* spp. is a stem-kinosternoid and *Hoplochelys* spp. is a representative of the kinosternid stem (Hutchison, 1991; Meylan & Gaffney, 1989; Joyce, 2007). The genus *Baptemys*, from the Eocene of North America, has been allied to *Dermatemys mawii* within

Dermatemydidae (Knauss, 2006). On the other hand, the oldest putative members of stem kinosternidae may be some undescribed remains from the Campanian of North America (Hutchison et al., 1998).

Taxonomic composition of Chelydridae and its relationships with remaining clades within Cryptodira are also still under debate. This family of turtles has a long fossil history from North America, Asia and Europe, far outside its present range. According to Eaton et al. (1999a, 1999b), the oldest crown chelydrid is *Protochelydra zangerli* from the Eocene of North Dakota and the oldest stem chelydrid is *Emarginachelys cretacea* from the Late Cretaceous (Turonian) of Montana. Following to Knauss et al., (2010), *Baltemys staurogastros, Xenochelys formosa* and *X. lostcabinensis,* from the Early Eocene of Wyoming, also belong to the crown clade Chelydridae. However, previous works placed *Baltemys* and *Xenochelys* within crown Kinosternidae (Joyce et al., 2004).

The crown clade Cryptoderinea contains *Platysternon megacephalum* and the crown taxa Testudinoidea (Joyce et al., 2004). *Platysternon megacephalum* is an extant freshwater turtle from Asia that forms a monotypic lineage sister to the Testudinoidea (Joyce et al., 2004; Krenz et al., 2005; Sterli, 2010). The fossil record of the *Platysternon* lineage is very fragmentary, with few and partial specimens coming from the Paleocene and Oligocene of Kazakhstan (Joyce et al., 2004 and references therein). Testudinoidea contains three major clades, Testudinidae, Emydidae and Geoemydidae called informally land tortoises and generally pond turtles. In addition to the last principal crown groups, Testudinoidea includes different basal families from the Cretaceous of Asia such as Haichemydidae, Sinochelyidae and Lindholmemydidae because of the development of an ossified bridge connecting the plastron with the carapace (Sukhanov, 2000; Danilov & Sukhanov, 2001).

The crow Testudinidae is represented by 43 extant species characterized by exclusive terrestrial habitats. This clade has an excellent fossil record but the majority of the basal forms, such as *Hadrianus, Stylemys, Manouria, Cheirogaster, Ergilemys* and others, lack skulls making phylogenetic analyses difficult. The oldest representatives are *Hadrianus majuscula* from the Early Eocene (Wasatchian) of New Mexico and *Achilemys cassouleti* from the Early Eocene (Ypresian) of France.

The crow Geoemydidae contains 61 species of freshwater, swamp, lagoon and humid environment turtles living in all the continents except to Australia and Antarctica.

Table 1. Conservation status of living turtles according to the International Union for Conservation of Nature (IUCN) database (IUCN, 2010). Numbers in parenthesis indicate the number of species within each turtle family. Remaining numbers are the number of species per genus classified within each threat category: CE, critically endangered; E, endangered; V, vulnerable; LR/NT, lower risk/near threatened; LR/LC, lower risk/least concern; DD, data deficient; NL, not listed in the IUCN Red List. The taxonomy of genera follows Joyce et al. (2004) appendixes

Major taxa	Genus	IUCN threat category						
		CE	E	V	LR/NT	LR/LC	DD	NL
Pleurodira								
Chelidae (52)	*Acanthochelys*			1	3			5
	Batrachemys	1						5
	Chelodina	1	1	1	3	2		1
	Chelus							1
	Elseya		1	1		1	2	3
	Elusor		1					
	Emydura					1		4
	Hydromedusa			1				1
	Mesoclemmys			1				1
	*Phynops**		1		2			4
	Platemys							1
	Pseudemydura	1						
	Rheodytes			1				
Pelomedusidae (17)	*Pelomedusa*							1
	Pelusios			1		3	1	11
Podocnemidae (8)	*Erymnochelys*	1						
	Podocnemis		1	3	1			1
	Peltocephalus			1				

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Table 1 (Continued)

Major taxa	Genus	IUCN threat category						
		CE	E	V	LR/NT	LR/LC	DD	NL
Cryptodira								
Dermatemydidae (1)	*Dermatemys*	1						
Kinosternidae (25)	*Claudius*				1			
	Kinosternon			4	2	6	3	3
	Staurotypus				2			
	Sternotherus			1			3	3
Trionychidae (24)	*Amyda*			1				
	Apalone					2		1
	Aspideretes			3				
	Chitra	1	1					
	Cyclanorbis				2			
	Cycloderma				2			
	Dogania					1		
	Lissemys					1	1	
	Nilssonia		1					
	Palea		1					
	Pelochelys		1	1				
	Pelodiscus			1				
	Rafetus	1	1					
	Trionyx							1
Carettochelyidae (1)	*Carettochelys*			1				
Chelydridae (3)	*Chelydra*			1		1		
	Macroclemys			1				
Dermochelyidae (1)	*Dermochelys*	1						
Cheloniidae (6)	*Caretta*		1					

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Major taxa	Genus	IUCN threat category						
		CE	E	V	LR/NT	LR/LC	DD	NL
	Chelonia	1	1					
	Eretmochelys	1						1
	Lepidochelys	1		1				1
	Natator						1	
Platysternidae (1)	*Platysternon*		1					
Testudinidae (43)	*Chersina*							1
	Dipsochelys							1
	*Geochelone***	3		6		1		1
	Gopherus			3		1		
	Homopus			1	1			3
	Indotestudo		2	1				
	Kinixys			1	1		1	2
	Malacochersus			1				
	Manouria		1	1	1			
	Psammobates		1	1				2
	Pyxis	2						
	Testudo	1		2	1	1		
Geoemydidae (61)	*Batagur*	2						
	Cuora	8	2	1				
	Cyclemys			1	1			3
	Geoclemys			1				
	*Geoemyda****		3		1			
	Hardella			1				
	Heosemys	2	1	1				
	Hieremys		1					
	Kachuga	1	2					

Table 1 (Continued)

Major taxa	Genus	IUCN threat category						
		CE	E	V	LR/NT	LR/LC	DD	NL
	Leucocephalon	1						
	Malayemys			1				
	Mauremys	1	3		1			2
	Melanochelys			1	1			
	Morenia			2				
	Notochelys			1				
	Orlitia		1					
	Pangshura		1		1			
	Rhinoclemmys				5	2		4
	Sacalia		2					
	Siebenrockiella			1	1			
Emydidae (48)	*Actinemys*			1	1			1
	Chrysemys							
	Clemmys			1				
	Deirochelys							1
	Emyoidea				1			
	Emys				1		1	
	Glyptemys		1	1				
	Graptemys		2	1	5			4
	Malaclemys				1			
	Pseudemys		1		2			4
	Terrapene		1		2		1	
	Trachemys		2	5	3			5

*, Includes genus *Rhinemys*

**, Includes genera *Astrochelys*, *Centrochelys* and *Chelonoidis*.

***, Includes genus *Vijayachelys*.

This group of turtles, informally called Eurasian pond, river turtles and Neotropical wood turtles, comprises a significant portion of the diversity of extant turtles and the major number of freshwater species. Nowadays, the oldest representative of geoemydids probably is *Echmatemys* ssp. from the Eocene of North America and Asia (Hirayama, 1985). Other undefined stem geoemydids are known from the Paleocene to Oligocene of various North American, Asian and probably European sites. Moreover, some basal taxa such as *Grayemy-Hokouchelys*, *Clemmydopsis*, *Epiemys* and *Elkemys* have been attributed to Geoemydidae but phylogenetic relationships among these taxa and extant forms are unclear (Mlynarsky, 1976).

The crow Emydidae contains 48 species of extant turtles most of which living in the New World, with the exception of *Emys orbicularis* from Europe, north Africa and western Asia. This group of turtles, informally called pond turtles, developed diverse ecological strategies and colonized a wide range of environments, from aquatic to fully terrestrial habitats. Nowadays, the oldest fossil emydid is *Gyremys sectabilis* from the Late Cretaceous of Judith River Formation of Montana, North America (Ernst & Barbour, 1989). Traditionally, a number of fossils have been associated (Mlynarsky, 1976) with this group but none has been integrated into a cladistic analysis and consequently cannot be referred with any confidence to Emydidae (Joyce et al., 2004). Recently, phylogenetic analyses have been carried out to clarify the phylogeny of some primitive forms, such as *Hummelemys, Palaeochelys, Juvemys, Merovemys* and others (Hervet, 2004). However, results do not elucidate their relationships with the Geoemydidae and Emydidae stem.

AN OVERVIEW OF THE TURTLE THREATENED PHYLOGENETIC DIVERSITY

Posadas et al. (2001) highlighted the fact that conservation of biodiversity requires the knowledge of its history. Phylogenies provide the ways to measure biodiversity, to quantify the evolutionary history of a set of species and to assess conservation priorities (Mace et al., 2003). Despite the large number of the recently published papers, key questions about the origins and evolutionary history of turtles remain unanswered, as it has been explained in the above paragraphs. Phylogenetic analyses have not resolved satisfactorily if turtles are sister to parareptiles (e.g. Lyson et al., 2010) or diapsids (e.g. Shedlock et al.,

2007). The Jurassic turtle fossil record is fragmentary and sparse making the understanding of the origins of extant lineages difficult (see Sterli, 2008). The phylogenetic relationships of extant Testudines are also unclear, with controversial results about the placement of Pleurodires (see Sterli, 2010 for an example) and other major lineages such as Chelonioidea, Kinosternoidea and Chelydridae (Barley et al., 2010 and references therein) in the tree of life of turtles. Some factors can explain disagreement in phylogenetic analyses carried out with different source of data (e.g. fossil evidence, morphology, DNA sequences). Firstly, morphological variation of turtles is still poorly understood from an evolutionary point of view. This is enhanced by large gaps in their fossil record, especially in key periods such as Jurassic, Cretaceous and Paleocene. Moreover, fossil turtles usually lack parts of the skeleton with characters of great systematic value (e.g. skulls). On the other hand, molecular trees show short internal branches, often weakly supported, and long terminal branches suggesting a rapid radiation of the living groups of turtles since the Late Jurassic (Sterli, 2010, but see Barley et al., 2010). This complicates the determination of interrelationships and the position of the root of major lineages of extant turtles.

Despite this bleak picture, we have estimated the amount of threatened phylogenetic diversity of turtles based, in part, on the results reported by Sterli (2010) and data from IUCN (2010) red list (Table 1, Figure 9). However, due the large disagreement among current studies, relationships among largest clades of living turtles are represented as a polytomy, especially within Cryptodira. Most of living major lineages of turtles are recognized in the fossil record since the Middle-Late Cretaceous (Figure 9). Only three of fourteen living lineages can be considered slightly endangered, two within Pleurodira (Chelidae and Pelomedusidae) and one within Cryptodira (Kinosternidae), containing 25% or less threatened species (Figure 9). At the opposite end, Podocnemidae, Carettochelyidae, Dermochelyidae, Cheloniidae, Dermatemydidae and Platysternidae are at high risk of extinction with 75% or more species threatened. The status is critical for Dermochelyidae, Dermatemydidae and Platysternidae because they are represented by a single species classified as endangered or critically endangered (Table 1).

This overview of the conservation status of the turtle tree of life clearly shows that most of the phylogenetic diversity generated during 90 million of years or more is in a real risk of extinction and the situation is extreme for an important number of lineages. Turtles agree with the prediction of Purvis et al. (2000) in that species on long branches (i.e. without close relatives) are particularly likely to be at risk.
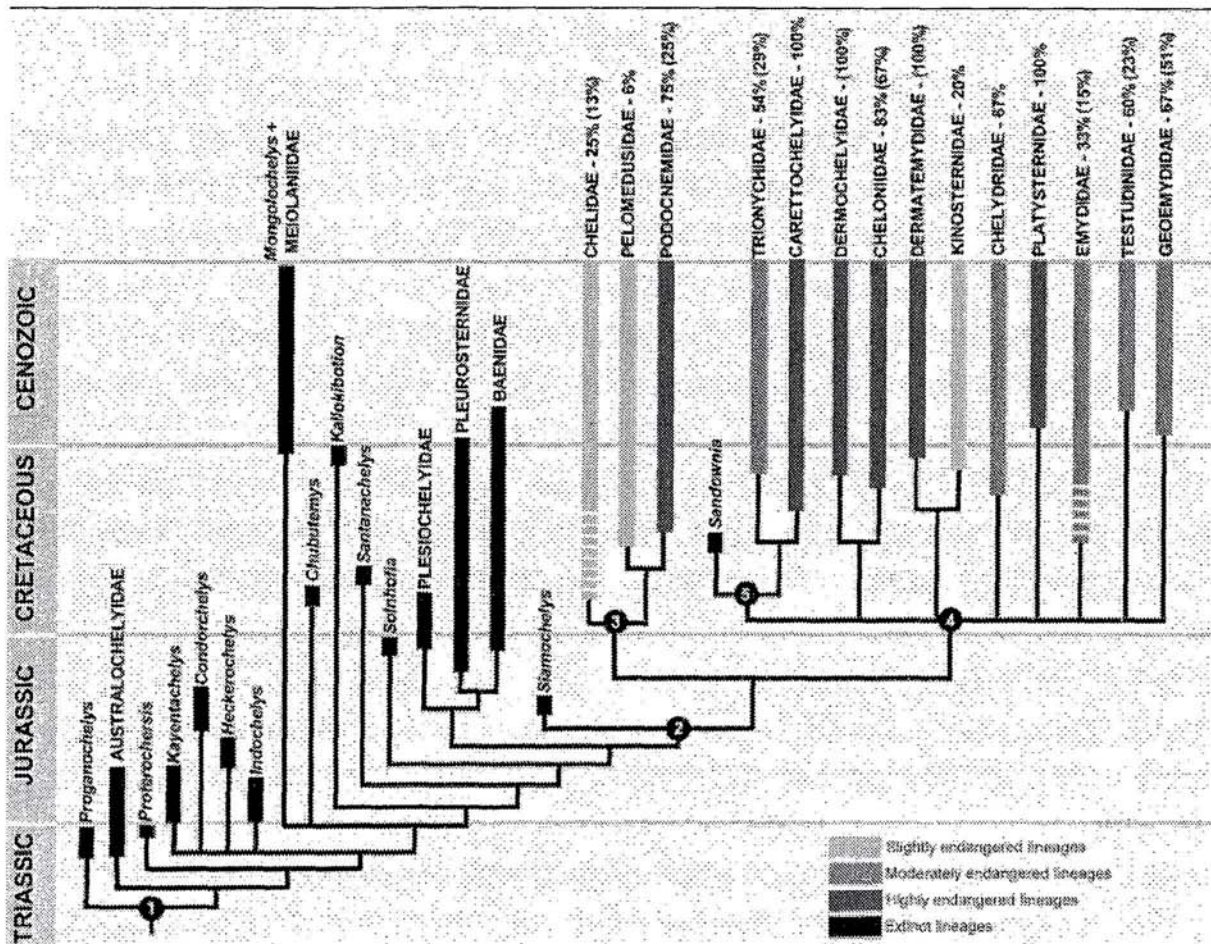
Figure 9. Evolutionary tree of turtles with phylogenetic relationships of stem taxa based on Sterli (2010). Phylogenetic relationships within Testudines (node 2) are not clarified because the lack of consensus among different authors (see text for details). The percentage of threatened species (vulnerable, endangered and critically endangered—see Table 1) is shown for each lineage. Percentages of endangered plus critically endangered species are within parenthesis. A quantification of the risk of lineage extinction is indicated based on Table 1: slightly endangered lineages (25% or less of species threatened), moderately endangered lineages (between 25% and 75% of species threatened), highly endangered lineages (75% or more of species threatened). Numbers in nodes mean: 1, Testudinata; 2, Testudines; 3, Pleurodira; 4, Cryptodira; 5, Trionychia.

Moreover, according to these authors, fossil record demonstrates that some clades (e.g. Pleurodira, Chelonioidea) were more diverse in the past and probably have suffered considerable extinction through geological time due to unknown phylogenetic factors promoting a greater risk of extinction for these lineages.

Nee & May (1997) noted that the importance assigned to a species is not necessarily proportional to the amount of evolutionary history it represents. For instance, conservation concern is often focused on their behavior, potential usefulness or their role in an ecosystem rather than simply on overall measures of evolutionary history. Moreover, from a systematic perspective, there has been

debate on what may be a greater loss: the demise of the sole survivor of an ancient lineage (for instance, the Central American river turtle, *Dermatemys mawii*) or the demise of a member of a rich species flock (for instance, the Roti Island snake-necked turtle, *Chelodina mccordi*) (Nee & May, 1997). Distinct taxa and 'living fossils' contribute disproportionately to overall biodiversity because the large amount of evolutionary history that may represent (Bowen, 1999). However, other authors have argued that these 'sole survivors' are a dead-end and conservation efforts should be focused on the species flock because its future evolutionary potential to restock biodiversity if a mass extinction episode occurs (Erwin, 1991). According to Bowen (1999), the leatherback sea turtle (*Dermochelys coriacea*) may illustrate the complexity of the decision making in conservation biology and that several perspectives (systematic, ecological and evolutionary) should be taken into account. This critically endangered species is the last survivor of a lineage that traces back to the Late Cretaceous or before. Thus it has a high relevance from the systematic point of view. In addition, it has a remarkable ecological and evolutionary significance because it is one of the few vertebrates that feeds on jellyfish (Scyphozoa) and has a suite of unique morphological and physiological adaptations allowing it to forage in freezing waters (Bowen, 1999).

This study demonstrates that the future of turtles is uncertain if no effective conservation measures are carried out. Turtles represent an exclusive group of reptiles and amniotes because their peculiar body plane and long evolutionary history, traced back since at least 225 million years ago, that justifies conservation efforts. Moreover, most endangered species of turtles inhabit aquatic environments. Their conservation may guarantee the conservation of fragile habitats such as rivers and wetlands that frequently suffer the impact of human activities.

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