

Palaeoecology of Triassic stem turtles sheds new light on turtle origins

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Competing hypotheses of early turtle evolution contrast sharply in implying very different ecological settings—aquatic versus terrestrial—for the origin of turtles. We investigate the palaeoecology of extinct turtles by first demonstrating that the forelimbs of extant turtles faithfully reflect habitat preferences, with short-handed turtles being terrestrial and long-handed turtles being aquatic. We apply this metric to the two successive outgroups to all living turtles with forelimbs preserved, *Proganochelys quenstedti* and *Palaeochersis talampayensis*, to discover that these earliest turtle outgroups were decidedly terrestrial. We then plot the observed distribution of aquatic versus terrestrial habits among living turtles onto their hypothesized phylogenies. Both lines of evidence indicate that although the common ancestor of all living turtles was aquatic, the earliest turtles clearly lived in a terrestrial environment. Additional anatomical and sedimentological evidence favours these conclusions. The freshwater aquatic habitat preference so characteristic of living turtles cannot, consequently, be taken as positive evidence for an aquatic origin of turtles, but must rather be considered a convergence relative to other aquatic amniotes, including the marine sauropterygians to which turtles have sometimes been allied.

Keywords: Testudines; *Proganochelys quenstedti*; *Palaeochersis talampayensis*; ancestral states; evolution; importance of fossils

1. INTRODUCTION

Although widely regarded as ‘primitive’, turtles display some of the most derived morphologies known among extant amniotes, thus obscuring their phylogenetic relations within that clade. Traditionally, turtles were regarded as living ‘stem’ amniotes (e.g. Zittel 1889; Williston 1917; Romer 1956; Parsons 1967) or, in cladistic terms, they were proposed to be sister to all other living amniotes (Gaffney 1980). More recently, however, the discussion has focused on their placement within a monophyletic reptilian clade (Gauthier *et al.* 1988a,b; Reisz & Laurin 1991; Lee 1994, 1995, 1996, 1997; Laurin & Reisz 1995). Based on molecular sequence data, virtually all possible relationships within Amniota have been proposed for turtles during the past decade, depending on the DNA sequences studied, taxa included and the methods of analysis. It has been suggested, for example, that turtles are the sister of Thecodontia (Mammalia + Archosauria; Gardiner 1993), Sauria (i.e. crown diapsids; Caspers *et al.* 1996), Lepidosauria (Hedges 1994; Zardoya & Meyer 2000), Archosauria (Platz & Conlon 1997; Kumazawa & Nishida 1999), Crocodylia (McJilton & Reeder 1999), *Sphenodon punctatus* (Fushitani *et al.* 1996) or even Aves (Pollock *et al.* 2000). Given the enormous importance of taxon sampling in phylogenetic inference (Hillis *et al.* 2003), estimating deep divergences based upon molecular (especially mtDNA) data alone could be problematic as only a tiny fraction of all the amniotes that have ever lived will ever be sampled using molecular techniques (Gauthier *et al.* 1989).

According to the two most prominent hypotheses based on extensive data from both extinct and extant amniotes, turtles are either part of a clade of basal terrestrial ‘anapsid’ reptiles (*sensu* Gauthier 1994), related specifically to pareiasaurs (Gregory 1946; Lee 1995, 1997) or procolophonoids (Reisz & Laurin 1991; Laurin & Reisz 1995), or they are the sister to sauropterygians (deBraga & Rieppel 1997), a clade of highly modified, aquatic saurian reptiles. The purported ecology of the ancestral turtle lineage has also been used to assess the plausibility of the competing hypotheses, which imply either a terrestrial or an aquatic origin for turtles (Lee 1996; Rieppel & Reisz 1999). Because the common ancestor of all crown turtles (*sensu* de Queiroz & Gauthier 1990) was clearly aquatic (see below), a key issue is the uncertain ecology of their closest extinct relatives, *Proganochelys quenstedti* and *Palaeochersis talampayensis* from the Upper Triassic of Germany and Argentina, respectively.

Assessing the ecology of extinct turtles has proven problematic because of imperfect correlations between the habitats of living turtles and such commonly used indicators as shell morphology and depositional environment (Gaffney *et al.* 1987; Lucas *et al.* 2000). For instance, although highly domed shells often correlate with terrestrial habits, that is by no means always the case, as demonstrated by the highly domed aquatic Asian box turtle *Cuora amboinensis* or the greatly flattened terrestrial African pancake tortoise *Malacochersus tornieri* (Ernst & Barbour 1989). Similarly, although it is plausible to infer that a turtle discovered in terrestrial sediments is not marine, it does not follow that a turtle found in fluvial or marine sediments cannot be of terrestrial origin, as rivers can bury terrestrial faunas or transport them to marine environments. It is well known that the forelimbs of living

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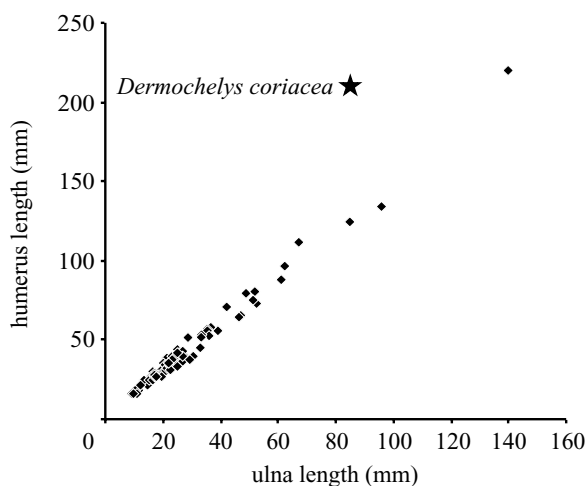


Figure 1. Correlation between the length of the humerus and the ulna in living turtles. Note that *Dermochelys coriacea* is the only turtle that deviates significantly from this relationship.

turtles generally reflect their ecology (Pritchard 1979; Ernst & Barbour 1989), but this relationship has never been quantified and applied to the fossil record. Previous analysis of the cryptodiran hindlimb proved inconclusive (Zug 1971). We therefore performed a morphometric analysis of the forelimbs of living turtles to test explicitly for a relationship between hand morphology and habitat preference.

2. MATERIAL AND METHODS

Measurements were obtained from the literature for the fossil stem turtles *P. quenstedti* and *P. talampayensis* and directly from 77 skeletons representing 71 species of extant turtles—ca. 25% of their total species diversity—selected so as to ensure estimation of ancestral conditions for all major clades. Measurements include the length of the humerus from the anterior (preaxial) process to the distal articular surface; the total length of the ulna along its lateral margin; and, from the hand, the combined length of metatarsal III and digit III, excluding the keratinous claw. This set of measurements was chosen primarily to enable the use of articulated skeletons. Measurements less than 5 cm were taken to the decimal point; greater lengths were rounded to the nearest millimetre. Habitat preferences of living turtles were obtained from the literature (Pritchard 1979; Ernst & Barbour 1989) and coded in six states. See electronic Appendix A (available on The Royal Society's Publications Web site) for primary data.

3. RESULTS AND DISCUSSION

We discovered that the length of the humerus and ulna are correlated in all turtles examined (figure 1). The humerus is, on average, 1.56 times longer than the ulna, while the full range of observed values is between 1.29 and 1.80 for individuals of *Kinixys homeana* and *Emydoidea* (or *Emys*) *blandingii*, respectively. The marine turtle *Dermochelys coriacea* is the only living turtle that does not exhibit this relationship ($p < 0.001$ that *D. coriacea* is part of the same population), its humerus being about 2.5 times longer than its ulna. We also found that relative hand

length varies enormously and is independent of either humerus or ulna length (figure 2a). For instance, the hand represents only 12% of the total forelimb length in the terrestrial tortoise *Geochelone radiata*, but 61% in the marine turtle *D. coriacea*. Limb ratios of different-sized individuals of three species with different habitat preferences—*Apalone spinifera*, *Chelydra serpentina* and *Terrapene ornata*—exhibit no marked differences, thus excluding size and/or ontogeny as potential sources of bias. Most significantly, relative hand length and habitat preference appear closely coupled in living turtles (figure 2b). There are clear phylogenetic signals in these data (Felsenstein 1985)—all testudinids are short-handed and terrestrial and all chelonoids are long-handed and aquatic—but it is striking that most clades cover a wide range of habitats and morphospace. For example, at least four turtle lineages invaded terrestrial habitats independently of one another according to current molecular and morphologic phylogenies (Gaffney & Meylan 1988; McCord *et al.* 2000; Feldman & Parham 2002). These clades include not only the archetypal terrestrial tortoises (Testudinidae), but also *Cuora* (Asian box turtles), *Rhinoclemmys* (Central American pond and wood turtles) and *Terrapene* (North American box turtles), among the 'pond turtles'. We find it particularly significant that all four terrestrial clades also exhibit shorter hands compared with their more aquatic relatives (figure 1b), supporting the idea that this relationship is neither purely historical nor accidental, but rather causal in nature.

This correlation probably reflects divergent selective forces that favour shorter hands in terrestrial environments to facilitate digital rollover during walking, and increasingly longer hands in aquatic environments for swimming. Interestingly, this correlation is not as tight in the hindlimb, perhaps because turtle feet point outward through much of the step cycle (Zug 1971), in contrast to turtle hands, which always point forward when in contact with the ground.

Although a full gradation exists in habitat preferences of living turtles, most species can readily be assigned to either terrestrial or aquatic categories, with some taxa in an 'intermediate' zone (figure 2b). It is important to note that our use of 'terrestrial' and 'aquatic' does not imply an inability to function in a different environment or even a mandatory aversion to the opposing medium, but should rather be taken as abbreviations for 'adapted to weight-bearing locomotion on land' versus 'adapted to effective swimming in water'. Naturally, both adaptive categories in themselves exhibit gradations that reflect changes in ecology relative to hand length. For instance, relatively short-handed aquatic turtles are typically adapted to restricted or slow-moving bodies of water, whereas progressively longer-handed aquatic turtles are adapted to increasingly stronger currents or larger bodies of water. Interestingly, aquatic 'bottom walkers' such as musk turtles (Kinosternidae) and snapping turtles (Chelydridae) exhibit hand lengths that have no resemblance to terrestrial weight-bearing walkers, but instead closely reflect their aquatic habitat preference.

This metric thus provides a powerful tool for assessing the palaeoecology of ancient turtles. Fossils that exhibit limb proportions similar to those of modern aquatic or terrestrial turtles can confidently be assigned to these

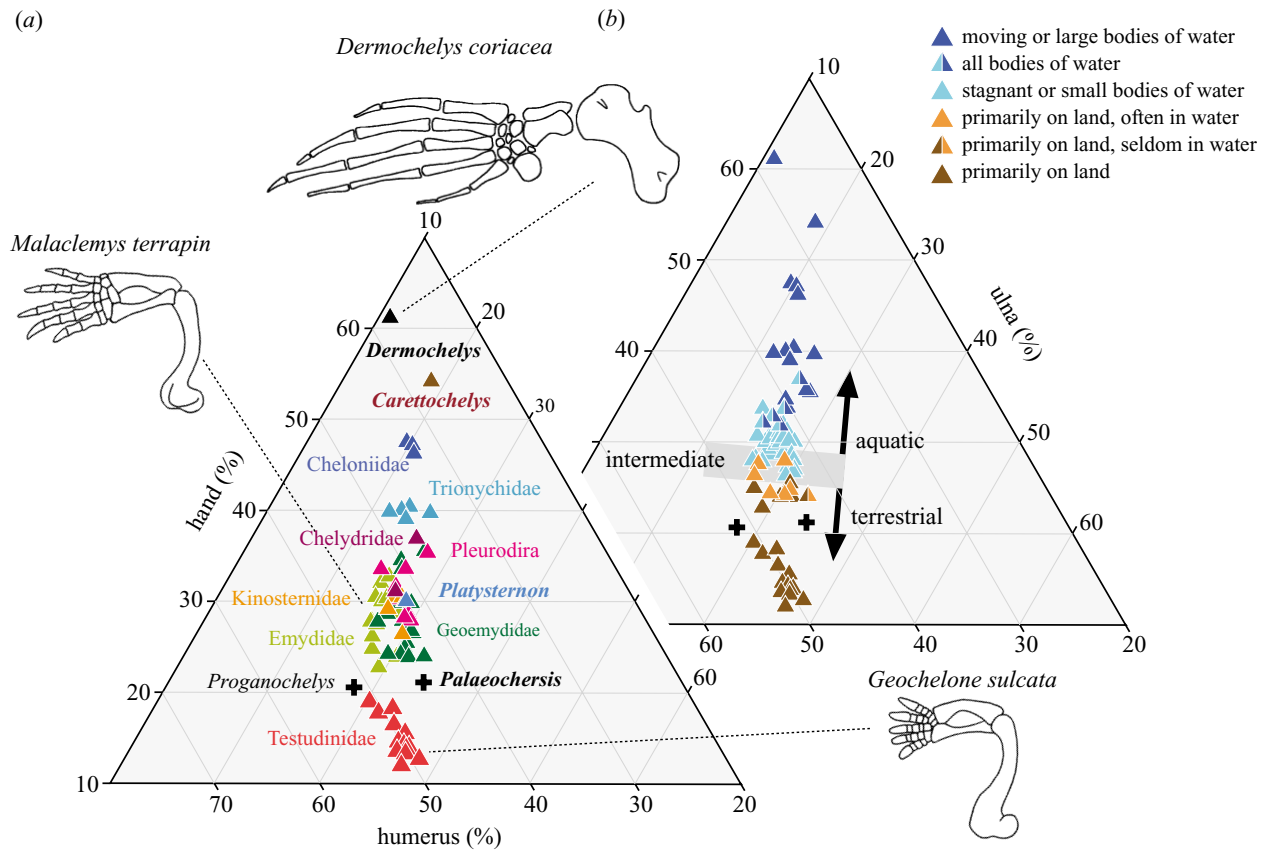


Figure 2. Distribution of (a) taxa and (b) habitat preferences on a ternary plot using turtle forelimb measurements. Turtles that live primarily on land or in aquatic habitats define the aquatic and terrestrial fields of ecology, respectively. The assemblage of turtles in the intermediate field is from both terrestrial and aquatic settings.

habitats. However, the palaeoecology of fossil turtles within the 'intermediate' zone must be considered uncertain, although it remains safe to assume that such turtles were indeed intermediate in their ecology, as is the case with all turtles that occupy this field today.

Among fossils with forelimbs preserved, only two indisputably represent the successive outgroups of crown turtles (figure 3): *P. quenstedti* (Gaffney 1990) and *P. talampayensis* (Rougier *et al.* 1995). *Proganochelys quenstedti* has been described as semi-aquatic (Gaffney 1990; Gaffney & Kitching 1994; Rieppel & Reisz 1999), whereas *P. talampayensis* (Rougier *et al.* 1995) has been said to be more terrestrial, thus supporting the notion that basal turtles were ecologically diverse (Gaffney & Kitching 1994; Rougier *et al.* 1995). Our analysis indicates, however, that *P. quenstedti* and *P. talampayensis* are located in the middle of the terrestrial field (figure 2b), thus indicating that both species were well adapted to terrestrial habitats and almost certainly not competent swimmers.

The ecology of the best-known Triassic stem turtle, *P. quenstedti*, has been a point of particular controversy, so it is interesting to note that additional anatomical evidence also favours the proposed terrestrial habitat for that species. For instance, the limbs of *P. quenstedti* are covered with thick osteoderms (bony scales), an attribute that is only paralleled in terrestrial tortoises and that is notably absent from all living aquatic turtles. Furthermore, the fore and hindlimbs of *P. quenstedti* are characterized by a greatly reduced phalangeal count, a feature previously

noted as being distinctive for terrestrial turtles in general by Zug (1971), and applied to *P. quenstedti* in particular by Lee (1994). Finally, the neck and tail of *P. quenstedti* are protected by spiked osteoderms and the distal part of the tail is fused to form a massive club (Gaffney 1990). Among vertebrates, heavy armour is typically associated with terrestrial habits. Tail clubs, which are also known in the extinct horned turtle *Meiolania* (Gaffney 1996), some ankylosaur dinosaurs (Weishampel *et al.* 1990) and glyptodontid armadillos (Scott 1937), are most plausibly used in defence. Terrestriality seems mandatory to such a function, because such bulky weapons are of little use under water.

The phylogenetic distribution of aquatic versus terrestrial habits among turtles indicates that the last common ancestor of crown turtles lived in fresh water (figure 3). At first sight, this conclusion appears counterintuitive, because terrestrial turtles are so conspicuous among arid-adapted terrestrial faunas (Ernst & Barbour 1989). Nevertheless, phylogenetic evidence (Gaffney & Meylan 1988; McCord *et al.* 2000; Feldman & Parham 2002) indicates that all living terrestrial turtles are deeply nested within the clade Testudinoidea, thus adoption of terrestrial habits is therefore most parsimoniously interpreted as an evolutionary novelty within crown turtles. Nevertheless, because the two successive outgroups of crown turtles, *P. quenstedti* and *P. talampayensis* (Gaffney 1990; Rougier *et al.* 1995), are demonstrably terrestrial based on their relatively short hands, the habitat preference of stem turtles,

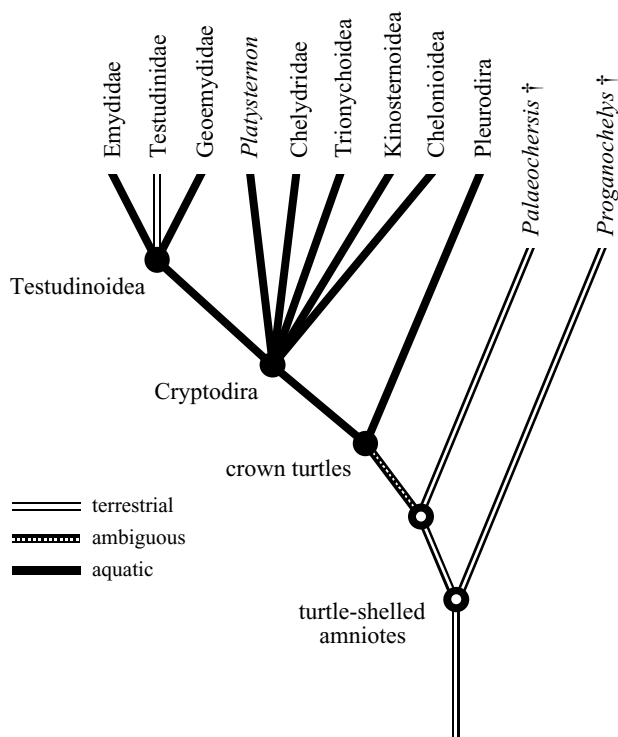


Figure 3. Simplified cladogram illustrating the observed and inferred habitat preferences of the major clades of turtles and their hypothetical ancestors. The informal term 'crown turtles' refers to the clade that originates from the last common ancestor of all living turtles. The more inclusive clade containing all amniotes with a carapace and plastron homologous to those in living turtles is referred to informally as 'turtle-shelled amniotes'. Taxa denoted with a '+' are extinct. Note that even if we choose the single tree among all those possible that is most biased against our conclusions, viz., (((((((((Emydidae + Geoemydidae) Testudinidae) (Platysternon + Chelydridae + Trionchoidea + Kinosternoidea + Chelonioidae)) Pleurodira) Palaeochoersis) Proganochelys)) Sauropterygia), it is still more parsimonious to assume terrestrial habits as ancestral for the entire clade, with convergent acquisition of aquatic habits in sauropterygians and crown turtles, and a subsequent reversal to terrestrial habits in Testudinidae, provided amniotes, reptiles and saurians are regarded as terrestrial ancestrally.

and as such the origin of turtles as a whole, must unambiguously (Maddison *et al.* 1984) have taken place in a terrestrial setting rather than in an aquatic environment (figure 3).

Sedimentological observations have recently been outlined that are consistent with a terrestrial origin for turtles (Lucas *et al.* 2000). Outcrops of Triassic sediments have been sampled worldwide and yielded a plethora of fossils from numerous localities. Triassic faunas are dominated by phytosaurs, temnospondyls and basal sauropterygians, indicating a strong bias towards preservation of aquatic assemblages. Furthermore, although stem turtle specimens are known from quarries across the globe (see Lucas *et al.* (2000) for a summary of localities), they are never associated with aquatic faunas but rather with other terrestrial vertebrates such as prosauropod dinosaurs (Lucas *et al.* 2000). If the origin of turtles occurred in an aquatic environment, then their absence from the well-sampled aquatic fossil biota is conspicuous, especially considering

the high fossilization potential of the heavy turtle shell. Following the Middle Jurassic, turtles became conspicuous elements in nearly every fossil vertebrate locality worldwide, which may indicate that they had not successfully invaded aquatic habitats until that time.

4. CONCLUSIONS

We conclude that although crown turtles appear to have lived in fresh water ancestrally, representatives of the turtle stem lineage lived on land. Turtles might still be sister to sauropterygians, but aquatic habits can no longer be taken as supporting that hypothesis. Indeed, the derived 'aquatic' habits shared by these taxa must now be regarded as convergent, a conclusion hinted at by the freshwater 'aquatic' habits of crown turtles versus the marine 'aquatic' habits of sauropterygians.

This study demonstrates the importance of an integrative approach to evolutionary biology that uses observations from both living and fossil organisms. Turtle evolution offers diverse examples because many living crown clades extend deep into the Mesozoic, permitting rigorous assessment of all manner of evolutionary properties, even in long-extinct species ('justified inferences' of de Queiroz and Gauthier (1992); 'extant phylogenetic bracket' of Witmer (1995)), including inferences regarding their palaeoecology. Habitat preference is corroborated further by the strong across-clade correlation between hand morphology and habitat preferences observed among living turtles. Without a firm grasp of the ecology and morphology of extant turtles, any assessment of the palaeoecology of fossil turtles is conjectural. A deeper understanding of living turtles is consequently the key to revealing the ecology of their fossil relatives. Conversely, only by considering fossils is it possible to reconstruct the full ecological history of turtles. If fossils had not been considered in this study, the origin of turtles would mistakenly have been thought to occur in an aquatic environment (an inference justified for the crown clade only). The inclusion of fossils from the ancient Triassic stem of the turtle crown reveals, however, that turtles first evolved in a terrestrial setting and only later invaded the aquatic niches in which they currently predominate.

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