

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.

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1. INTRODUCTION

According to the two most prominent hypotheses based

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.* 1988*a,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).

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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

