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Rafael Zardoya · Axel Meyer

The evolutionary position of turtles revised

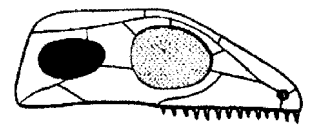
Abstract Consensus on the evolutionary position of turtles within the amniote phylogeny has eluded evolutionary biologists for more than a century. This phylogenetic problem has remained unsolved partly because turtles have such a unique morphology that only few characters can be used to link them with any other group of amniotes. Among the many alternative hypotheses that have been postulated to explain the origin and phylogenetic relationships of turtles, a general agreement among paleontologists emerged in favoring the placement of turtles as the only living survivors of the anapsid reptiles (those that lack temporal fenestrae in the skull). However, recent morphological and molecular studies have radically changed our view of amniote phylogenetic relationships, and evidence is accumulating that supports the diapsid affinities of turtles. Molecular studies favor archosaurs (crocodiles and birds) as the living sister group of turtles, whereas morphological studies support lepidosaurs (tuatara, lizards, and snakes) as the closest living relatives of turtles. Accepting these hypotheses implies that turtles cannot be viewed any longer as primitive reptiles, and that they might have lost the temporal holes in the skull secondarily rather than never having had them.

Living turtles (order Testudines) are among the most striking and strangest tetrapods. Early on in their evolutionary history, these reptiles evolved distinctive shells as effective defense (Burke 1989). This innovation is probably the key to their evolutionary success and persistence, and has constrained the evolution of the rest of their morphology (Lee 1996). The general Baüplan of turtles has barely changed since the Triassic (200 MYA), yet their carapaces show a great variety of shapes that reflect adaptations to terrestrial, freshwater and marine

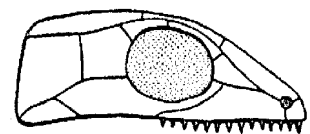
niches (Pough et al. 1998). Based on the mechanism of retraction of their heads into the shell, extant turtles are classified into two main suborders, Cryptodira (turtles that bend their neck vertically) and Pleurodira (side-necked turtles) (Shaffer et al. 1997). Cryptodires (approximately 200 species) have a worldwide distribution (though rare in Australia) whereas pleurodires (approximately 50 species) are currently found only in South America, Africa and Australia.

The exact phylogenetic position of turtles within the Amniota (reptiles, birds, and mammals) is the subject of a lively debate that dates back for over a century (Benton 1991). The current classification of amniotes is consistent with a single key morphological character, the presence and type of temporal fenestration of the skull (Fig. 1) (Günther 1867; Willinston 1917). Extant amniotes that show a completely roofed skull (i.e., turtles) are

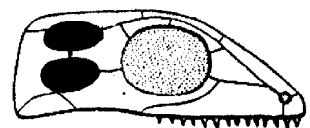
Fig. 1 Temporal fenestration of the amniote skull. *Anapsida*: the skull of early amniotes shows complete dermal roofing of the temporal region. Turtles also have no true temporal openings. *Diapsida*: the skull of crocodiles and the tuatara has two temporal windows (shown in black) that accommodate jaw muscles. Birds, lizards, and snakes have modified the primitive diapsid pattern by the lost of one or more of the bone arches that defined the original two openings. *Synapsida*: the skull of mammals presents a single lower temporal hole (shown in black)



Synapsida



Anapsida



Diapsida

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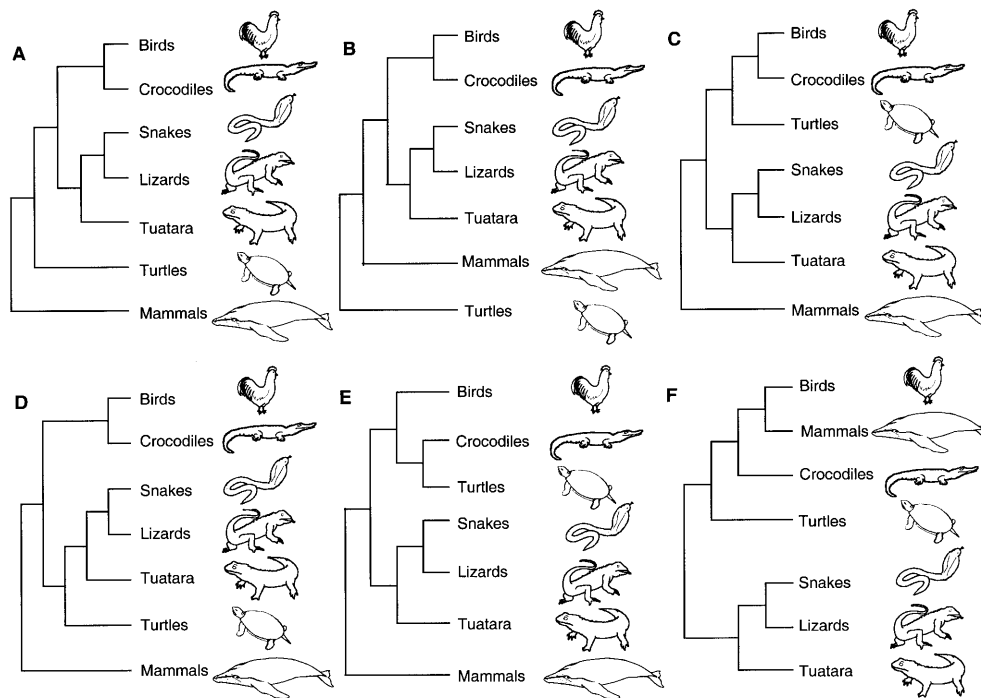


Fig. 2A–F Alternative hypotheses explaining the phylogenetic position of turtles within living amniotes. **A** Mammals are the most basal living amniotes. Turtles are the only living representatives of anapsid reptiles. Living diapsid reptiles include Lepidosauria (the tuatara, snakes, and lizards) and Archosauria (crocodiles and birds) (e.g. Laurin and Reisz 1995; Lee 1997). **B** Turtles represent the sister group of all other extant amniotes (Gaffney 1980). **C** Turtles have diapsid affinities, and are the sister group of Archosauria (e.g. Kumazawa and Nishida 1999; Zardoya and Meyer 2001). **D** Turtles have diapsid affinities, and are the sister group of Lepidosauria (e.g. deBraga and Rieppel 1997). **E** Turtles have archosaurian affinities, and are the sister group of crocodiles (Hedges and Poling 1999; Mannen and Li 1999; Cao et al. 2000). **F** The Haemathermia hypothesis: birds are the sister group of mammals (e.g. Gardiner 1993)

called anapsids. Those that have two fenestrae in the temporal region of the skull (tuatara, lizards, snakes, crocodiles, and birds) are the diapsids. Finally, living amniotes that possess a single lower temporal hole in their skulls (mammals) are the synapsids. According to the fossil record, the first branching event in amniote evolution appears to have separated the synapsids from anapsids and diapsids (Carroll 1988; Gauthier et al. 1988; Laurin and Reisz 1995; Caspers et al. 1996; Rieppel and deBraga 1996; Lee 1997; Reisz 1997; Cao et al. 1998; Zardoya and Meyer 1998). Within reptiles (Sauropsida), the anapsid condition shown by turtles is regarded by some as primitive with respect to the more advanced condition of diapsids (Fig. 2A) (e.g. Carroll 1988; Laurin and Reisz 1995; Lee 1997, 2001; Reisz 1997; Cao et al. 1998).

However, the traditional phylogenetic position of turtles as the only surviving representatives of anapsids is highly controversial (Benton 1991; Rieppel and deBraga 1996; deBraga and Rieppel 1997; Platz and Conlon 1997; Zardoya and Meyer 1998, 2001; Hedges and

Poling 1999; Kumazawa and Nishida 1999; Mannen and Li 1999; Rieppel and Reisz 1999; Cao et al. 2000). Alternative hypotheses, based either on morphological or on molecular evidence, have placed turtles as the most basal amniotes (Fig. 2B) (Gaffney 1980), as sister group of the Archosauria (crocodiles and birds) (Fig. 2C) (Hennig 1983; Platz and Conlon 1997; Zardoya and Meyer 1998, 2001; Kumazawa and Nishida 1999), as sister group of the Lepidosauria (tuatara, lizards, and snakes) (Fig. 2D) (Rieppel and deBraga 1996; deBraga and Rieppel 1997), as sister group of crocodiles (Fig. 2E) (Hedges and Poling 1999; Mannen and Li 1999; Cao et al. 2000), or basal to crocodiles and the Haemathermia clade (mammals and birds) (Fig. 2F) (Owen 1866; Gardiner 1982, 1993; Løvtrup 1985).

Living turtles are highly derived reptiles which also retain numerous amniote ancestral characters. It is difficult to estimate with confidence their phylogenetic affinities based on morphological data due to a general lack of shared derived characters with other amniotes and due to conflicting phylogenetic signal in different data sets (Rieppel and deBraga 1996). Moreover, the major lineages of amniotes (including turtles) show significantly different rates of molecular evolution, complicating phylogenetic inference based on molecular data (Kumazawa and Nishida 1999).

In recent years, new morphological and molecular data sets bearing on the phylogenetic position of turtles, and on amniote relationships, have accumulated. Most current phylogenetic information seems to be able to distinguish between some of the competing hypotheses and provides stunning new insights into our view of this long-standing phylogenetic issue.

Morphological evidence

The monophyly of turtles is supported by many derived features such as their shell, strengthened skull, absence of teeth, and the position of the limb girdles inside the rib cage (Gaffney and Meylan 1988). Other undisputed monophyletic groups within the amniotes are: mammals (diagnosed by, e.g., possession of hair and mammary glands; Rowe 1988), squamates, i.e., lizards and snakes (diagnosed by, e.g., their skin and paired copulatory organs; Estes et al. 1988), crocodylians (diagnosed by, e.g., their posterior skull bones and elongated wrist bone; Benton and Clark 1988), and birds (diagnosed by, e.g., their feathers and furcula; Ostrom 1976). Furthermore, a close relationship of the tuatara (*Sphenodon*) and squamates to form the monophyletic clade Lepidosauria, and a sister group relationship of crocodylians and birds to form the monophyletic clade Archosauria are accepted generally among paleontologists. The debate about the position of turtles with respect to mammals, lepidosaurs, and archosaurs is still ongoing.

It is now widely accepted that mammals represent the sister group of all other living amniotes (Carroll 1988; Gauthier et al. 1988; Laurin and Reisz 1995; Rieppel and deBraga 1996; Lee 1997; Reisz 1997). However, in the past, two alternative hypotheses have been postulated. Gaffney (1980) proposed that mammals and diapsid reptiles (lepidosaurs and archosaurs) were sister groups because they shared a lower temporal hole in the skull and the development of a Jacobson's organ at some stage in ontogeny. Alternatively, a putative close relationship of birds and mammals, the Haematothermia hypothesis, as originally proposed by Owen (1866), has recently been revived (Gardiner 1982, 1993; Løvtrup 1985). Many authors have noticed that evidence in support of either hypothesis is rather weak and a number of characters supporting them are questionable (e.g., Gauthier et al. 1988). None of these latter hypotheses have been supported by new morphological or molecular phylogenetic data.

Hence, assuming that mammals are the outgroup to the rest of amniotes, turtles are typically placed basal to diapsid reptiles (Fig. 2A), as the sister group of Archosauria (Fig. 2C) or as the sister group of Lepidosauria (Fig. 2D).

Turtles as anapsids

Ever since Günther (1867) started classifying reptiles based on skull fenestration, many authors (Carroll 1988; Laurin and Reisz 1995; Lee 1997, 2001; Reisz 1997) have accepted the anapsid condition of turtles, i.e., they retain the primitively complete temporal roofing of the skull. Early studies proposed that turtles are derived either from extinct diadectids (Romer 1966) or captorhinids (Gaffney and Meylan 1988; Gauthier et al. 1988). At present, diadectids are thought to be basal to amniotes,

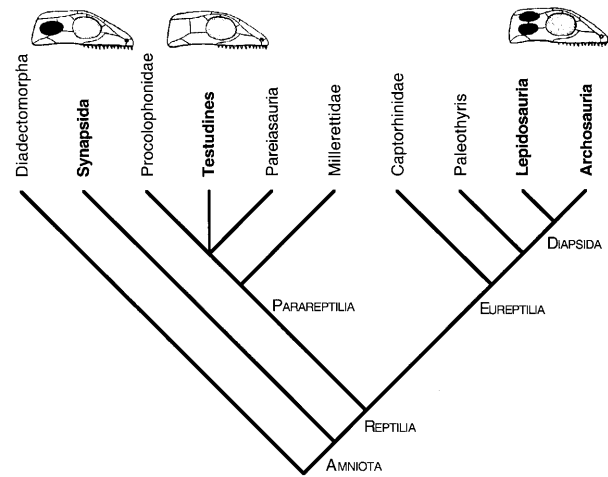


Fig. 3 Turtles as anapsid reptiles. Traditional phylogenetic hypotheses based on morphological and paleontological data place Synapsida (mammals and extinct relatives) as the most basal Amniota. Turtles (Testudines) are considered anapsid reptiles and are grouped either with extinct procolophonids (Laurin and Reisz 1995) or with extinct pareiasaurs (Lee 1997, 2001) in the Parareptilia clade. Living taxa are shown in *bold*

captorhinids are commonly placed basal to diapsids in the Eureptilia clade, and turtles are grouped either with procolophonids (Laurin and Reisz 1995) or with pareiasaurs (Gregory 1946; Lee 1995, 1996, 1997, 2001) in the Parareptilia clade (Fig. 3). If turtles are grouped with procolophonids or pareiasaurs, the origin of the lineage that led to turtles has to be placed in the Upper Permian (around 255 MYA) (Reisz 1997). However, the earliest fossil turtles such as *Proganochelys* are only from the Late Triassic (215 MYA) (Gaffney 1990; Rougier et al. 1995). Hence, both hypotheses imply the existence of a rather extensive gap of 40 Myr (million years) in the fossil record (deBraga and Rieppel 1997). At least 14 shared derived characters that group together Upper Permian procolophonids, such as *Procolophon* and *Hypsognathus*, to testudines were proposed by Laurin and Reisz (1995). This grouping was supported by a 82% bootstrap value and a decay index of 5 (Laurin and Reisz 1995). On the other hand, up to seven features associated with the shell were found to relate turtles and dwarf pareiasaurs such as *Nanoparia*, *Anthodon* and *Pumiliopareia* (Lee 1996, 1997). Such a grouping was supported in a very recent morphological study by a bootstrap value of 93% and a decay index of 12 (Lee 2001). Lee (1996) proposed that the distinct carapace of turtles evolved gradually from the dermal armor of dwarf pareiasaurs which initially had a supporting function, and later in certain lineages become co-opted for protection (in a paradigmatic case of exaptation; Gould and Vrba 1982). Other striking unique traits of turtles would have arisen, influenced by the evolution of the shell, i.e., by correlated progression (Lee 1996).

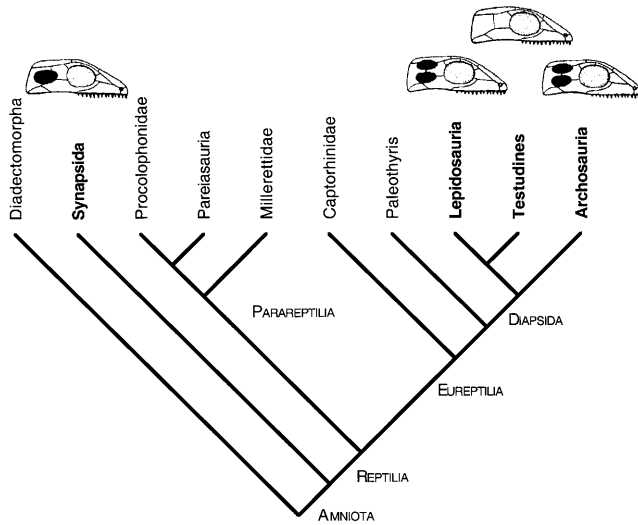


Fig. 4 Turtles as diapsid reptiles. Recent phylogenetic analyses (deBraga and Rieppel 1997) place turtles (Testudines) as advanced diapsid reptiles closely related to extinct Sauropterygia (marine plesiosaur and pliosaur reptiles). Lepidosauria (the tuatara, snakes, and lizards) are identified as the closest living relatives of turtles to the exclusion of Archosauria (crocodiles and birds). According to this hypothesis, turtles lost secondarily their original two openings in the tempora region of the skull. Living taxa are shown *in bold*

Turtles as diapsids

The traditional assumption that turtles were the only survivors of the anapsid lineage restricted most early cladistic analyses that tested turtle interrelationships exclusively to Paleozoic amniote taxa, i.e., excluded derived diapsid reptiles. However, a recent analysis based on 168 morphological characters that also included Mesozoic and living diapsids revealed that support for the anapsid affinities of turtles is rather weak (Rieppel and deBraga 1996; deBraga and Rieppel 1997). Instead, turtles were placed as advanced diapsid reptiles closely related to extinct Sauropterygia (marine plesiosaur and pliosaur reptiles) (Rieppel and deBraga 1996; deBraga and Rieppel 1997) (Fig. 4). In this phylogenetic analysis, Lepidosauria were identified as the closest living relatives of turtles (Rieppel and deBraga 1996; deBraga and Rieppel 1997) (Fig. 4). The Testudines+Sauropterygia clade was supported only by a 43% and two steps were needed to collapse it (deBraga and Rieppel 1997). Similarly, the Diapsida and Eureptilia clades (Fig. 4) were weakly supported by bootstrap values below 50% (deBraga and Rieppel 1997). To explain this apparent lack of strong bootstrap support, the authors pointed out that their phylogenetic analysis showed a higher rate of homoplasy because of the large data set and numerous taxa (Rieppel and deBraga 1996; deBraga and Rieppel 1997; Rieppel and Reisz 1999; but see Wilkinson et al. 1997). The osteological data set of deBraga and Rieppel (1997) was recently revised and expanded by Lee (2001). The phylogenetic analysis of this expanded osteological data set

recovered a single most parsimonious tree that supported the anapsid condition of turtles (Lee 2001). This result was highly dependent on the inclusion of fossil taxa in the phylogenetic analysis. When fossils were excluded, and the phylogenetic analysis was performed only with living taxa, three equally most parsimonious trees were recovered in which turtles were either placed as sister group of diapsids, or grouped with archosaurs, or grouped with lepidosaurs (Lee 2001).

Recent analyses show that it is the Sauropterygia that places turtles deep within the diapsids (Rieppel and Reisz 1999). Interestingly, there is morphological evidence that may place plesiosaurs and pliosaurs basal to the Archosauria (Merck 1997). Hence, it is possible that both turtles and sauropterygians could be closely related to the Archosauria rather than to the Lepidosauria. A close relationship of turtles and archosaurs had previously been proposed on the basis of neontological characters (e.g., deBeer 1937; Ax 1984; Løvtrup 1985; Gardiner 1993). However, a recent study showed that most, but not all, of the neontological characters that relate turtles to archosaurs were invalid (Rieppel 2000).

The hypothesis that turtles are crown-group diapsids implies that the anapsid condition of the turtle skull developed secondarily. In fact, *Proganochelys* (Gaffney 1990) and extant turtles show a squamosal configuration in the temporal region of the skull that does not match the primitive pattern found in Paleozoic anapsids, and it would be consistent with the former presence of a lateral temporal hole (deBraga and Rieppel 1997). It has been suggested that it might be possible that a dorsal expansion of the quadratojugal could have closed a putative fenestra in the ancestor of turtles (deBraga and Rieppel 1997). Given the very specialized body plan of turtles, it may not be too far-fetched to propose that the turtle skull is also highly derived (Carroll 1988). Apparently, the loss of the temporal skull window may be a more frequent event than previously thought. In fact, it has been demonstrated in several extinct reptiles, such as, e.g., some araucoscelid diapsids (deBraga and Rieppel 1997). The diapsid affinities of turtles may be also supported by developmental patterns of ossification which are shared by turtles and extant diapsids (Rieppel 1995). Furthermore, if turtles are diapsids, their ancestor likely had to evolve in the Lower to Middle Triassic (245–235 MYA). This evolutionary scenario shortens the gap in the fossil record between the origin of the turtle lineage and *Proganochelys* to less than 20 Myr (deBraga and Rieppel 1997).

Molecular evidence

It has been suggested that molecular data may be helpful in resolving the morphological controversy on the phylogenetic position of turtles (Wilkinson et al. 1997). However, many phylogenetic analyses of relatively small molecular data sets were rather weak in their conclusions. Phylogenetic analyses of amino acid sequences from α

A-crystallin, α - and β -hemoglobin, myoglobin, histone H2B, cytochrome *c*, and insulin were unable to resolve the relationships of turtles, birds, and crocodiles (Hedges et al. 1990 and references therein). The Haemathermia hypothesis (Owen 1866; Gardiner 1993) (Fig. 2F) seemed plausible based on 18S rRNA evidence (Hedges et al. 1990). However, subsequent reanalyses of this nuclear data set (Hedges et al. 1990) with weighted parsimony (Marshall 1992), a total evidence approach that combined molecular and morphological data (Eernisse and Kluge 1993), and the use of a tree reconstruction method that takes into account the among-site rate variation of the rRNA molecule (Van de Peer et al. 1993), rejected the mammal+bird clade, and supported mammals as the sister group of all other living amniotes. More recently, larger molecular data sets have been collected, and the basal position of mammals among living amniotes has been firmly established (Hedges 1994; Caspers et al. 1996; Strimmer and von Haeseler 1996; Janke and Arnason 1997; Cao et al. 1998; Zardoya and Meyer 1998, 2001; Hedges and Poling 1999; Mannen and Li 1999; Mindell et al. 1999; Cao et al. 2000). However, recent phylogenetic analyses of relatively large mitochondrial and nuclear sequence data sets differ on the relative position of turtles with respect to diapsids (Lepidosauria and Archosauria).

Mitochondrial evidence

A maximum parsimony (MP) analysis of complete mitochondrial 12S and 16S rDNA sequences supported the traditional anapsid position of turtles, i.e., basal to lepidosaurs and archosaurs (Hedges 1994) (Fig. 2A). The same study, based on neighbor-joining (NJ) analysis, however, favored a sister group relationship between turtles and lepidosaurs with low bootstrap support (Hedges 1994) (Fig. 2D). A maximum likelihood (ML) analysis of the same molecular data set supported with high bootstrap values the anapsid nature of turtles (Strimmer and von Haeseler 1996; Cao et al. 1998) (Fig. 2A). However, these results appeared to be sensitive to taxon sampling (Zardoya and Meyer 1998), and obviously the phylogenetic method used. Further phylogenetic analyses (MP, NJ, ML) of the same genes with additional taxa (including representatives of the two major lineages of turtles, Pleurodira and Cryptodira) recovered a turtle+Archosauria clade supported by moderately high bootstrap values (Zardoya and Meyer 1998) (Fig. 2C). Alternative hypotheses [turtles as anapsids (Fig. 2A) or turtles as sister group of lepidosaurs (Fig. 2D)] could not be statistically rejected based on this data set (Zardoya and Meyer 1998).

A ML analysis (using the mtREV model; Adachi and Hasegawa 1996) of concatenated amino acid sequences of 12 complete mitochondrial protein-coding genes further supported the archosaurian affinities of turtles and statistically rejected alternative hypotheses (Kumazawa and Nishida 1999). The turtle+archosaurian clade was

supported by a 100% bootstrap value (Kumazawa and Nishida 1999). A very recent and comprehensive ML analysis accounting for among-site rate variation, which combined the amino acid sequences of 12 mitochondrial proteins, and the nucleotide sequences of the two mitochondrial rRNA genes, also strongly supported the close relationship of turtles and archosaurs (Fig. 5A) (Cao et al. 2000). The phylogenetic analyses (with MP, NJ, and ML) of a molecular data set which included complete mitochondrial protein-coding, rRNA, and tRNA genes further supported the phylogenetic position of turtles as sister group of archosaurs (crocodiles+birds) (Zardoya and Meyer 2001) (Fig. 5B).

Nuclear evidence

Phylogenetic analyses (with MP, NJ, and ML) of a data set that combined the nucleotide sequences of the lactate dehydrogenase (LDH-A and LDH-B) and α -enolase genes from several amniotes strongly supported crocodiles as the closest living relatives of turtles (Mannen and Li 1999) even to the exclusion of birds (Fig. 2E). A more comprehensive study that included amino acid sequences from 11 nuclear proteins also strongly supported (100, 99, and 97% bootstrap values in the ML, NJ, and MP analyses, respectively) the turtle+crocodile clade (Fig. 2E) (Hedges and Poling 1999). However, three of those nuclear proteins (α A-crystallin, α -enolase, and calcitonin) supported individually a turtle+archosaurian grouping (Hedges and Poling 1999). These analyses did not include the tuatara (*Sphenodon*) because few genes have been sequenced in this species (Mannen and Li 1999; Hedges and Poling 1999). A smaller data set of sequences from four nuclear protein-coding genes for which sequences of the tuatara are available recovered a tree in which squamates were basal to an unresolved clade including tuatara, turtles, crocodiles, and birds (Hedges and Poling 1999). The nuclear 18S and 28S rRNA genes supported crocodiles as the closest living sister group of turtles (Hedges and Poling 1999) (Fig. 2E). A recent reanalysis of Hedges and Poling's (1999) data taking into account among-site rate variation and rate heterogeneity among genes also favored the turtle+crocodile grouping (although with lower bootstrap support) (Cao et al. 2000). Furthermore, the combined mitochondrial and nuclear evidence favored crocodiles as the closest living relatives of turtles but could not statistically reject a turtle+archosaurian grouping (Cao et al. 2000).

A turtle+crocodilian clade is completely unorthodox from a morphological and paleontological perspective (osteology and soft anatomy clearly support a monophyletic Archosauria) (Gauthier et al. 1988; deBraga and Rieppel 1997). Similarly, there is strong morphological and paleontological evidence linking tuataras to squamates (Gauthier et al. 1988; deBraga and Rieppel 1997). Both crocodiles and turtles show significantly long branches which might introduce biases into the phyloge-

Rieppel's (1997) data seems to favor the anapsid condition of turtles (as sister group of pareiasaurs), and statistically rejects the putative diapsid affinities of turtles (Lee 2001). This result is dependent on the inclusion of fossil taxa in the phylogenetic analysis. Moreover, a total evidence analysis, including mitochondrial and morphological data, seems also to group turtles with anapsid parareptiles (Lee 2001). The molecular and morphological combined data set can statistically reject a turtle+lepidosaurian grouping but not a turtle+archosaurian sister group relationship (Lee 2001).

The synapomorphies uniting turtles and diapsids are distributed all over the skeleton (Rieppel and Reisz 1999). Therefore, turtles can no longer be assumed to provide the ancestral condition against which to interpret comparative studies involving reptiles (Rieppel and deBraga 1996). A phylogenetic position of turtles within Diapsida would imply that turtles had windows in the temporal region of the skull which were secondarily closed. The true anapsid condition would be restricted to Parareptilia fossils and the diapsid condition would be a shared derived character of all living reptiles, indicating their monophyly.

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