Phylogenetic Relationships of Mesozoic Turtles

Walter G. Joyce

Division of Vertebrate Paleontology, Peabody Museum of Natural History, Yale University,
P.O. Box 208118, New Haven, CT 06520-8118 USA — *email:* walter.joyce@yale.edu

ABSTRACT

Presented herein is the first morphological analysis of turtle relationships to examine the monophyly of many turtle groups by using only single species as terminals and by integrating a large number of primitive fossil taxa. The data matrix consists of 136 osteological parsimony informative characters with 169 derived character states for 45 fossil and 22 living species of the clade TESTUDINATA. The results corroborate the monophyly of a large number of previously hypothesized clades, but refute the accepted hypothesis regarding the basal split of living turtles. In particular, the primitive turtles *Proterochersis robusta, Kayentachelys aprix, Mongolochelys efremovi, Meiolania platyceps,* and *Kallokibotion bajazidi* are removed from their current position as crown turtles and placed along the phylogenetic stem of this clade. The age of the turtle crown is thereby adjusted from the Late Triassic to the Late Jurassic, which is relevant to testing molecular clock hypotheses. This revised topology has important implications for the evolution of several character complexes, because it implies that the common ancestor of all living turtles must have had a partially braced brain case and a primitive trochlear mechanism. Other noteworthy conclusions include the tentative exclusion of protostegids from CHELONIOIDEA, the placement of *Platysternon megacephalum* outside of CHELYDRIDAE, and the tentative interpretation of *Sandownia harrisi* as a basal eucryptodire.

KEYWORDS

Phylogeny, phylogenetic nomenclature, basal turtles, trochlear mechanism, ecology, TESTUDINATA, TESTUDINES, PANPLEURODIRA, PLEURODIRA, PANCRYPTODIRA, CRYPTODIRA.

Introduction

Among living vertebrates, turtles are an ideal group for phylogenetic analysis because they are morphologically diverse and have an excellent fossil record (Gaffney et al. 1991). Indeed, turtles were among the first groups of vertebrates to be analyzed within a cladistic framework (Gaffney 1972b) and the history of phylogenetic study of this group mirrors the development of cladistic methodology over the last 30 years.

Early studies of turtle relationships sought progress by developing characters and using them to hypothesize the monophyly of the primary groups of turtles (e.g., Gaffney 1975a). Relationships within these groups were subsequently analyzed in detail (e.g., Baenidae by Gaffney 1972b; CHELYDRIDAE by Gaffney 1975b; CHELIDAE by Gaffney 1977; KINOSTERNOIDEA by Hutchison and Bramble 1981; TESTUDINIDAE by Crumly 1982; BATAGURIDAE by Hirayama 1985) and their monophyly was scrutinized through the addition of new characters and taxa, reanalysis of scorings, and reassessment of primary homology statements (e.g., Gaffney 1984; Gaffney and Meylan 1988; Gaffney et al. 1991).

Due to computational limitations, all exploratory studies of turtle relationships demanded

Bulletin of the Peabody Museum of Natural History 48(1):3–102, April 2007.

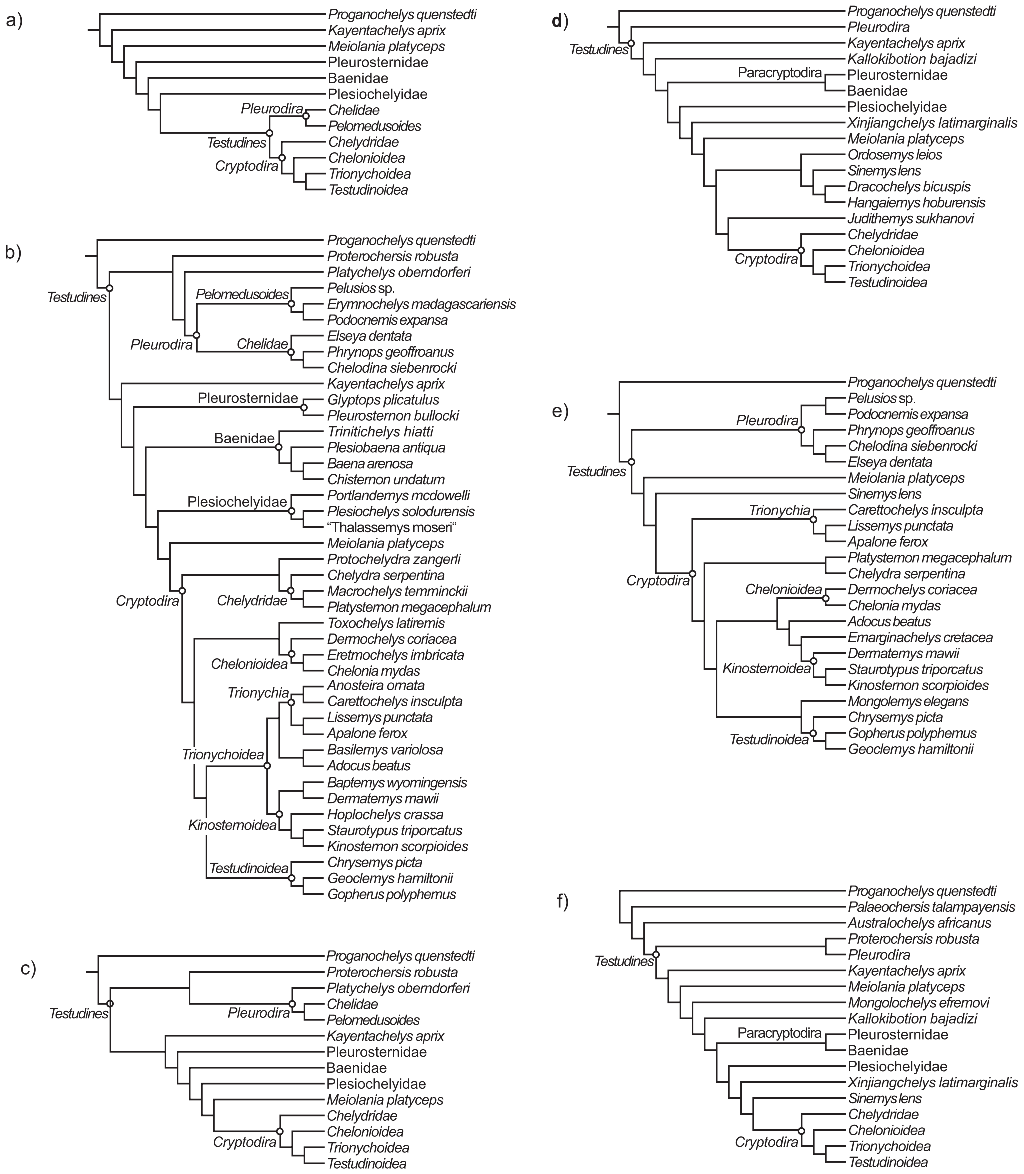


Figure 1. Previous hypotheses of relationships among turtles used in this study. **a.** Phylogenetic hypothesis of Dryden (1988) based on a data matrix of 59 characters for 12 terminal turtle taxa. Numerous terminals are replaced with equivalent ones used in this study to allow for better comparison. **b.** Phylogenetic hypothesis of Gaffney and Meylan (1988), a composite cladogram based on numerous earlier phylogenetic hypotheses. To date this is the only phylogenetic hypothesis that contains all living genera and virtually all better understood fossil genera. Numerous terminals are replaced with equivalent ones used in this study to allow for better comparison. **c.** Phylogenetic hypothesis of Gaffney et al. (1991) based on a data matrix of 39 characters for 14 terminal turtle taxa. Numerous terminals are replaced with equivalent ones used in this study to allow for better comparison. **d.** Phylogenetic hypothesis of Gaffney (1996) based on a data matrix of 40 characters for 17 terminal turtle taxa. Numerous terminals are replaced with equivalent ones used in this study to allow for better comparison. **e.** Phylogenetic hypothesis of Shaffer et al. (1997) based on the combined analysis of cytochrome *b* and 12S rDNA data and 115 morphological characters for 23 living and 7 fossil turtle taxa. To date this is the only extensive analysis to combine molecular and morphological data. Numerous terminals are replaced with equivalent ones used in this study to allow for better comparison. **f.** Phylogenetic hypothesis of Hirayama et al. (2000) based on a data matrix of 76 characters for 21 terminal turtle taxa. Numerous terminals are omitted or replaced with equivalent ones used in this study to allow for better comparison.

simplifying assumptions. In particular, analyses of relationships between higher groups of turtles had to assume that these groups were indeed monophyletic. Likewise, any analysis of relationships within a group had to assume the monophyly of the ingroup. Naturally, a cladistic analysis must make assumptions regarding the monophyly of the ingroup and its terminals. However, in the case of turtles, these assumptions can be reduced by expanding the ingroup to all turtles, a clade of organisms currently united by dozens of characters relative to any potential outgroup, and by restricting the terminals to single species or single specimens only. Aided by the availability of modern computing technology, recent studies have made significant progress by expanding their ingroups to include all turtles (e.g., Dryden 1988; Gaffney et al. 1991; Rougier et al. 1995; Gaffney 1996; Hirayama et al. 2000; Figure 1). Although all of these analyses still used higher taxa as terminals, few did not do so exclusively, and this sometimes produced surprising conclusions. In particular, Dryden (1988) scored the putative PANCRYPTODIRAN turtle *Kayentachelys aprix* as a separate terminal, only to conclude that it is more parsimoniously is placed along the phylogenetic stem of crown TESTUDINES. Conversely, Rougier et al. (1995) scored the putative PANPLEURODIRAN turtle *Proterochersis robusta* as a separate terminal, only to conclude that this taxon may represents a stem turtle as well.

The integration of fossils should be a primary goal for any rigorous phylogenetic analysis, because parsimony analysis of living taxa alone may incorrectly group distantly related lineages based on homoplastic characters (Gauthier et al. 1988). Early investigators of turtle relationships were limited in their choice of fossil taxa because virtually no single fossil turtle had been described in detail beyond the external surface of the shell. The situation has changed substantially in recent years, stimulated by cladistic analyses, with many fossil taxa now described with special reference to phylogenetically useful characters that pertain to all anatomical systems.

This paper presents a global analysis of turtle relationships that attempts to reduce a priori assumptions by restricting all terminals to single species only while significantly enlarging the number of fossil species included. This approach allows the first independent assessment of the monophyly of many groups of turtles. The results are intriguing in that they imply a pathway for the evolutionary development of the trochlear system of living turtles that is different from previous, cladistically supported hypotheses.

Abbreviations and Nomenclature

Anatomical terms of the cranium follow those summarized by Gaffney (1972a). Nomenclature of the shell and scutes follows the recommendation of Zangerl (1969) as updated by Hutchison and Bramble (1981). The preliminary phylogenetic nomenclature developed by Joyce et al. (2004) is used herein. However, because many useful taxon names governed by the International Code on Zoological Nomenclature have not yet been converted to phylogenetically defined taxon names, traditional rank-based taxon names have been retained herein. The application of these names (i.e., their referred content) follows that of Gaffney and Meylan (1988). To help distinguish both sets of names, phylogenetically defined names (including all of their grammatical derivatives) are placed in small capitals throughout.

The following institutional abbreviations are used: AMNH, American Museum of Natural History, New York, New York, USA; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CCMGE, Chernyshev's Central Museum of Geological Exploration, St. Petersburg, Russia; CJB, Collection of Christopher J. Bell, Texas Memorial Museum, Austin, Texas, USA; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; DCM, Dorset County Museum, Dorset, England; MB, Museum für Naturkunde, Berlin, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; NS, Naturmuseum Solothurn, Solothurn, Switzerland; SMM, The Science Museum of Minnesota, St. Paul, Minnesota, USA; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; USNM, United States National Museum, Washington, D.C., USA; UMZC Cambridge University Museum of Zoology, Cambridge, England; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

Materials and Methods

Taxon Sampling

Extant ingroup taxa were selected primarily for availability, while attempting to cover the greatest amount of tree space. All major clades of living turtles were sampled. When choosing extinct taxa, emphasis was placed on including as many species as possible that could reasonably reflect stem representatives of extant clades, but sampling was ultimately limited to species that were either well described or that were accessible for the duration of the study. Fossil taxa known from complete skeletons or single, well-preserved skulls were given preference to avoid the pitfalls associated with including chimeras. Although coverage of fossil forms was generally good, a demonstrable bias exists towards North American and European faunas and taxa described after the advent of cladistic study.

Unlike all previous studies, this analysis only uses single species as terminal taxa to avoid a priori assumptions about the monophyly of the terminals. Future analysis will be able to significantly improve on this study, by adding more terminals. A list of included species and the sources of information used in their scoring is given in Appendix 1.

Character Sampling

In an attempt to compile the most comprehensive morphological data set pertaining to the phylogenetic relationships of turtles, numerous previous analyses were scanned for discrete skeletal characters. These included Dryden (1988), Meylan and Gaffney (1989), Gaffney et al. (1991), Rougier et al. (1995), Gaffney (1996), Shaffer et al. (1997), Brinkman and Wu (1999), and Hirayama et al. (2000) (see Figure 1). Additional characters were derived from Hirayama and Chitoku (1996), Gaffney and Meylan (1988), and Fuente and Iturralde-Vinent (2001) to allow improved resolution within Cryptodira and Pleurodira.

A significant number of characters derived from previous studies were omitted before the analysis and are consequently not described in detail (see Character Discussion, below). Only three reasons were considered permissible for omitting characters. First, many characters were omitted because they were parsimony uninformative for the selected ingroup by either being present in a single terminal taxon or by being present in all ingroup taxa. Second, within the context of this analysis many previously used characters were continuous. The continuous nature of these characters is typically the result of more extensive taxon sampling, which rendered previously discrete characters continuous. Finally, a few characters were omitted due to problems associated with primary homology assessments or the availability of primary data. Future workers will likely be able to tackle the difficulties associated with these characters and extract the phylogenetic information that they likely contain using either different ingroups or alternative coding methods. The list of characters removed from the analysis and the rationale for omission of each is provided in Appendix 2.

It is inherently difficult to avoid phrasing redundant morphological characters in large cladistic analyses, because many objectively redundant characters pertain to different anatomical structures and may thus be overlooked. For instance, the acquisition of a clear jugal–squamosal contact on the skull surface of a turtle will automatically result in the loss of a postorbital–quadratojugal contact. To help organize such large sets of morphological characters, this paper lists all characters that pertain to a given anatomical structure and provides cross-references to redundant characters. For instance, the loss of a contact between the postorbital and squamosal due to the development of temporal emarginations is listed as "Character 18" under the heading "Squamosal," but cross-referenced in the sections "Postorbital," "Upper Temporal Emargination," and "Lower Temporal Emargination." This organization should allow future researchers to more easily find characters, establish synonymies, and integrate new characters into analyses.

Outgroup

Currently there is little reason to doubt that *Proganochelys quenstedti* Bauer from the Upper Triassic of Europe is the most primitive well-understood representative of Testudinata (see Joyce and Karl 2006 for a potentially more primitive taxon that is known only from a single fragment). This assertion is supported by a large series of morphological characteristics of *P. quenstedti* that are present in primitive tetrapods, but not in any other known turtle. In particular, *P. quenstedti* is the only turtle known to have palatine and vomerine teeth, a basicranium that is only loosely attached to the surrounding palatoquadrate and dermal roofing elements, and a primitive ear consisting of a massive stapes that articulates directly with the quadrate and not the tympanum (Gaffney 1990). *P. quenstedti* is consequently an ideal outgroup taxon for any analysis of turtle relationships. However, some characters cannot be scored for *P. quenstedti* and thus cannot be polarized using this species. As an alternative, this analysis uses a hypothetical outgroup taxon constructed with the known morphology of *P. quenstedti* and supplemented with information obtained from the ingroup. A rationale for each supplementary character polarization is provided with each problematic character (see Character Discussion, below).

Phylogenetic Analyses

The data matrix includes 136 osteological characters with 169 derived parsimony informative character states for 45 fossil and 22 living representatives of Testudinata and the hypothetical outgroup. Of these characters, 27 are multistate characters of which 15 can be ordered into morphoclines. The data matrix was assembled using McClade 3.08 (Maddison and Maddison 1999) and is given in Appendix 3.

Three principal phylogenetic analyses, which differ in the ordering of the morphoclinic multistate characters and in the omission of rogue taxa, were performed using PAUP 4.0b10 (Swofford 2002). Characters were considered reversible and assigned equal weight in all analyses. Under parsimony settings, branches were set to collapse if their minimum length was zero, to avoid supporting nodes with missing data. The most parsimonious solution was sought using heuristic algorithms with 1,000 randomly seeded replications and by filtering all retained trees for the optimal solutions only.

Two tests were performed to assess the rigor of the topologies obtained in the third, and later preferred, phylogenetic analysis (see Discussion). The first test consisted of calculating decay indices using TreeRot version 2 (Sorenson 1999) for the 50% consensus tree. The second test consisted of running 1,000 bootstrap replicates using PAUP 4.0b10 with the same settings used in the third analysis (i.e., removal of rogue taxa and ordering of morphoclinic multistate characters). However, due to computational limitations, each bootstrap replicate was restricted to 25 randomly seeded searches and a maximum of 1,000 most parsimonious trees, thus rendering the test less rigorous but accomplishable within a reasonable time frame.

Character Discussion

Nasals

CHARACTER 1: NASAL A

Character definition. Nasals (Dryden 1988, 22; Gaffney et al. 1991, 18; Gaffney 1996, 1; Brinkman and Wu 1999, 1; Hirayama et al. 2000, 1): 0 = present; 1 = absent.

Morphology and distribution. Primitive turtles, such as *Proganochelys quenstedti* and *Kayentachelys aprix* Gaffney, Hutchison, Jenkins and Merker, are characterized by the presence of a pair of nasal bones situated along the dorsal rim of the external nares (Figure 2a–e). Nasals are absent in numerous PANPLEURODIRES and PANCRYPTODIRES and in *Baena arenosa* Leidy (Figure 2f). At least within CRYPTODIRA, this loss of the nasals is due to their failure to ossify during development (e.g., *Emys orbicularis,* Kunkel 1912; *Chelydra serpentina,* Rieppel 1993; *Apalone spinifera,* Sheil 2003). There generally is no disagreement regarding the distribution of nasals within TESTUDINATA; however, in some fossils the anterior margin of the skull may be eroded, making it impossible to verify whether or not nasals were present (e.g., *Neurankylus eximius* Lambe, *Judithemys sukhanovi* Parham and Hutchison).

Character evolution. Using DELTRAN optimization, nasals are lost four times in the preferred phylogenetic hypothesis (Figure 18; CI = 0.25): along the phylogenetic stems of PELOMEDUSOIDES, *Baena arenosa,* CHELONIOIDEA, and the clade formed by the remaining CRYPTODIRES (i.e., CHELYDRIDAE + TESTUDINOIDEA + TRIONYCHOIDEA). Using ACCTRAN optimization, nasals are lost along the phylogenetic stems of PELOMEDUSOIDES, *Baena arenosa,* and CRYPTODIRA, but subsequently reacquired in *Toxochelys latiremis* Cope. The lack of additional, putative PANCHELONIOIDS makes is currently impossible to favor one evolutionary pathway over the other. Additional losses not encompassed by this analysis occurred in *Chelus fimbriatus* Schneider (Gaffney and Meylan 1988).

CHARACTER 2: NASAL B

Character definition. Medial contact of nasals (Shaffer et al. 1997, 49): 0 = nasals contact one another medially along their entire length; 1 = medial contact of nasals partially or fully hindered by long anterior frontal process.

Morphology and distribution. Among turtles that possess nasals, including *Proganochelys quenstedti* and *Kayentachelys aprix,* these bones are squarish elements that contact another along the midline for their entire length (Figure 2a–d). In several representatives of CHELIDAE, this medial contact is partially reduced due to the development of an elongate process of the frontal that extends anteriorly to fully separate the prefrontals and partially or fully separate the nasals (Figure 2e). This character was originally developed as a synapomorphy of CHELIDAE only (Gaffney and Meylan 1988; Shaffer et al. 1997); however, partially or fully

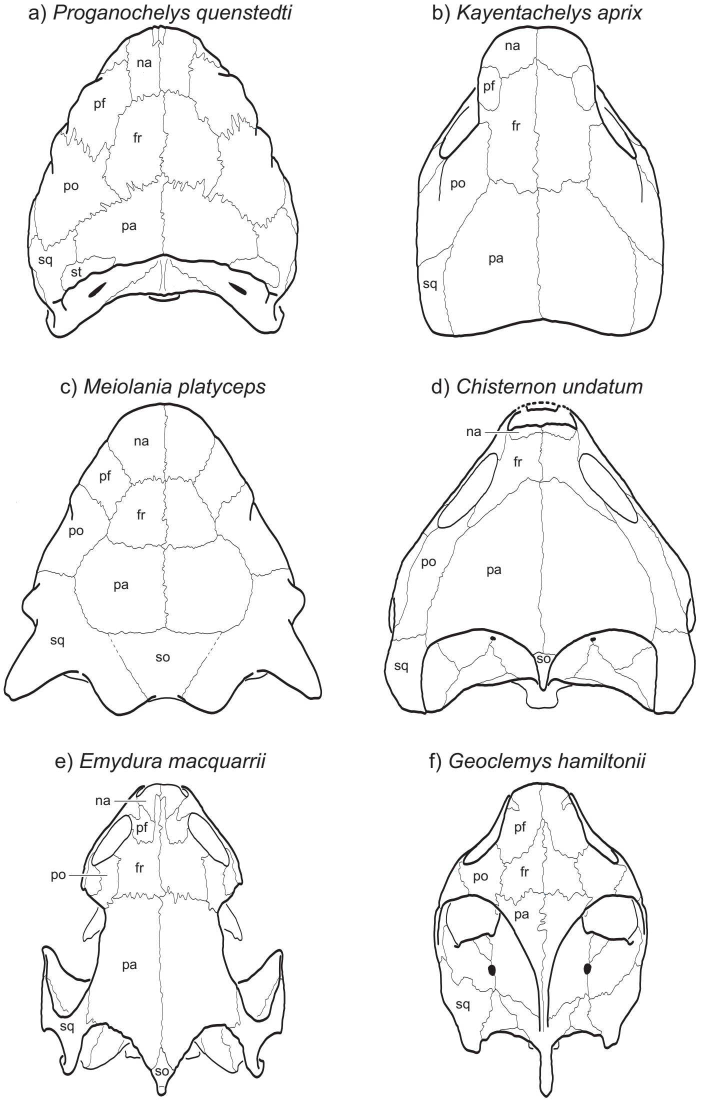

a) *Proganochelys quenstedti*
b) *Kayentachelys aprix*
c) *Meiolania platyceps*
d) *Chisternon undatum*
e) *Emydura macquarrii*
f) *Geoclemys hamiltonii*

Figure 2. Dorsal views of skulls of select *Testudinata.* **a.** *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **b.** *Kayentachelys aprix* Gaffney, Hutchison, Jenkins and Meeker 1987, redrawn from Gaffney et al. (1987). **c.** *Meiolania platyceps* Owen 1886, redrawn from Gaffney (1983). **d.** *Chisternon* (orig. *Baena*) *undatum* (Leidy 1871), redrawn from Gaffney (1972b). **e.** *Emydura* (orig. *Hydraspis*) *macquarrii* (Gray 1831b), redrawn from Gaffney (1979a). **f.** *Geoclemys* (orig. *Emys*) *hamiltonii* (Gray 1831b), redrawn from McDowell (1964). *Abbreviations:* fr, frontal; na, nasal; pa, parietal; pf, prefrontal; po, postorbital; so, supraoccipital; sq, squamosal; st, supratemporal.

separated nasals are present in *Pleurosternon bullockii* Owen and *Glyptops plicatulus* (Cope) as well. The condition is unclear for *Dinochelys whitei* Gaffney (Brinkman et al. 2000).

Character evolution. The medial contact of the nasals is lost twice in the preferred phylogenetic hypothesis (Figure 18; CI = 0.5). In the first instance, this loss occurs along the phylogenetic stem of Chelidae; in the second instance it occurs along the phylogenetic stem of Pleurosternidae. The loss of a medial contact is thus predicted for *Dinochelys whitei.* Given that all representatives of Pelomedusoides lack nasals and that the anterior skull region of no stem-pleurodire is documented, it is unclear if the loss of the medial nasal contact is a true synapomorphy of Chelidae or of a much more inclusive clade of panpleurodires.

CHARACTER 3: NASAL C

Character definition. Size of nasals (Gaffney 1996, M11): 0 = dorsal exposure of nasals large; 1 = dorsal exposure of nasals greatly reduced relative to that of the frontals.

Morphology and distribution. The nasals of *Proganochelys quenstedti, Palaeochersis talampayensis* Rougier, Fuente and Arcucci, *Meiolania platyceps* Owen, *Mongolochelys efremovi* Khosatsky, and *Kayentachelys aprix* are large square elements, which commonly match or exceed the frontals in the amount of exposure to the dorsal skull surface (Figure 2a–c). In contrast, the nasals of all other turtles are significantly smaller than the frontals when present (Figure 2d–e). The presence of (unusually) large nasals was initially observed by Gaffney (1996) in meiolaniids only and served as a synapomorphy for this group. However, large nasals are present in most primitive turtles, indicating that the presence of large nasals is primitive for TESTUDINATA.

Character evolution. Nasals are reduced in size twice in the preferred phylogenetic hypothesis using DELTRAN optimization (Figure 18; CI = 0.5). The first reduction occurs as an autapomorphy for the taxon *Mongolochelys efremovi* and the second reduction in the clade formed by *Kallokibotion bajazidi* Nopska + TESTUDINES. Using ACCTRAN optimization, nasals are reduced in size only once for the clade that originates from the common ancestor of *Meiolania platyceps* and TESTUDINES, but subsequently reversed for *Meiolania platyceps.* At present, both evolutionary pathways seem equally plausible.

NASAL FRONTAL CONTACT

See character 4.

SUBDIVISION OF EXTERNAL NARES

See character 22.

Prefrontal

CHARACTER 4: PREFRONTAL A

Character definition. Medial contact of prefrontals on dorsal skull surface (Dryden 1988, 25; Gaffney et al. 1991, 19; Gaffney 1996, 2; Brinkman and Wu 1999, 3; Hirayama et al. 2000, 3): 0 = absent; 1 = present, prefrontal contact with frontal absent.

Morphology and distribution. The prefrontals of *Proganochelys quenstedti, Kayentachelys aprix* and of most other primitive turtles contribute a significant portion to the dorsal surface of the skull, but do not meet one another along the midline due to a large contact of the nasals with the frontals (Figure 2a–e). This differs from the condition seen in PELOMEDUSOIDS and all eucryptodires with the exception of "Thalassemys marina," *Santanachelys gaffneyi* Hirayama, *Sinemys lens* Wiman, and *Ordosemys leios* Brinkman and Peng (Figure 2f). There is no disagreement regarding the distribution of this character.

Character evolution. The medial contact of the prefrontals is a relatively homoplastic character within the context of the preferred phylogenetic hypothesis (Figure 18; CI = 0.25). It occurs as independent synapomorphies of PELOMEDUSOIDES and PANCRYPTODIRA, but is reversed twice within PANCRYPTODIRA ("Thalassemys moseri" + *Santanachelys gaffneyi* and *Ordosemys leios* + *Sinemys lens*). The medial contact of the prefrontals thus appears to be an unreliable character for diagnosing PANCRYPTODIRA.

CHARACTER 5: PREFRONTAL B

Character definition. Prefrontal–vomer contact (Dryden 1988, 16a; Gaffney et al. 1991, 8; Rougier et al. 1995, 7; Gaffney 1996, 3; Brinkman and Wu 1999, 3; Hirayama et al. 2000, 5): 0 = absent; 1 = present.

Morphology and distribution. The prefrontals of *Proganochelys quenstedti* and *Palaeochersis talampayensis* have a descending process that forms the anterior wall of the orbit and contacts the palatine, but not the vomer (Figure 3a). A contact with the vomer is also absent in all PLEURODIRES (Figure 3b, c). All remaining turtles, including *Kayentachelys aprix, Mongolochelys efremovi,* and *Meiolania platyceps* show a well-developed descending process that contacts the vomer within the orbit (Figure 3d, f). In contrast to most previous cladistic analyses, several fossil TESTUDINATES, such as *Pleurosternon bullockii, Kallokibotion bajazidi, Dinochelys whitei, Neurankylus eximius,* and *Judithemys sukhanovi* are scored as unknown, because the available fossil material is not sufficient to score this character with certainty.

Character evolution. The presence of a vomer–prefrontal contact has previously been thought to have a consisteny index (CI) of 1.00 and was thus considered to be one of the most reliable features for diagnosing the entire PANCRYPTODIRAN clade (e.g., Gaffney and Meylan 1988; Gaffney et al. 1991). However, like Dryden (1988), the present paper indicates this character is a synapomorphy to the clade that includes *Kayentachelys aprix + Meiolania platyceps + Mongolochelys efremovi + Kallokibotion bajazidi* + TESTUDINES, and that the absence of a contact in PLEURODIRES is not the primitive condition, but rather a reversal (Figure 18; CI = 0.5).

CHARACTER 6: PREFRONTAL C

Character definition. Prefrontal–palatine contact (Dryden 1988, 16b): 0 = present; 1 = absent.

Morphology and distribution.The prefrontal of most turtles, including *Proganochelys quenstedti* and *Kayentachelys aprix,* is characterized by a well-developed descending process that forms the anterior wall of the orbit and contacts the palatine within the orbit (Figure 3a, c–d, f). This contact is absent in *Dermochelys coriacea* (Vaudellius), TRIONYCHIDAE, and many representatives of PLEURODIRA, particularly due to the poor development of the anterior portions of the palatine in these taxa (Figure 3b, e). In contrast to Dryden (1988), this character is scored separately from the presence or absence of a prefrontal–vomer contact, because these two characters are not correlated, as evidenced by comparing the condition displayed in PLEURODIRA and TRIONYCHIDAE.

Character evolution. According to the preferred phylogeny, this character was acquired independently three times within Testudinata (Figure 18; CI = 0.33). A loss of a palatine vomer contact occurred along the phylogenetic stem of PLEURODIRA, TRIONYCHIA, and *Dermochelys coriacea.*

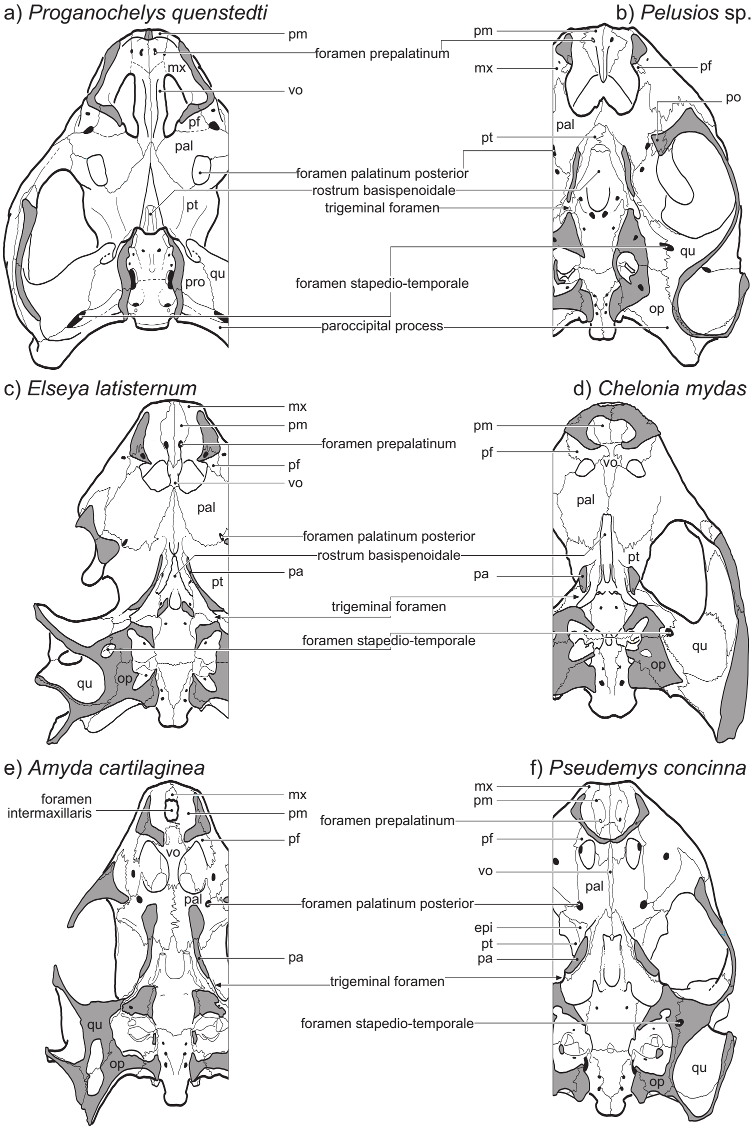


Figure 3. Dorsal views of horizontally sectioned skulls of select *Testudinata*. **a.** *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **b.** *Pelusios* sp., redrawn from Gaffney (1979a). **c.** *Elseya latisternum* Gray 1867, redrawn from Gaffney (1979a). **d.** *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus 1758), redrawn from Gaffney (1979a). **e.** *Amyda* (orig. *Testudo*) *cartilaginea* (Boddaert 1770), redrawn from Gaffney (1979a). **f.** *Pseudemys* (orig. *Testudo*) *concinna* (LeConte 1830), redrawn from Gaffney (1979a). *Abbreviations:* epi, epipterygoid; mx, maxilla; op, opisthotic; pal, palatine; pf, prefrontal; pm, premaxilla; pro, prootic; pt, pterygoid; qu, quadrate; vo, vomer.

Character 7: Prefrontal D

Character definition. Dorsal prefrontal exposure (Gaffney and Meylan 1988, C2.1): 0 = large; 1 = reduced; 2 = absent or near absent.

Morphology and distribution. The dorsal exposure of the prefrontals varies considerably among turtles. In *Proganochelys quenstedti* and *Meiolania platyceps* the prefrontals are relatively large elements that cover a significant portion of the interorbital area. A similar morphology is apparent in PELOMEDUSOIDS and all CRYPTODIRES (Figure 2a, c, f). In contrast, the dorsal prefrontal plate of *Kayentachelys aprix*, “Thalassemys moseri,” *Sinemys lens*, CHELIDS, and numerous baenids is greatly reduced in size (Figure 2b, e), and may even disappear in the remaining representatives of Baenidae (Figure 2d). Even though this character seems to contain a genuine phylogenetic signal, it may be difficult to reproduce objectively, because the character states are continuous and not clearly defined. Scoring this character as a step matrix may help alleviate this problem in the future (Wiens and Etheridge 2003).

Character evolution. The CI of this character is 0.33 with six steps for two derived character states (Figure 18). A reduction of the prefrontal exposure occurs as independent autapomorphies in *Kayentachelys aprix,* "Thalassemys moseri," and *Sinemys lens.* It also occurs as independent synapomorphies of CHELIDAE and Paracryptodira. Within Paracryptodira, the near absence of a dorsal prefrontal exposure unites Baenidae.

CHARACTER 8: PREFRONTAL E

Character definition. Prefrontals heavily sculptured with prominences and bosses (Rougier et al. 1995, 5): 0 = present; 1= absent.

Morphology and distribution. The interorbital region of *Proganochelys quenstedti* is characterized by numerous large prominences and ridges that resemble the brow ridges of basal humans (Figure 4a). The interorbital region of all other known turtles lacks such broad prominences (Figure 4b–h).

Character evolution. Because the morphology of *Proganochelys quenstedti* is the predominant source for polarizing characters in this analysis, the loss of prefrontal prominences and bosses is operationally revealed to be an unambiguous synapomorphy of the clade comprised of all turtles to the exclusion of *Proganochelys quenstedti* (Figure 18; CI = 1.00). Given the sole presence of this characteristic in Proganochelys quenstedti, however, it is unclear whether the presence of this character is an autapomorphy for this taxon or whether its loss is a synapomorphy of all remaining turtles.

PREFRONTAL–POSTORBITAL CONTACT

See character 10.

Lacrimal

CHARACTER 9: LACRIMAL A

Character definition. Lacrimal (Gaffney et al. 1987, 2d; Dryden 1988, 15; Gaffney et al. 1991, 1; Rougier et al. 1995, 4; Hirayama et al. 2000, 6): 0 = present; 1 = absent.

Morphology and distribution. Lacrimal bones and the centrally located lacrimal duct foramina are present along the anterior wall of the orbit in *Proganochelys quenstedti, Palaeochersis talampayensis,* and *Australochelys africanus* Gaffney and Kitching only (Figure 4a). Lacrimal bones and the associated lacrimal duct are absent in all remaining turtles, but the actual glands remain present (Figure 4b–h).

Character evolution. The loss of lacrimal bones and lacrimal duct foramina unambiguously unites all turtles to the exclusion of *Proganochelys quenstedti, Palaeochersis talampayensis,* and *Australochelys africanus* (Figure 18; CI = 1.00).

Frontal

CHARACTER 10: FRONTAL A

Character definition. Frontal contribution to orbit (Meylan and Gaffney 1989, 16; Shaffer et al. 1997, 97; Brinkman and Wu 1999, 48; Hirayama et al. 2000, 4): 0 = absent, prefrontal contacts postorbital; 1 = present.

Morphology and distribution. The frontal of *Proganochelys quenstedti* and *Palaeochersis talampayensis* is a relatively large element barred from contributing to the orbital rim by a strong prefrontal–postorbital contact along the orbit rim. Among other taxa, this condition is also present in *Mongolochelys efremovi, Meiolania platyceps,* and some representatives of CRYPTODIRA (Figure 2a, c, f). In all remaining turtles, including *Kayentachelys aprix,* the frontal clearly contributes to the dorsal orbital rim, so there is no contact between the prefrontal and postorbital (Figure 2b, d–e). In contrast to Hirayama et al. (2000), this analysis scores *Proganochelys quenstedti* and *Palaeochersis talampayensis* as having a broad contact between the prefrontal and postorbital, rendering the absence of a frontal contribution to the orbital rim primitive for TESTUDINATA.

Character evolution. According to the preferred hypothesis, this character is highly homoplastic, requiring eight evolutionary steps (Figure 18; CI = 0.125). The acquisition of a frontal contribution to the orbital rim occurs twice, once as an autapomorphy of *Kayentachelys aprix* and once as a synapomorphy of TESTUDINES. Within TESTUDINES, particularly CRYPTODIRA, this character shows several reversals (*Dermochelys coriacea,* KINOSTERNIDAE, CHELYDRIDAE, *Platysternon megacephalum* Gray, *Zangerlia neimongolensis* Brinkman and Peng, and *Geoclemys hamiltonii* Gray). Inclusion of a larger sample of TESTUDINOIDS in particular is expected to further increase the homoplasy of this character (Joyce and Bell 2004).

FRONTAL–NASAL CONTACT

See character 4.

FRONTAL CONTRIBUTION
TO UPPER TEMPORAL RIM

See character 11.

ANTERIOR FRONTAL PROCESS

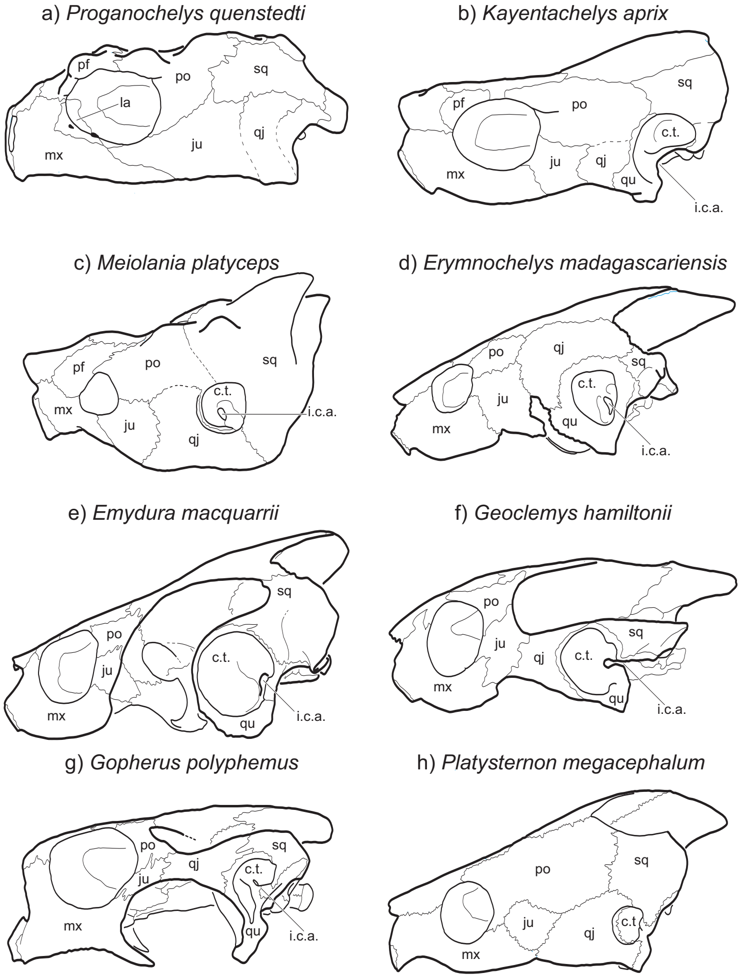
See characters 2 and 4.

Parietal

CHARACTER 11: PARIETAL A

Character definition. Parietal–squamosal contact (Dryden 1988, 24; Gaffney et al. 1991, 15; Gaffney 1996, 17–18; Hirayama et al. 2000, 8–9; Rougier et al. 1995, 32–33; Brinkman and Wu 1999, 17–18): 0 = present, upper temporal emargination absent or only poorly developed; 1 = absent, upper temporal emargination well developed.

Morphology and distribution. The upper temporal region of most primitive turtles, including *Proganochelys quenstedti* and *Kayentachelys aprix,* is fully covered by dermal bones, particularly the parietal, postorbital, and squamosal. A contact between the parietal and squamosal is typically present in



a) *Proganochelys quenstedti*
b) *Kayentachelys aprix*
c) *Meiolania platyceps*
d) *Erymnochelys madagascariensis*
e) *Emydura macquarrii*
f) *Geoclemys hamiltonii*
g) *Gopherus polyphemus*
h) *Platysternon megacephalum*

Figure 4. Lateral views of skulls of select *Testudinata.* **a.** *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **b.** *Kayentachelys aprix* Gaffney et al. 1987, redrawn from Gaffney et al. (1987). **c.** *Meiolania platyceps* Owen 1886, redrawn from Gaffney (1983). **d.** *Erymnochelys* (orig. *Dumerilia*) *madagascariensis* (Grandidier 1867), redrawn from Gaffney (1979a). **e.** *Emydura* (orig. *Hydraspis*) *macquarrii* (Gray 1831b), redrawn from Gaffney (1979a). **f.** *Geoclemys* (orig. *Emys*) *hamiltonii* (Gray 1831b), redrawn from McDowell (1964). **g.** *Gopherus* (orig. *Testudo*) *polyphemus* (Daudin 1802), redrawn from Gaffney (1979a). **h.** *Platysternon megacephalum* Gray 1831a, redrawn from Gaffney (1979a). *Abbreviations:* c.t., cavum tympani; i.c.a., incisura columella auris; ju, jugal; la, lacrimal; mx, maxilla; pf, prefrontal; po, postorbital; qj, quadratojugal; qu, quadrate; sq, squamosal.

those taxa that have no, or very little, upper temporal emargination (Figure 2a–e). In numerous CHELIDS and PANCRYPTODIRES, the temporal roofing is reduced by a posterior emargination that disrupts the contact between the parietal and squamosal (Figure 2f). Unlike Gaffney et al. (1991) and Gaffney (1996), this analysis recognizes the absence of a parietal–squamosal contact in plesiochelyids and several baenids.

The presence or absence of an upper temporal emargination is a commonly used character in analyses of turtle relationships. However, the amount of emargination to the temporal roofing of turtles varies gradually, making it difficult to score this character objectively. To avoid the problems associated with scoring continuous characters, this analysis uses three independent and discrete characters that approximate the amount of temporal emargination in the skull roof: the presence or absence of a parietal–squamosal contact (a proxy for slight emargination, see this character); the presence or absence of a squamosal–postorbital contact (a proxy for intermediate emargination, see character 18); and the contribution of the jugal to the upper temporal rim (a proxy for deep emargination, see character 15).

Character evolution. The parietal–squamosal contact must be considered highly homoplastic with a CI of 0.14 (Figure 18). In the preferred cladogram, a parietal–squamosal contact is lost independently five times along the phylogenetic stems of *Chelodina elongata,* PELOMEDUSOIDES, Baenidae, *Santanachelys gaffneyi*, and CRYPTODIRA. Within Baenidae this contact is reacquired in the clade formed by *Baena arenosa* + *Chisternon undatum* Leidy and within CRYPTODIRA the contact is reacquired in CHELONIOIDEA.

CHARACTER 12: PARIETAL B

Character definition. Parietal contact with the pterygoid, epipterygoid, or palatine (Hirayama et al. 2000, 7a): 0 = absent, trigeminal foramen only developed as a notch; 1 = present, trigeminal foramen clearly formed by the descending process of the parietal.

Morphology and distribution. The parietal of all turtles produces a descending, inferior process that forms an anterior extension to the lateral braincase wall. In *Proganochelys quenstedti,* this inferior process is clearly present, but it only contacts the supraoccipital and prootic, leaving the trigeminal foramen open anteriorly (Figure 3a). A similar condition is seen in the poorly ossified cranium of mature specimens of *Dermochelys coriacea.* In all other known turtles, the inferior process of the parietal is well developed anteroventrally and contacts in addition to the supraoccipital and prootic the pterygoid, epipterygoid, or the palatine. The trigeminal foramen is consequently enclosed from all sides (Figure 3b–f).

Character evolution. In the preferred cladogram, a contact of the inferior parietal process with the pterygoid, epipterygoid, or palatine is a synapomorphy of a clade comprised of *Mongolochelys efremovi* + *Meiolania platyceps* + *Kallokibotion bajazidi* + TESTUDINES, but a singular reversal occurs along the phylogenetic stem of *Dermochelys coriacea* (Figure 18; CI = 0.5). Given that the descending parietal process is not well documented in numerous primitive turtles, including *Proterochersis robusta* Fraas, *Palaeochersis talampayensis, Australochelys africanus,* and *Kayentachelys aprix,* it is not clear whether this character should be considered a synapomorphy of a more inclusive clade of turtles excluding only *Proganochelys quenstedti.*

CHARACTER 13: PARIETAL C

Character definition. Length of anterior extension of the lateral braincase wall (Hirayama et al. 2000, 7b): 0 = short, inferior parietal process only produces a narrow strut anterior to trigeminal foramen, palatine contact absent; 1 = elongate, inferior parietal process produces an extended process anterior to trigeminal foramen, palatine contact commonly present.

Morphology and distribution. With the known exception of *Proganochelys quenstedti* and *Dermochelys coriacea,* all turtles have an inferior parietal process that contacts the palatoquadrate elements ventrally (see character 12), but the extent of the resulting anterior extension to the lateral braincase wall differs markedly. A distinctly short anterior extension to the lateral braincase wall is present in the primitive turtles *Meiolania platyceps* and *Mongolochelys efremovi.* The condition is unclear for *Kayentachelys aprix.* A short extension is also present in PANCHELONIIDAE (Figure 3d), *Solnhofia parsonsi* Gaffney, *Plesiochelys solodurensis* Rütimeyer, and *Santanachelys gaffneyi,* and was previously interpreted as indirect evidence for salt glands in fossil taxa, because the presence of salt glands seems to be correlated with this character in living CHELONIOIDS (Hirayama 1998). All remaining turtles have significantly more extensive anterior extensions to the lateral braincase walls that commonly reach the palatines anteriorly (Figure 3b–c, e–f).

Polarity. This character cannot be polarized using *Proganochelys quenstedti* because this taxon scores as nonapplicable. A short contact is nevertheless considered primitive for turtles, because this condition is present in the primitive turtles *Mongolochelys efremovi* and *Meiolania platyceps* and, more importantly, because a short contact is morphologically intermediate between no contact (as seen in *Proganochelys quenstedti*) and a large contact (as seen in most derived TESTUDINES).

Character evolution. This character requires five character steps in the preferred cladogram (Figure 18; CI = 0.20), with four gains and one subsequent reversal. The acquisition of an extended anterior extension to the lateral braincase wall is an autapomorphy of "Thalassemys moseri," and a synapomorphy of PLEURODIRA, Paracryptodira, and the clade that originates from the common ancestor of *Hangaiemys hoburensis* Sukhanov and Narmandakh and CRYPTODIRA. Within CRYPTODIRA, a short lateral anterior extension of the braincase wall is reacquired as a synapomorphy of CHELONIOIDEA. Interestingly, this hypothesis of character evolution implies that the short extension in such turtles as *Plesiochelys solodurensis* and *Santanachelys gaffneyi* may not be an adaptive feature for marine habitats (Hirayama 1998), but rather just a symplesiomorphy without any specific purpose.

Jugal

CHARACTER 14: JUGAL A

Character definition. Jugal–squamosal contact (Rougier et al. 1995, 8): 0 = present; 1 = absent, contact between postorbital and quadratojugal commonly present.

Morphology and distribution. The jugal of *Proganochelys quenstedti* and *Dermochelys coriacea* is a large element that reaches posteriorly to contact the large squamosal (Figure 4a). In contrast, the jugal and squamosal of *Kayentachelys aprix* and all other turtles are much reduced in size relative to *Proganochelys quenstedti* and do not meet each other, resulting in a broad contact between the postorbital and quadratojugal whenever the temporal region is ossified (Figure 4b–h).

Character evolution. This character requires two character steps in the preferred hypothesis (Figure 18; CI = 0.5). As a first step, a loss of the jugal–squamosal contact unites the clade of turtles that originates from the common ancestor of *Kayentachelys aprix* and TESTUDINES (Clade 4). Given that this character is not documented for *Australochelys africanus, Palaeochersis talampayensis,* and *Proterochersis robusta,* it is not clear if this character should be considered a synapomorphy of a more inclusive clade of turtles to the exclusion of *Proganochelys quenstedti.* The second step occurs as a reversal along the phylogenetic stem of *Dermochelys coriacea.*

CHARACTER 15: JUGAL B

Character definition. Jugal participation to upper temporal rim: 0 = absent; 1 = present, upper temporal emargination extensive.

Morphology and distribution. The upper temporal area of *Proganochelys quenstedti, Kayentachelys aprix,* and most other turtles is ossified well enough to hinder the jugal from contributing to the upper temporal emargination (Figure 4a–e, g–h). This differs from the condition seen in TRIONYCHIDAE, where the upper temporal emargination is so deep that the jugal contributes clearly to its anterior margin. A contribution to the upper temporal emargination is also present in *Geoclemys hamiltonii* and *Staurotypus triporcatus* (Wiegmann) (Figure 4f). This discrete character is a proxy for the development of a deep upper temporal emargination (see character 11).

Character evolution. The acquisition of a contribution of the jugal to the upper temporal rim occurs in the preferred phylogeny once as a synapomorphy of TRIONYCHIDAE and twice as independent autapomorphies of *Staurotypus triporcatus* and *Geoclemys hamiltonii* (Figure 18; CI = 0.33).

JUGAL CONTRIBUTION TO LOWER TEMPORAL RIM

See character 17.

Quadratojugal

CHARACTER 16: QUADRATOJUGAL A

Character definition. Quadratojugal (Shaffer et al. 1997, 47): 0 = present; 1 = absent, due to the presence of a deep lower temporal emargination.

Morphology and distribution. Among turtles, chelids are unique in having an extremely deep lower temporal emargination and the associated loss of the quadratojugal (Figure 4e). The quadratojugal is also lost in several TESTUDINOIDS, such as *Terrapene ornata* (Agassiz), *Heosemys grandis* (Gray), and *Cuora galbinifrons* Bourret (Joyce and Bell 2004). In these taxa, the quadratojugal is not lost because of the absence of a temporal bar, however, but rather due to a lack of ossification of the temporal bar. It is thus reasonable to assert that the condition seen in TESTUDINOIDS is nonhomologous with the condition seen in *chelids*. Quadratojugals are also absent in *Sinemys lens* and *Sinemys gamera* Brinkman and Peng, but this seems to be in conjunction with a lack of ossification of the temporal bar. All other turtles, including *Proganochelys quenstedti* and *Kayentachelys aprix,* clearly have a quadratojugal (Figure 4a–d, f–h).

Character evolution. In the context of the preferred cladogram, the loss of the quadratojugal due to the development of a deep lower temporal emargination is an unambiguous synapomorphy of CHELIDAE (Figure 18; CI = 1.00).

CHARACTER 17: QUADRATOJUGAL B

Character definition. Quadratojugal–maxilla contact (Meylan and Gaffney 1989, 17; Shaffer et al. 1997, 98): 0 = absent; 1 = present.

Morphology and distribution. The quadratojugal and maxilla of *Proganochelys quenstedti, Kayentachelys aprix,* and most other turtles do not contact one another in the cheek region because the jugal lies between them along the lower temporal rim (Figure 4a–g). This condition differs from that seen in an eclectic group of CRYPTODIRES that includes KINOSTERNIDS, *Carettochelys insculpta* Ramsay, and *Platysternon megacephalum,* in which the quadratojugal contacts the maxilla ventral to the lateral exposure of the jugal (Figure 4h). There is no disagreement on the distribution of this character.

Character evolution. A quadratojugal–maxilla contact is acquired three times in the preferred phylogenetic hypothesis (Figure Figure 18; CI = 0.33). This contact is synapomorphic for KINOSTERNIDAE and autapomorphic for *Platysternon megacephalum* and *Carettochelys insculpta.*

QUADRATOJUGAL–POSTORBITAL CONTACT

See character 14.

QUADRATE–OPISTHOTIC CONTACT

See character 49.

FORMATION OF THE FORAMEN STAPEDIO-TEMPORALE

See character 53.

Squamosal

CHARACTER 18: SQUAMOSAL A

Character definition. Squamosal–postorbital contact (Dryden 1988, 28; Meylan and Gaffney 1989, 42; Gaffney et al. 1991, 27; Gaffney 1996, 19; Shaffer et al. 1997, 46, 111; Brinkman and Wu 1999, 19; Hirayama et al. 2000, 11): 0 = present; 1 = absent, temporal roofing well developed, but postorbital short; 2 = absent, due to lower temporal emargination; 3 = absent, due to upper temporal emargination.

Morphology and distribution. The temporal region of *Proganochelys quenstedti, Kayentachelys aprix, Mongolochelys efremovi, Meiolania platyceps,* and most basal PANCRYPTODIRES is characterized by the presence of a large squamosal–postorbital contact on the dorsal skull surface (Figures 2a–d, 4a–c, g). This contact is lost in numerous derived taxa. However, a brief review of the ingroup reveals that this loss is not always due to the development of an upper temporal emargination as previously stated by Gaffney et al. (1991) and Gaffney (1996). In *Podocnemis, Peltocephalus dumerilianus* (Schweigger), *Erymnochelys madagascariensis* (Grandidier), and *Pseudemydura umbrina* Siebenrock, the temporal region is well ossified, but the postorbital is so greatly reduced in size that it is barred from contacting the squamosal posteriorly (Figure 4d). In most representatives of CHELIDAE, a postorbital–squamosal contact is not possible due to the extensive development of the lower temporal emargination (Figures 2e, 4e). Finally, in *Pelomedusa subrufa* (Lacepede) and several derived CRYPTODIRES, this contact is disrupted by the extensive development of the upper temporal emargination (Figures 2f, 4f–g). To document properly the observed range of morphological variation, this character is extended to contain three derived character states.

Character evolution. According to the preferred phylogenetic hypothesis, this character with three derived states requires five evolutionary steps (Figure 18; CI = 0.60). The absence of a squamosal–postorbital contact due to the presence of short postorbitals is a synapomorphy of PELOMEDUSOIDES. The absence of a squamosal–postorbital contact due to the presence of a well-developed lower temporal emargination is a synapomorphy of CHELIDAE. Within PELOMEDUSOIDES, a loss of the squamosal–postorbital contact occurs in *Pelomedusa subrufa* because of the development of a deep upper temporal emargination. The squamosal–postorbital contact is lost two times independently within PANCRYPTODIRA, as an autapomorphy for *Sinemys lens* and as a synapomorphy for the clade formed by TESTUDINOIDEA and TRIONYCHOIDEA.

CHARACTER 19: SQUAMOSAL B

Character definition. Squamosal supraoccipital contact (Hirayama et al. 2000, 10): 0 = absent; 1 = present.

Morphology and distribution. The temporal region of *Proganochelys quenstedti, Kayentachelys aprix,* and most other turtles lack a contact between the squamosal and supraoccipital (Figure 2a–b, d–f). In contrast, an extensive contact between these two bones exists on the dorsal skull surface of meiolaniids and *Mongolochelys efremovi* (Figure 2c). An extensive contact also occurs in the chelid *Pseudemydura umbrina* Siebenrock.

Character evolution. The presence of a squamosal supraoccipital contact is an unambiguous synapomorphy for the clade comprised of *Mongolochelys efremovi* + *Meiolania platyceps* (Figure 18; CI = 1.00).

SQUAMOSAL–JUGAL CONTACT

See character 14.

SQUAMOSAL–PARIETAL CONTACT

See character 11.

FORMATION OF THE ANTRUM POSTOTICUM

See character 35.

SQUAMOSAL–OPISTHOTIC CONTACT

See character 49.

Postorbital

CHARACTER 20: POSTORBITAL A

Character definition. Postorbital–palatine contact (Dryden 1988, 1, 12; Gaffney et al. 1991, 23; Shaffer et al. 1997, 54, 109): 0 = absent; 1 = present, foramen palatinum posterius situated posterior to the orbital wall.

Morphology and distribution. The postorbital of *Proganochelys quenstedti, Kayentachelys aprix, Mongolochelys efremovi, Meiolania platyceps,* and all PANCRYPTODIRES is a rather flat dermal element, which is only thickened slightly along the posterior rim of the orbit (Figure 3a, d–f). In all PLEURODIRES, the postorbital produces a large descending process that forms an ossified posterior orbital wall and contacts the palatine ventrally (best seen in Figure 3b). This ossified posterior orbital wall is probably a supportive structure related to the development of the processus trochlearis pterygoideus, but both structures are coded independently because they are not necessarily correlated. The foramen palatinum posterius is always situated posterior to the orbital wall. Unfortunately, many fossil PANCRYPTODIRES cannot be scored for this character, because the available material is either crushed or not prepared sufficiently to allow observation of the relevant area.

This character is the fusion of two previously used characters: the presence of a postorbital–palatine contact and the position of the foramen palatinum posterius relative to the orbit. The latter character is difficult to score objectively, because the "orbit" of all nonpleurodires is an anatomical region without discrete boundaries. Nevertheless, the foramen palatinum posterius of several PANCRYPTODIRE taxa is clearly situated posterior to the orbital rim (e.g., *Chinemys reevesii* (Gray) and representatives of TRIONYCHIDAE) and seems to be intermediately placed in others. In contrast, because PLEURODIRES have a clearly defined posterior orbital wall due to the postorbital–palatine contact, scoring the relative position of the foramen palatinum posterius is vastly simplified. Because the unambiguous posterior position of the foramen in PLEURODIRES is based on the presence of a posterior orbital wall, both characters are considered correlated here and are thus combined.

Character evolution. The postorbital–palatine contact combined with the formation of a massive posterior orbital wall and the placement of the foramen palatinum posterius posterior to this orbital wall is an unambiguous synapomorphy of PLEURODIRA (Figure 18; CI = 1.00). Given that the anterior skull region is currently not known from any PANPLEURODIRE, it remains possible that this feature may prove to be diagnostic of a more inclusive clade of PANPLEURODIRAN turtles.

POSTORBITAL–PREFRONTAL CONTACT

See Character 10.

POSTORBITAL–SQUAMOSAL CONTACT

See Character 18.

POSTORBITAL–QUADRATOJUGAL CONTACT

See Character 14.

Supratemporal

CHARACTER 21: SUPRATEMPORAL A

Character definition. Supratemporal (Gaffney et al. 1991, 24; Rougier et al. 1995, 35; Hirayama et al. 2000, 12): 0 = present; 1 = absent.

Morphology and distribution. The basal taxa *Proganochelys quenstedti* and *Palaeochersis talampayensis* are unique

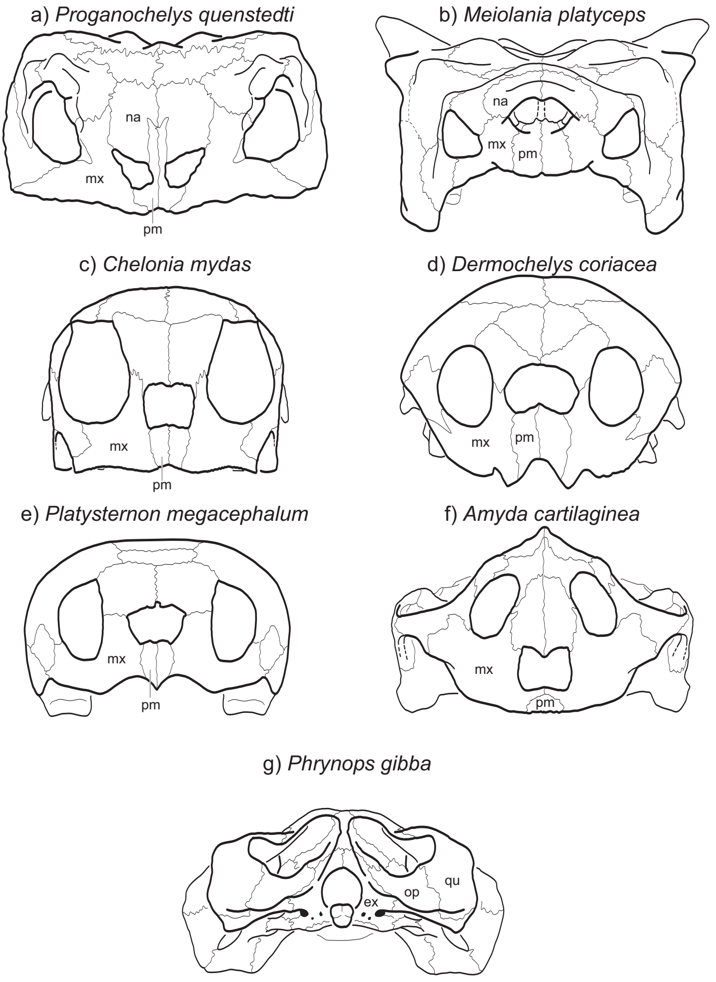

a) *Proganochelys quenstedti*
b) *Meiolania platyceps*
c) *Chelonia mydas*
d) *Dermochelys coriacea*
e) *Platysternon megacephalum*
f) *Amyda cartilaginea*
g) *Phrynops gibba*

Figure 5. Anterior and posterior views of skulls of select *Testudinata.* **a.** *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **b.** *Meiolania platyceps* Owen 1886, redrawn from Gaffney (1983). **c.** *Chelonia* (orig. *Testudo*) *mydas* Linnaeus 1758, redrawn from Meylan (1987). **d.** *Dermochelys* (orig. *Testudo*) *coriacea* (Vandellius 1761), redrawn from Gervais (1872). **e.** *Platysternon megacephalum* Gray 1831a, based on YPM R 12621. **f.** *Amyda* (orig. *Testudo*) *cartilaginea* (Boddaert 1770), redrawn from Meylan (1987). **g.** *Phrynops* (orig. *Emys*) *gibbus* (Schweigger 1812), redrawn from Gaffney (1975b). *Abbreviations:* ex, exoccipital; mx, maxilla; na, nasal; op, opisthotic; pm, premaxilla; qu, quadrate.

among turtles in having a supratemporal bone along the posterior edge of the temporal roof (Figure 2a). It is unclear whether or not this bone is present in *Australochelys africanus.* A supratemporal is clearly absent in all other known turtles, including *Kayentachelys aprix* (Figure 2b–f). There is no disagreement on the distribution of this character.

Character evolution. The loss of a supratemporal is an unambiguous synapomorphy that unites a clade comprised of *Kayentachelys aprix* + *Mongolochelys efremovi* + *Meiolania platyceps* + *Kallokibotion bajazidi* + Testudines (Figure 18; CI = 1.00).

Upper Temporal Emargination

See characters 11, 18, and 15.

Lower Temporal Emargination

See characters 16, 17, and 18.

Premaxilla

Character 22: Premaxilla A

Character definition. Subdivision of external nares by internarial process of premaxilla (Dryden 1988, 11; Rougier et al. 1995, 1; Hirayama et al. 2000, 2): 0 = present; 1 = absent.

Morphology and distribution. The external nares of *Proganochelys quenstedti* and *Palaeochersis talampayensis* are subdivided by a bony internarial process that is formed by the premaxillae, which is a primitive feature seen in most tetrapods (Figure 5a). The external nares are also subdivided by an internarial process in *Kallokibotion bajazidi* as well as some individuals of *Meiolania platyceps* (Figure 5b). The internarial processes of these taxa are different, as they seem to be formed by the nasals in *Kallokibotion bajazidi* and the premaxillae and nasals in the *Meiolania platyceps*. Given that the bony sutures are not preserved well in most taxa with bony septa, all variations regarding the subdivision of the external nares are united into one character state. All remaining turtles, including *Kayentachelys aprix,* have fully confluent bony external nares (Figure 5c–f). In contrast to Hirayama et al. (2000), this analysis scores *Xinjiangchelys latimarginalis* Young and Chow as unknown, because I am unaware of any skulls for this taxon.

Character evolution. In the preferred cladogram, the loss of a nasal septum is a synapomorphy of a clade comprised of *Kayentachelys aprix, Mongolochelys efremovi + Meiolania platyceps + Kallokibotion bajazidi* + TESTUDINES, but a singular reversal occurs along the phylogenetic stem of *Kallokibotion bajazidi* (Figure 18; CI = 0.5). A reversal is also apparent for some *Meiolania platyceps.* However, this reversal is not included in the calculation of the CI in the available phylogenetic software because *Meiolania platyceps* is scored as polymorphic.

CHARACTER 23: PREMAXILLA B

Character definition. Fusion of premaxillae (Meylan and Gaffney 1989, 7; Shaffer et al. 1997, 81): 0 = absent; 1 = present.

Morphology and distribution. The premaxillae of *Proganochelys quenstedti, Kayentachelys aprix,* and most other turtles are paired elements situated at the anterior tip of the snout (Figure 5a–e). This contrasts to the condition seen in all known representatives of TRIONYCHIA, which only have a single, centrally located premaxilla, the likely result of a medial fusion of paired premaxillae (Figure 5f). There is no disagreement on the distribution of this character.

Character evolution. The presence of fused premaxillae unambiguously unites TRIONYCHIA (Figure 18; CI = 1.00).

CHARACTER 24: PREMAXILLA C

Character definition. Foramen praepalatinum (Meylan and Gaffney 1989, 8): 0 = present; 1 = absent, premaxillae well ossified; 2 = absent, foramen intermaxillaris present.

Morphology and distribution. The premaxillae of *Proganochelys quenstedti, Kayentachelys aprix,* and most other turtles are well-developed elements that form much of the anterior rim of the palate and are pierced by paired foramina, known as the foramina praepalatinum (Figure 3a–c, f). The premaxillae of CHELONIIDS are also well-developed elements, but foramina praepalatinum are absent (Figure 3d). In contrast, the anterior palate of TRIONYCHIANS is ossified poorly, with a gaping foramen intermaxillaris (Figure 3e). Given that the bony portions of the premaxillae that normally form the foramina praepalatinum are absent, these foramina are not developed in TRIONYCHIANS either. However, as in turtles with a bony foramen praepalatinum, the anterior nasal artery traverses the foramen intermaxillaris (Albrecht 1967). This analysis disagrees with that of Meylan and Gaffney (1989) in that it does not acknowledge the presence of a foramen intermaxillaris in *Staurotypus triporcatus.* Rather, a simple medially fused foramen praepalatinum similar to that of *Dermochelys coriacea* is recognized. This character is also scored as uncertain for *Santanachelys gaffneyi,* because the vomeral and premaxillary morphology apparent from the figure seems to contradict the observations made by Hirayama (1998).

Character evolution. With two character evolutions for two character states, the CI of this character is 1.00 (Figure 18). The absence of praepalatine foramen, despite the presence of well-ossified premaxillae, is a synapomorphy of CHELONIIDAE. The absence of this foramen due to the development of a large foramen intermaxillaris is an unambiguous synapomorphy for Trionychia.

CHARACTER 25: PREMAXILLA D

Character definition. Exclusion of premaxillae from apertura narium externa (Shaffer et al. 1997, 87): 0 = absent; 1 = present.

Morphology and distribution. The premaxillae of *Proganochelys quenstedti, Kayentachelys aprix,* and most other TESTUDINATES are well-developed elements that not only form significant portions of the anterior labial margin, but also the anteroventral rim of the apertura narium externa (Figure 5a–e). This condition differs from that in all TRIONYCHIDS where the premaxillae are reduced in size and excluded from contribution to the ventral rim of the apertura narium externa by medial contact of the maxillae (Figure 5f). A medial contact of the maxillae also exists in some TESTUDINOIDS, but in these taxa the maxillae meet ventral to the premaxillae and consequently do not exclude them from the external narial margin (Joyce and Bell 2004). There is no disagreement on the distribution of this character.

Character evolution. The medial contact of the maxillae along the ventral rim of the apertura narium externa is a unique synapomorphy for the clade comprised of all representatives of TRIONYCHIDAE (Figure 18; CI = 1.00).

CHARACTER 26: PREMAXILLA E

Character definition. Distinct, medial premaxillary hook along the labial margin of the premaxillae (Brinkman and Wu 1999, 44): 0 = absent; 1 = present.

Morphology and distribution. The upper labial margin of *Proganochelys quenstedti, Kayentachelys aprix,* and most other turtles is a toothless, even ridge that bears a horny beak (Figure 5a–d, f). In *Dinochelys whitei, Glyptops plicatulus, Dracochelys bicuspis* Gaffney and Ye, *Platysternon megacephalum, Staurotypus triporcatus,* and CHELYDRIDS, a distinct medial hook predominantly formed by the premaxillae adorns the upper labial margin (Figure 5e). Other morphologies to the upper labial margin are possible (e.g., fine serrations or distinct paired maxillary "teeth"), but they are not considered homologous herein. This character is nondiscrete and is subject to a considerable amount of interspecific variation, as is the case with most characters pertaining to the sculpturing of the labial jaw margin (see Joyce and Bell 2004).

Character evolution. The presence of a medial premaxillary hook is a rather homoplastic character within the context of the preferred phylogenetic hypothesis (Figure 18; CI = 0.20). It occurs as independent synapomorphies for the clades comprised of *Dinochelys whitei* + *Glyptops plicatulus* and *Chelydra serpentina* + *Macroclemys temminckii* (Troost). This character furthermore arose independently as autapomorphies for *Platysternon megacephalum, Chelonia mydas* L., and *Staurotypus triporcatus.* More homoplasies will likely result from the addition of more taxa.

Maxilla

MAXILLA–QUADRATOJUGAL CONTACT

See character 17.

MEDIAL CONTACT OF MAXILLAE

See character 25.

MAXILLA FORM ANTEROVENTRAL RIM OF EXTERNAL NARES

See character 25.

Vomer

CHARACTER 27: VOMER A

Character definition. Vomer (Dryden 1988, 7; Gaffney et al. 1987, 2b; Meylan and Gaffney 1989, 9; Gaffney et al. 1991, 3; Rougier et al. 1995, 6; Hirayama et al. 2000, 15): 0 = paired; 1 = single; 2 = single, greatly reduced or absent.

Morphology and distribution. *Proganochelys quenstedti* and *Palaeochersis talampayensis* are unique among turtles in having a paired vomer, which is the ancestral amniote condition (Figure 6a). All remaining turtles with vomers, including *Kayentachelys aprix,* have a single, fused vomer (Figure 6b–c, e–f). This unpaired vomer is greatly reduced or even absent in representatives of PELOMEDUSOIDES (Figure 6d). The assertion that the vomer is reduced in size in representatives of TRIONYCHIA relative to the condition seen in other CRYPTODIRES (Meylan and Gaffney 1989) is factually correct. However, the vomer of these taxa is still significantly larger than those seen in PELOMEDUSOIDS (Figure 6d, f). This analysis consequently scores TRIONYCHIANS as having a regularly sized vomer.

Character evolution. This character is highly consistent with a CI of 1.00 (Figure 18). The medial fusion of the paired vomer is an unambiguous synapomorphy of a clade comprised of *Kayentachelys aprix* + *Meiolania platyceps* + *Mongolochelys efremovi* + *Kallokibotion bajazidi* + TESTUDINES. Within this clade, the vomer is greatly reduced along the phylogenetic stem of Pelomedusoides.

CHARACTER 28: VOMER B

Character definition. Vomer–pterygoid contact in palatal view (Shaffer et al. 1997, 75; Hirayama et al. 2000, 17): 0 = present; 1 = absent, medial contact of palatines present.

Morphology and distribution. The paired vomer of *Proganochelys quenstedti* consists of elongate elements that articulate with the premaxilla anteriorly and the pterygoid posteriorly (Figure 6a). The same topological relationship holds true for the single vomer of most other turtles (Figure 6b–c, d). *Solnhofia parsonsi,* "Thalassemys moseri," *Santanachelys gaffneyi*, and representatives of TRIONYCHIA have a well-developed vomer, but in dorsal and ventral view, it is separated from the pterygoid by an extensive medial contact of the palatines (Figure 6f). In some CHELIDS, the vomer is greatly reduced in size, but it maintains a small contact with the pterygoid within the interorbital cavity. The vomer is greatly reduced in PELOMEDUSOIDS and a posterior contact with the pterygoid is absent whenever the vomer is present (Figure 6d). This loss of a contact was not acknowledged by Shaffer et al. (1997). The vomer and palatines are not preserved in *Pleurosternon bullockii* and are consequently scored as uncertain. *Sinemys* is scored absent, following Hirayama et al. (2000).

Character evolution. Within the context of the preferred phylogenetic hypothesis, the absence of a vomer–pterygoid contact in palatal view must be considered an independently derived synapomorphy for three clades of turtles (Figure 18; CI = 0.33): PELOMEDUSOIDES, TRIONYCHIA, and the clade comprised of *Solnhofia parsonsi,* "Thalassemys moseri," and *Santanachelys gaffneyi.* No reversals occur within these clades.

CHARACTER 29: VOMER C

Character definition. Vomerine and palatine teeth (Rougier et al. 1995, 10; Hirayama et al. 2000, 14, 16): 0 = present; 1 = absent.

Morphology and distribution. *Proganochelys quenstedti* is unique among turtles in having several rows of palatal teeth on its vomers and palatines (Figure 6a). All other turtles, including *Kayentachelys aprix,* clearly lack vomerine and palatine teeth (Figure 6b–f).

Character evolution. The loss of vomerine and palatine teeth is an unambiguous synapomorphy that unites all turtles to the exclusion of *Proganochelys quenstedti* (Figure 18; CI = 1.00).

VOMER BASISPHENOID CONTACT

See character 44.

Palatine

CHARACTER 30: PALATINE A

Character definition. Palatine contribution to anterior extension of lateral braincase wall (Shaffer et al. 1997, 68): 0 = absent; 1 = present, well developed.

Morphology and distribution. The anterior extension of the lateral braincase wall anterior to the trigeminal foramen is not ossified in *Proganochelys quenstedti* and *Dermochelys coriacea* (see character 12). In most other turtles, the descending process of the parietal is well developed and forms the entire extension anterior to the trigeminal foramen with minor contribution from the pterygoid (Figure 3b–d, f). In contrast, in representatives of TRIONYCHIA and KINOSTERNOIDEA the extension is formed or supported by a distinct ascending process of the palatines (Figure 3e). There is no disagreement on the distribution of this character.

Character evolution. According to the preferred phylogenetic hypothesis, a strong contribution of the palatine to the formation of the anterior extension of the lateral braincase wall is a unique synapomorphy of TRIONYCHOIDEA (Figure 18; CI = 1.00).

MEDIAL CONTACT OF PALATINES

See character 28.

PALATINE–POSTORBITAL CONTACT

See character 20.

PALATINE–PREFRONTAL CONTACT

See character 6.

PALATINE–BASISPHENOID CONTACT

See character 44.

Quadrate

CHARACTER 31: QUADRATE A

Character definition. Flooring of cavum acustico-jugulare and recessus scalae tympani (Gaffney et al. 1987, 4; Dryden 1988, 6, 8; Gaffney et al. 1991, 9, 21; Gaffney 1996, 8; Rougier et al. 1995, 26; Brinkman and Wu 1999, 8; Hirayama et al. 2000, 22): 0 = absent; 1 = fully or partially present, produced by the posterior process of the pterygoid; 2 = fully or partially present, produced by the ventral process of the quadrate or the prootic, or both.

Morphology and distribution. The middle ear of *Proganochelys quenstedti* and *Kayentachelys aprix* are only poorly ossified (Figure 6a–b). The position and size of the cavum acustico-jugulare and recessus scalae tympani (perilymphatic sinus and perilymphatic sac of Romer 1956) can thus only be estimated. In all known PANPLEURODIRES with skulls preserved, the cavum acustico-jugulare and cavum labyrinthicum are partially floored by a process that ascends from the main body of the quadrate or by a ventral expansion of the prootic, or both. (Figure 6d). In contrast, the cavum acustico-jugulare and cavum labyrinthicum of all remaining turtles is floored by an elongate posterior process of the pterygoid (Figure 6c, e–f). Previous analyses refer in their definitions to the flooring of the middle ear. Given that the middle ear includes all structures between the tympanum and the fenestra ovalis (e.g., cavum tympani, antrum postoticum, stapes, and cavum acustico-jugulare) and that many of these structures are not floored by the pterygoid or quadrate, it seems appropriate to restrict the character definition to the flooring of the acustico-jugulare and recessus scalae tympani only.

This character complex was originally conceived by Gaffney (1975a) to support his proposed dichotomy of living cryptodires and pleurodires. To underline the conclusion that both derived character states must have originated independently from one another, all subsequent analyses scored both derived character states as separate characters (e.g., Dryden 1988; Gaffney et al. 1991; Shaffer et al. 1997), or simply omitted one of the derived character states (e.g., Gaffney 1996; Hirayama et al. 2000).

Some may criticize the placement of both derived morphologies into one character, because it seems to force the homology between both derived states. Operationally, however, both solutions (i.e., two characters, or one character with two derived states) are the same, because both scoring systems will favor the same topology. Nevertheless, if future researchers prefer splitting this character complex into two separate characters once again, modifications are imperative to previous character definitions. In particular, the character definitions of Dryden (1988), Gaffney et al. (1991), and Shaffer et al. (1997) are problematic, because the primitive character states are composites. For instance, the primitive state of the character that pertains to PLEURODIRAN-type flooring of the cavum acustico-jugulare and recessus scalae tympani not only includes the primitive condition seen in *Proganochelys quenstedti* but also the derived morphology seen in PANCRYPTODIRES. However, like derived character states, ancestral character states should only contain one type of ancestral morphology. As an alternative, it would be more appropriate to restrict the primitive character state to the condition seen in *Proganochelys quenstedti* and to score all PANCRYPTODIRES as nonapplicable, because they neither have the primitive nor the derived condition. Failure to do so will weigh against any potential transition between the derived character states implied by the tree, because the transition from one derived character state to another would require two steps (loss of one derived trait, acquisition of the other derived trait) instead of one (transition from one derived state to the other).

Character evolution. The CI of this character with two derived character states is 1.00 (Figure 18). The flooring of the acustico-jugulare and recessus scalae tympani by the pterygoid is an unambiguous synapomorphy for a clade that includes *Meiolania platyceps* + *Mongolochelys efremovi* + *Kallokibotion bajazidi* + TESTUDINES. Within that clade, however, the flooring of the acustico-jugulare and recessus scalae tympani transforms to the quadrate within PANPLEURODIRA.

CHARACTER 32: QUADRATE B

Character definition. Central constriction of the middle ear (Gaffney et al. 1987, 2c; Gaffney et al. 1991, 4; Rougier et al. 1995, 17; Hirayama et al. 2000, 24): 0 = absent; 1 = present, formed by quadrate.

Morphology and distribution. The middle ear (the anatomical region between the tympanum and fenestra ovalis) of *Proganochelys quenstedti* is completely open posteriorly and is not visibly subdivided into chambers (see character 31). In contrast, the middle ear cavity of all TESTUDINES is subdivided by a constriction of the quadrate around the columella into two distinct chambers: the lateral cavum tympani and the medial cavum acustico-jugulare. Previous analysis termed this constriction of the quadrate the lateral wall of the middle ear (e.g., Gaffney et al. 1987; Gaffney et al. 1991; Rougier et al. 1995; Hirayama et al. 2000). This term is imprecise, however, because the tympanum is the lateral, unossified margin of the middle ear. As an alternative, it may be appropriate to call the constriction of the quadrate the lateral wall of the cavum acustico-jugulare.

Australochelys africanus and *Palaeochersis talampayensis* seem to have an intermediate morphology that was attributed to the primitive state by Hirayama et al. (2000) and the derived state by Rougier et al. (1995). Given that *Australochelys*

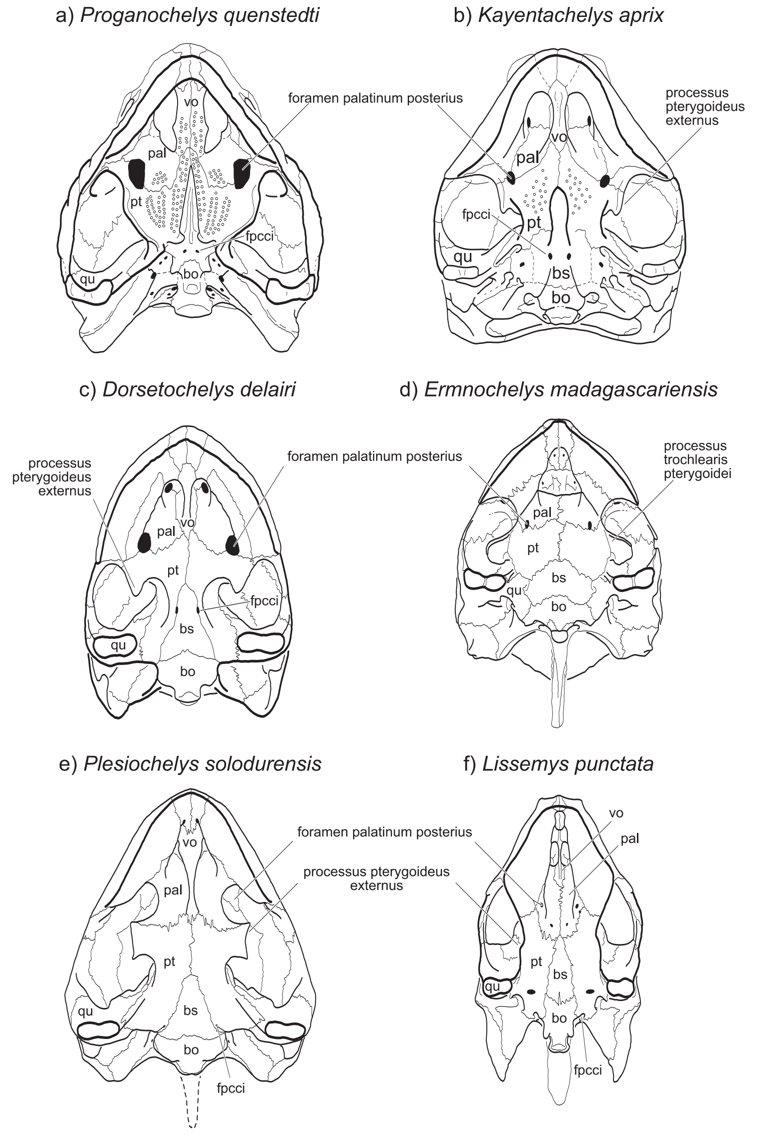


FIGURE 6. Palatal views of skulls of select *Testudinata.* **a.** *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **b.** *Kayentachelys aprix* Gaffney et al. 1987, redrawn from Gaffney et al. (1987). **c.** *Meiolania platyceps* Owen 1886, redrawn from Gaffney (1983). **d.** *Erymnochelys* (orig. *Dumerilia*) *madagascariensis* (Grandidier 1867), redrawn from Gaffney (1979a). **e.** *Plesiochelys solodurensis* Rütimeyer 1873, redrawn from Gaffney (1975d). **f.** *Lissemys* (orig. *Testudo*) *punctata* (Bonnaterre 1789), redrawn from Gaffney (1979a). *Abbreviations:* bo, basioccipital; bs, basisphenoid; fpcci, foramen posterius canalis carotic interni; pal, palatine; pt, pterygoid; qu, quadrate; vo, vomer.

africanus does not show a distinct constriction of the middle ear, this taxon is assigned the primitive state in this analysis. In contrast, *Palaeochersis talampayensis* is designated as uncertain, because the illustrations provided by Rougier et al. (1995) are not sufficient to allow rescoring of the character.

Character evolution. The formation of a central constriction of the middle ear is an unambiguous synapomorphy for the clade comprised of *Kayentachelys aprix* + *Mongolochelys efremovi* + *Meiolania platyceps* + *Kallokibotion bajazidi* + TESTUDINES (Figure 18; CI = 1.00).

CHARACTER 33: QUADRATE C

Character definition. Cavum tympani (Dryden 1988, 31; Rougier et al. 1995, 15): 0 = absent; 1 = partially developed; 2 = fully developed.

Morphology and distribution. The middle ear of *Proganochelys quenstedti* is unique among turtles in lacking any trace of an osseous subdivision into chambers (see character 32). A formed cavum tympani, the outer chamber of the middle ear that bears the tympanum, is consequently absent (Figure 4a). In contrast, all living turtles have a defined cavum tympani, recognizable as a funnel-shaped bony structure that surrounds much of the incisura stapes (Figure 4b–h). The condition seen in *Palaeochersis talampayensis* and *Australochelys africanus* is intermediate and is consequently given its own character state. However, the condition seen in *Australochelys africanus* seems significantly more primitive than *Palaeochersis talampayensis. Kayentachelys aprix* clearly shows a formed cavum tympani (Figure 4b).

Character evolution. This character of two steps has a CI of 1.00 in the preferred hypothesis (Figure 18). The partial formation of a cavum tympani is an unambiguous synapomorphy for the clade that includes all turtles but *Proganochelys quenstedti.* A fully developed cavum tympani is diagnostic for a clade nested within the previous one, to the exclusion of *Australochelys africanus* and *Palaeochersis talampayensis.*

Character 34: Quadrate D

Character definition. Precolumellar fossa (Shaffer et al. 1997, 45): 0 = absent; 1 = large and deep.

Morphology and distribution. Within Testudinata, the cavum tympani was originally formed by the quadrate as a simple, funnel-shaped structure that partially surrounds the stapes (Figure 4b–c, e–h). In contrast, in *Sinemys lens, Ordosemys leios, Dracochelys bicuspis,* and representatives of Pelomedusoides, a deep depression is formed just anterior to the columella, which is called the precolumellar fossa (Figure 4d). According to Shaffer et al. (1997), a precolumellar fossa is only developed among pleurodires in representatives of Pelomedusidae; however, the precolumellar fossa of podocnemids is just as distinctive and, consequently, scored as present here too.

Character evolution. The acquisition of a precolumellar fossa is an independently acquired synapomorphy for two clades (Figure 18; CI = 0.5): Pelomedusoides and the clade comprised of *Sinemys lens + Ordosemys leios + Dracochelys bicuspis*. No reversals occur within these clades.

Character 35: Quadrate E

Character definition. Antrum postoticum (Dryden 1988, 29; Meylan and Gaffney 1989, 13; Rougier et al. 1995, 29): 0 = absent; 1 = present, quadrate does not fully enclose the anterior perimeter of the antrum; 2 = present, quadrate fully encloses the anterior perimeter of the antrum.

Morphology and distribution. As discussed above (see characters 33 and 34), the middle ear region of *Proganochelys quenstedti* does not have any osseous subdivisions into chambers. An antrum postoticum is thus absent (Figure 4a). Based on the central constriction of the quadrate, the middle ear region of all other turtles is subdivided into an inner chamber called the cavum acustico-jugulare and an outer chamber called the cavum tympani (see character 33). In all turtles that have a cavum tympani, this air-filled chamber has a posterior extension called the antrum postoticum, but two morphologies can be distinguished that differ in the degree of ossification to the anterior rim of this structure. In *Kayentachelys aprix, Meiolania platyceps, Mongolochelys efremovi,* and an eclectic mix of pancryptodires, the anterior perimeter of the antrum is not fully formed by the quadrate. As a result, the posterodorsal rim of the cavum tympani is formed by the squamosal, not the quadrate (Figure 4b–c, h). In all remaining turtles, including all pleurodires and numerous cryptodires, the antrum postoticum is fully surrounded by the quadrate along its anterior margin. If the squamosal is removed, the outline of the antrum and the cavum tympani is still visible (Figure 4d–g).

Character evolution. The acquisition of an antrum postoticum is a character that unambiguously unites Clade 4 (Figure 18). Using DELTRAN optimization, a well-ossified anterior rim to the antrum postoticum on the preferred cladogram requires five evolutionary steps, with four acquisitions and a secondary loss (overall CI = 0.16). The acquisitions occur separately along the phylogenetic stems of Pleurodira, *Sinemys lens,* Chelydridae, and the clade comprised of Trionychoidea + Testudinoidea. The secondary loss occurs for Trionychidae. Using ACCTRAN optimization, four acquisitions are required with two subsequent losses. The acquisitions occur independently along the phylogenetic stems of Pleurodira, *Sinemys lens,* and the clade comprised of Chelydridae + Trionychoidea + Testudinoidea. The subsequent losses occur for *Platysternon megacephalum* and Trionychidae.

Character 36: Quadrate F

Character definition. Incisura columellae auris (Dryden 1988, 30; Meylan and Gaffney 1989, 13; Rougier et al. 1995, 21, 22; Shaffer et al. 1997, 59; Hirayama et al. 2000, 26–28): 0 = absent, stapes articulates along the medial side of the quadrate; 1 = present, but open posteroventrally; 2 = present and closed, but only enclosing the stapes; 3 = present and closed, enclosing stapes and the Eustachian tube.

Morphology and distribution. The stapes of *Proganochelys quenstedti* displays the primitive amniote condition in being massive and short, and by articulating laterally with a small facet along the medial side of the quadrate (see Gaffney 1990, fig. 53). In all more derived turtles, including *Australochelys africanus* and *Palaeochersis talampayensis,* the stapes lies in a groove called the incisura columellae auris, which guides the slender columella outwards to articulate directly with the tympanic membrane. Ancestrally, this groove is open posteroventrally (Figure 4b, f), but it may close posteriorly to the stapes to form a canal that completely surrounds and guides the stapes. In numerous cryptodires, the canal is very tight and only contains the actual columella (Figure 4g–h). In contrast, in numerous pleurodires and *Meiolania platyceps,* the incisura columellae auris is closed off much further posteroventrally. The resulting large opening not only contains the stapes but also the Eustachian tube (Figure 4c–e). There is no substantial disagreement regarding the distribution of this character.

Characters that were previously developed to encompass the shape of the stapes (Rougier et al. 1995, 21) and the presence of a stapedial foramina (Dryden 1988, 30) are tentatively synonymized with the presence of an incisura stapes. This is because all three characters seem to be tightly correlated with the development of the impedance matching ear seen in derived turtles.

Character evolution. The evolution of the incisura stapes optimizes to be relatively homoplastic with nine evolutionary steps for two derived characters (Figure 18; CI = 0.22). The primary formation of the incisura is an unambiguous synapomorphy that unites all turtles to the exclusion of *Proganochelys quenstedti*. Within that clade, a tightly closed incisura optimizes as an autapomorphy of *Sinemys lens* and a synapomorphy of the clade comprised of CHELYDRIDAE + TESTUDINOIDEA + TRIONYCHOIDEA, but is subsequently lost independently three times as an autapomorphy of *Adocus beatus* Leidy, a synapomorphy of KINOSTERNOIDEA, and a synapomorphy to the clade formed by *Chrysemys picta* (Schneider) + *Geoclemys hamiltonii*. A closed incisura that includes the Eustachian tube evolved three times independently along the phylogenetic stem of *Meiolania platyceps, Kallokibotion bajazidi,* and PLEURODIRA. No reversals are apparent.

FORMATION OF THE FORAMEN STAPEDIO-TEMPORALE

See character 53.

Epipterygoid

CHARACTER 37: EPIPTERYGOID A

Character definition. Epipterygoid (Dryden 1988, 17; Gaffney et al. 1991, 17): 0 = present; 1 = absent.

Morphology and distribution. Epipterygoids are ancestrally present among tetrapods and should consequently be present in primitive turtles as well. However, the skulls of *Proganochelys quenstedti, Palaeochersis talampayensis,* and *Kayentachelys aprix* are not sufficiently preserved to allow unambiguous assessment. Epipterygoids are present in *Mongolochelys efremovi, Meiolania platyceps,* and all sufficiently preserved PANCRYPTODIRES (best seen in Figure 3f). In contrast, epipterygoids are absent in pleurodires and *Dermochelys coriacea* (Figure 3b–c). Following Gaffney (1975a), baenids are also scored as lacking epipterygoids. However, it is not clear whether this is due to lack of ossification (as in *Dermochelys coriacea*), lack of condrification (as speculated by Gaffney [1975a] for PLEURODIRA), or fusion with surrounding elements (as suggested by Gaffney [1979a]). There is no disagreement regarding the distribution of this character.

Character evolution. According to the preferred hypothesis, epipterygoids are lost three times within TESTUDINATA (Figure 18; CI = 0.33): as an autapomorphy for *Dermochelys coriacea* (due to lack of ossification) and as a synapomorphy for PLEURODIRA (perhaps due to lack of condrification) and Baenidae (perhaps due to fusion).

EPIPTERYGOID PARIETAL CONTACT

See characters 12 and 13.

Pterygoid

CHARACTER 38: PTERYGOID A

Character definition. Pterygoid teeth (Dryden 1988, 2; Gaffney et al. 1991, 10b; Rougier et al. 1995, 9b): 0 = present; 1 = absent.

Morphology and distribution. The pterygoids of *Proganochelys quenstedti, Palaeochersis talampayensis,* and *Kayentachelys aprix* have several rows of small palatal teeth (Figure 6a–b). In all other turtles with palates preserved, pterygoid teeth are lacking (Figure 6c–f). The distribution of this character is generally unambiguous, perhaps with the exception of *Australochelys africanus,* which is expected to have pterygoid teeth based on its overall unmodified morphology and antiquity. Unfortunately, it is not preserved sufficiently to determine the presence of these elements.

Character evolution. The loss of pterygoid teeth is an unambiguous synapomorphy for the clade of turtles comprised of *Mongolochelys efremovi* + *Meiolania platyceps* + *Kallokibotion bajazidi* + TESTUDINES (Figure 18; CI = 1.00).

CHARACTER 39: PTERYGOID B

Character definition. Basipterygoid articulation (Gaffney et al. 1987, 2a; Dryden 1988, 23; Gaffney et al. 1991, 2; Rougier et al. 1995, 24; Hirayama et al. 2000, 19): 0 = open; 1 = fused.

Morphology and distribution. Among tetrapods, the braincase articulates ancestrally with the palatoquadrate elements by means of two kinetic joints. As implied by its name, the anterior of these two joints, the basipterygoid articulation, is formed between the basisphenoid and the pterygoids. A kinetic basipterygoid articulation is present in *Proganochelys quenstedti* (Figure 6a). In all other turtles, the braincase is rigidly attached to the palatoquadrate elements. In particular, the pterygoid broadly contacts the basisphenoid along its palatal surface locking the basipterygoid joint (Figure 6b–f). There is no disagreement on the distribution of this character.

Character evolution. A fused basipterygoid articulation is an unambiguous synapomorphy for all turtles except Proganochelys quenstedti (Figure 18; CI = 1.00).

CHARACTER 40: PTERYGOID C

Character definition. Interpterygoid vacuity (Dryden 1988, 4; Gaffney et al. 1991, 11; Rougier et al. 1995, 11; Gaffney 1996, 6; Brinkman and Wu 1999, 6; Hirayama et al. 2000, 20): 0 = present; 1 = absent.

Morphology and distribution. The pterygoids of *Proganochelys quenstedti* only have a minimal anteromedial contact with one another. The remaining portion of their medial rim frames a long and narrow triangular gap, called the interpterygoid vacuity. The interpterygoid vacuity measures almost the full length of the pterygoids in *Proganochelys quenstedti* (Figure 6a). An interpterygoid vacuity is also present in *Australochelys africanus, Palaeochersis talampayensis,* and *Kayentachelys aprix,* but it is reduced in size relative to the condition seen in *Proganochelys quenstedti* due to a more significant anteromedial contact of the pterygoids (Figure 6b). All remaining turtles lack an interpterygoid vacuity, due to a full medial contact of the pterygoids with one another and with the basisphenoid (Figure 6c–f). There is no disagreement on the distribution of this character.

Character evolution. A closed interpterygoid vacuity is an unambiguous synapomorphy for the clade of turtles comprised of *Mongolochelys efremovi* + *Meiolania platyceps* + *Kallokibotion bajazidi* + TESTUDINES (Figure 18; CI = 1.00).

CHARACTER 41: PTERYGOID D

Character definition. Pterygoid–basioccipital contact (Shaffer et al. 1997, 103; Hirayama et al. 2000, 25): 0 = absent; 1 = present.

Morphology and distribution. The pterygoid of *Proganochelys quenstedti, Palaeochersis talampayensis,* and *Kayentachelys aprix* is a relatively short element that lacks any posterior contact with the basioccipital (Figure 6a–b). With the exception of an eclectic group of more derived turtles, including *Mongolochelys efremovi, Sinemys lens,* all PLEURODIRES (Figure 6d), and some EMYDIDS, the pterygoids of all other turtles have well-developed posterior pterygoid processes that contact the basioccipital (Figure 6c, e–f). This posterior process of the pterygoid should not be confused with the batagurine process of some TESTUDINOIDS (see Joyce and Bell 2004). This analysis differs from Hirayama et al. (2000) by scoring *Kayentachelys aprix, Mongolochelys efremovi,* and *Sinemys lens* as lacking a pterygoid–basioccipital contact.

Character evolution. Using DELTRAN optimization, a pterygoid–basioccipital contact is acquired twice independently and reversed three times (Figure 18; CI = 0.20). The two independent acquisitions occur along the phylogenetic stems of *Meiolania platyceps* and Clade 7. The reversals occur separately for PANPLEURODIRA, *Sinemys lens,* and *Chrysemys picta.* Using ACCTRAN optimization this contact is only acquired once in the common ancestor of *Kallokibotion bajazidi* and TESTUDINES, but is subsequently lost four times.

CHARACTER 42: PTERYGOID E

Character definition. Processus trochlearis pterygoideus (Dryden 1988, 18–19; Gaffney et al. 1987, 3b; Meylan and Gaffney 1989, 11; Gaffney et al. 1991, 7, 20; Rougier et al. 1995, 12–13; Gaffney 1996, 4; Shaffer et al. 1997, 77; Brinkman and Wu 1999, 4; Hirayama et al. 2000, 18): 0 = absent; 1 = present.

Morphology and distribution. The lateral margin of the processus pterygoideus externus of *Proganochelys quenstedti, Palaeochersis talampayensis, Australochelys africanus,* and *Meiolania platyceps* is rounded, revealing no positive evidence of any structures relating to the jaw closure mechanism (Figure 6a). Despite this lack of direct anatomical evidence, the processus pterygoideus externus of primitive turtles likely assisted jaw closure, by guiding the mandible. Many CRYPTODIRES have a vertical flange along the lateral margin of the processus pterygoideus externus (Figure 6b–c, e–f), which is known to guide the mandible during jaw closure (Schumacher 1954). However, this flange is extremely small or even absent in many living CRYPTODIRES, rendering it continuous with the primitive condition. Given that this vertical flange does not seem to have a function that differs from the primitive condition, and given that it is often difficult to distinguish the vertical flange from the primitive morphology, this analysis does not recognize the flange as a derived morphology and includes it in the primitive character state.

In representatives of PLEURODIRA, the processus pterygoideus externus is hypertrophied to form the processus trochlearis pterygoideus (Figure 6d). This processes not only guides the mandible during jaw closure, but also redirects the main adductor tendon posteriorly (Schumacher 1954).

Similar to the flooring of the acustico-jugulare and recessus scalae tympani (character 31), the vertical flange and the processus trochlearis pterygoidei were used by Gaffney (1975a) to underline the putative dichotomy between CRYPTODIRES and PLEURODIRES. All later analyses treated these morphologies as the derived states of two separate characters (e.g., Dryden 1988; Gaffney et al. 1991; Rougier et al. 1995; Gaffney 1996; Shaffer et al. 1997; Hirayama et al. 2000). However, the primitive character states proposed in these studies once again combined the primitive morphology and the derived morphology of the other character into the primitive character state. The difficulties that such an approach will cause are discussed in detail under character 31. Admittedly, the present analysis seems to fall into the same trap by combining the morphology seen in *Proganochelys quenstedti* and CRYPTODIRES into the primitive character state. Within the context of this analysis, however, this is not problematic, because the CRYPTODIRAN morphology is not recognized as a derived character state.

Character evolution. The presence of a processus trochlearis pterygoidei is an unambiguous synapomorphy of Pleurodira (Figure 18; CI = 1).

CHARACTER 43: PTERYGOID F

Character definition. Foramen palatinum posterius (Shaffer et al. 1997, 66): 0 = present; 1 = present, but open laterally; 2 = absent.

Morphology and distribution. Almost all turtles, including *Proganochelys quenstedti* and *Kayentachelys aprix,* have a clearly defined fenestra or foramen along the palatine–pterygoid suture, called the foramen palatinum posterius (Figures 3a–c, e–f, and 6a–d, f). In some primitive marine turtles, including *Plesiochelys solodurensis,* this fenestra is not fully enclosed posterolaterally but its general outline remains intact (Figure 6e). Finally, a foramen palatinum posterius is fully lost in all living CHELONIOIDS (Figure 3d). Because the loss of the foramen palatinum posterius in extant chelonioids could have derived either from the opening of the foramen palatinum posterius (as seen in *Plesiochelys solodurensis*) or from the successive size reduction of the foramen, this character is left unordered. There is no disagreement on the distribution of the derived character states.

Character evolution. According to the preferred phylogenetic hypothesis, this character requires three steps for two derived character states (Figure 18; CI = 0.66). A laterally open foramen palatinum posterius occurs as an autapomorphy for *Plesiochelys solodurensis*, and as a synapomorphy for the clade formed by "Thalassemys moseri" + *Santanachelys gaffneyi.* In contrast, the absence of a foramen palatinum posterius is an unambiguous synapomorphy of CHELONIOIDEA.

CHARACTER 44: PTERYGOID G

Character definition. Medial contact of pterygoids (Dryden 1988, 9; Meylan and Gaffney 1989, 12; Shaffer et al. 1997, 79):

0 = pterygoids in medial contact with one another for at least part of their length; 1 = absent, contact of the basisphenoid with the vomer or palatines, or both, present.

Morphology and distribution. The pterygoids of primitive turtles, such as *Proganochelys quenstedti, Palaeochersis talampayensis,* and *Kayentachelys aprix,* are separated from one another medially due to the presence of an interpterygoid vacuity (see character 40), but they nevertheless meet anteriorly for at least part of their length (Figure 6a–b). In most derived turtles with a closed interpterygoid vacuity, the pterygoids meet medially for significant portions of their length (Figure 6c–e). The only exception is seen in *Pleurosternon bullockii, Glyptops plicatulus,* and representatives of TRIONYCHIA (Figure 6f), in which a medial contact of the pterygoids is lost owning to a contact of the substantially elongated basisphenoid with the vomer or palatines, or both. There is no disagreement on the distribution of this character.

Character evolution. The medial contact of the pterygoids is lost three times within TESTUDINATA (Figure 18; CI = 0.33). The contact is lost as an autapomorphy for *Hangaiemys hoburensis* and as a synapomorphy for TRIONYCHIA. It also occurs as a synapomorphy for Pleurosternidae, thus predicting the presence of this morphology in *Dinochelys whitei.*

CHARACTER 45: PTERYGOID H

Character definition. Pterygoid contribution to foramen palatinum posterius (Brinkman and Wu 1999, 49): 0 = present; 1 = absent.

Morphology and distribution. The foramen palatinum posterius of *Proganochelys quenstedti, Kayentachelys aprix, Meiolania platyceps,* most PLEURODIRES, and most stem–cryptodires is delimited by the palatine anteriorly and the pterygoid posteriorly (Figures 3a–d and 6a–d). In representatives of *Podocnemis* and most CRYPTODIRES the pterygoid is excluded from contributing to the foramen palatinum posterius whenever this foramen is developed. The foramen is thus enclosed solely in the palatine (Figures 3e–f and 6f). Unfortunately, this character is truly gradual and seems to be subject to a considerable amount of ontogenetic variation (see Joyce and Bell 2004 for TESTUDINOIDEA).

Character evolution. The exclusion of the pterygoid from the posterior palatine foramen is a highly homoplastic character that optimizes using DELTRAN to four evolutionary acquisitions and one subsequent reversal (Figure 18; CI = 0.20). Of the four acquisitions, three occur as autapomorphies for *Podocnemis expansa* (Schweigger), *Boremys pulchra* (Lambe), and *Chisternon undatum.* The fourth acquisition unites a highly inclusive clade of CRYPTODIRES that consists of CHELYDRIDAE + TRIONYCHOIDEA + TESTUDINOIDEA. Within that clade, this character is lost as an autapomorphy of Zangerlia neimongolensis. The evolution of this character is rather similar when using ACCTRAN optimization; however, within Baenidae an acquisition optimizes to be a synapomorphy to the clade formed by *Boremys pulchra* + *Chisternon undatum* + *Baena arenosa,* but it is subsequently lost in the latter of these three terminals.

PTERYGOID–VOMER CONTACT

See character 28.

PTERYGOID–PARIETAL CONTACT

See characters 12 and 13.

FLOORING OF CAVUM ACUSTICO-JUGULARE AND CAVUM LABYRINTHICUM

See character 31.

TROCHLEAR SYSTEMS

See characters 20 and 42, and Appendix 2.

Supraoccipital

CHARACTER 46: SUPRAOCCIPITAL A

Character definition. Crista supraoccipitalis (Rougier et al. 1995, 30): 0 = poorly developed; 1 = protruding significantly posterior to the foramen magnum.

Morphology and distribution. The supraoccipital of all turtles has a vertical crest called the crista supraoccipitalis. In *Proganochelys quenstedti, Kayentachelys aprix, Pleurosternon bullockii, Glyptops plicatulus,* "Thalassemys moseri," baenids, and some CHELIDS, the crista supraoccipitalis is only poorly developed and does not reach posteriorly much beyond the foramen magnum, if at all (Figure 6a–c). In contrast, all remaining turtles have a well-developed crista supraoccipitalis that may protrude far beyond the level of the foramen magnum (Figure 6d–f).

The character originally developed by Rougier et al. (1995) only pertains to the presence of a supraoccipital crest. However, given that all turtles, including *Proganochelys quenstedti,* have minimally a poorly developed supraoccipital crest, this character is uninformative. In this analysis, the character is reworded to encompass the variation that does exist among turtles and to better capture the character definition probably originally intended by Rougier et al. (1995).

Character evolution. The presence of a supraoccipital crest is a rather homoplastic character within the context of the preferred phylogenetic hypothesis (Figure 18; CI = 0.25). Primarily, it occurs as a synapomorphy for an inclusive clade that includes *Mongolochelys efremovi* + *Meiolania platyceps* + *Kallokibotion bajazidi* + TESTUDINES. Within that clade, however, three reversals occur along the phylogenetic stems of "Thalassemys moseri," Paracryptodires, and the clade formed by *Chelodina siebenrocki* Werner + *Phrynops geoffroanus* (Schweigger).

CHARACTER 47: SUPRAOCCIPITAL B

Character definition. Large supraoccipital exposure to dorsal skull roof: 0 = absent; 1 = present.

Morphology and distribution. The roofing of the temporal region of most turtles, including *Proganochelys quenstedti* and *Kayentachelys aprix,* does not include a large contribution from the supraoccipital (Figure 2a–b, f), although the supraoccipital may have a minute dorsal plate along the posterior margin of the temporal roofing (Figure 2d–e). In contrast, the skull roofing of *Meiolania platyceps* and *Mongolochelys efremovi* has a large dorsal exposure of the supraoccipital (Figure 2c). A large, dorsal exposure of the supraoccipital is also present in the CHELID *Pseudemydura umbrina* Siebenrock. It seems that a large contribution of the supraoccipital to the dorsal skull surface is restricted to taxa with well-ossified temporal roofing. However, a correlation is not apparent, given that many well-ossified taxa lack such a dorsal exposure of the supraoccipital.

Character evolution. A large supraoccipital exposure to the dorsal skull roof is an unambiguous synapomorphy to the clade formed by *Mongolochelys efremovi* + *Meiolania platyceps* (Figure 18; CI = 1.00).

SUPRAOCCIPITAL SQUAMOSAL CONTACT

See character 19.

EXCLUSION OF SUPRAOCCIPITAL FROM FORAMEN MAGNUM

See character 48.

Exoccipital

CHARACTER 48: EXOCCIPITAL A

Character definition. Medial contact of exoccipitals dorsal to foramen magnum (Shaffer et al. 1997, 51): 0 = absent; 1 = present.

Morphology and distribution. The exoccipitals are paired bones that frame most of the lateral aspect of the foramen magnum in most turtles. The dorsal rim of the foramen magnum is formed by the supraoccipital ancestrally in amniotes (Romer 1956). In contrast, in some CHELIDS the supraoccipital is excluded from participating to the rim of the foramen magnum by a medial contact of the exoccipitals (Figure 5g). This distribution of this character is not controversial.

Character evolution. A medial contact of the exoccipitals above the foramen magnum is an unambiguous synapomorphy to the clade formed by *Chelodina siebenrocki* + *Phrynops geoffroanus* (Figure 18; CI = 1.00).

BASIOCCIPITAL PTERYGOID CONTACT

See character 41.

Prootic

FLOORING OF CAVUM ACUSTICO-JUGULARE AND CAVUM LABYRINTHICUM

See character 31.

FORMATION OF THE FORAMEN STAPEDIO-TEMPORALE

See character 53.

Opisthotic

CHARACTER 49: OPISTHOTIC A

Character definition. Processus paroccipitalis (Gaffney et al. 1991, 5; Rougier et al. 1995, 34; Hirayama et al. 2000, 23): 0 = loosely articulated to squamosal and quadrate; 1 = tightly sutured to squamosal and quadrate.

Morphology and distribution. The skull of *Proganochelys quenstedti* is unique among turtles in having cranial joints between the braincase and the surrounding palatoquadrate elements, the primitive condition seen in tetrapods (Romer 1956). Anteriorly, the braincase articulates with the pterygoid via the basipterygoid joint (see character 39). Posteriorly the braincase is only lightly attached to the quadrate and squamosal via the paroccipital process (Figure 3a). In all other turtles, the paroccipital processes is tightly connected with the quadrate and commonly with the squamosal as well (Figure 3b–f). The distribution of this character is not controversial.

Character evolution. The fusion of the paroccipital process with the palatoquadrate and dermal skeleton is an unambiguous synapomorphy to a highly inclusive clade that includes all taxa but *Proganochelys quenstedti* (Figure 18; CI = 1.00).

Basisphenoid

CHARACTER 50: BASISPHENOID A

Character definition. Rostrum basisphenoidale (Shaffer et al. 1997, 63): 0 = flat; 1 = rod-like, thick, and rounded.

Morphology and distribution. The shape of the rostrum basisphenoidale differs widely among turtles, making it difficult to find discrete characters. Among others, the rostrum can be flat or rounded, long or short, have fully separated and fully fused trabeculae, and have a well-defined or nondefined sella turcica. Any combination of the above listed morphologies seems to be present, underlining the potential benefits associated with using the rostrum basisphenoidale for phylogenetic reconstruction.

The character that was originally developed by Shaffer et al. (1997) as a synapomorphy for the CHELONIOIDEA refers to the fusion of the trabeculae to a rod-like rostrum basisphenoidale (Figure 3d). Given that many other taxa, particularly PLEURODIRES, also have fused trabeculae (Figure 3b–c), this analysis slightly redefined this character to refer specifically to the thick and rounded rostrum basisphenoidale only found among CHELONIOIDS.

Character evolution. The presence of a rod-like rostrum basisphenoidale is an unambiguous synapomorphy of CHELONIOIDEA (Figure 18; CI = 1.00).

CHARACTER 51: BASISPHENOID B

Character definition. Paired pits on ventral surface of basisphenoid (Gaffney 1996, 16; Brinkman and Wu 1999, 16): 0 = absent; 1 = present.

Morphology and distribution. The basisphenoid of several primitive PANCRYPTODIRES, such as *Xinjiangchelys latimarginalis, Sinemys lens, Ordosemys leios,* and *Judithemys sukhanovi*, is characterized by a pair of pits along the ventral surface. These pits are likely associated with the neck retraction musculature as seen in recent turtles (e.g., Ogushi 1911; Shah 1963). According to Gaffney (1996), these pits are absent in *Dracochelys bicuspis,* but Parham and Hutchison (2003) contest that they are present. As the relevant material was unavailable for farther clarification, this taxon is scored as uncertain.

Brinkman and Wu (1999) postulated that these double pits may be homologous with the V-shaped crest of the basisphenoid associated with the neck retraction musculature in recent CHELONIID turtles. Although this primary homology assessment is generally plausible, it does not necessarily follow and is thus not used here.

Character evolution. The presence of paired pits on the ventral side of the basisphenoid delimits a paraphyletic group of turtles that includes all PANCRYPTODIRES more derived than *Xinjiangchelys latimarginalis* to the exclusion of CRYPTODIRA (Figure 18; CI = 0.50).

BASISPHENOID QUADRATE CONTACT

See character 31.

BASISPHENOID PTERYGOID CONTACT

See character 39.

BASISPHENOID VOMER AND PALATINE CONTACT

See character 44.

Hyomandibular Nerve

CHARACTER 52: HYOMANDIBULAR NERVE A

Character definition. Path of hyomandibular branch of the facial nerve (Dryden 1988, 14; Rougier et al. 1995, 19; Gaffney et al. 1991, 22): 0 = hyomandibular nerve passes through cranio-quadrate space parallel to vena capitis lateralis; 1 = hyomandibular nerve runs independent from vena capitis lateralis.

Morphology and distribution. The exact path of the hyomandibular branch of the facial (VII) nerve is unclear for such primitive turtles as *Proganochelys quenstedti*, because the cranio-quadrate space (i.e., the gap between the basicranium and the surrounding palatoquadrate elements) is unossified in this taxon, leaving no trace of this structure. However, based on outgroup and ingroup comparison, it seems certain that the hyomandibular nerve passed through the cranio-quadrate space somewhat parallel to the vena capitis lateralis in these taxa. In more derived taxa, including all PANCRYPTODIRES, the hyomandibular nerve passes parallel to the vena capitis lateralis through the canalis cavernosus, the ossified canal that primarily contains these structures. In contrast, in all PLEURODIRES the hyomandibular nerve passes through its own canal parallel to the canalis cavernosus, a condition that also occurs in *Meiolania platyceps.* Because the crania of many potentially close relatives of these taxa are not well preserved or described (e.g., *Kallokibotion bajazidi* and *Mongolochelys efremovi*) they were scored here as uncertain.

Character evolution. According to the preferred phylogeny, the formation of a pathway for the hyomandibular nerve separate from the vena capitis lateralis occurred twice during the evolution of turtles (Figure 18; CI = 0.5), as an autapomorphy for *Meiolania platyceps* and as a synapomorphy for PLEURODIRA. Given the many turtles for which this character could not be scored, it is possible that this character actually unites a more inclusive clade.

Stapedial Artery

CHARACTER 53: STAPEDIAL ARTERY A

Character definition. Position of stapedio-temporal canal (Rougier et al. 1995, 23): 0 = posterior to fenestra ovalis between paroccipital process and quadrate; 1 = anterior to fenestra ovalis between quadrate and prootic.

Morphology and distribution. The position of the stapedio-temporal canal, the canal that transmits the stapedial artery, is unique among turtles in *Proganochelys quenstedti* in passing posterior to the fenestra ovalis and exiting between the quadrate and the paroccipital process of the opisthotic (Figure 3a). This is the ancestral amniote condition (Romer 1956). In all other turtles, this structure passes anterior to the fenestra ovalis and exits between the quadrate and the prootic (Figure 3b–f).

Character evolution. The anterior position of the stapedio-temporal canal is an unambiguous synapomorphy that unites all turtles to the exclusion of *Proganochelys quenstedti* (Figure 18; CI = 1.00).

CHARACTER 54: STAPEDIAL ARTERY B

Character definition. Size of foramen stapedio-temporale (Meylan and Gaffney 1989, 1; Shaffer et al. 1997, 67, 92): 0 = relatively large (the size of a large blood foramina); 1 = significantly reduced in size (the size of a nerve foramina); 2 = absent.

Morphology and distribution. The foramen stapedio-temporale (e.g., the dorsal exit of the stapedio-temporal canal into the upper temporal fossa) in most turtles is a large foramen situated between the quadrate and the prootic in the upper temporal fossa (see character 53). Because this foramen marks the exit for the stapedial artery, a major artery to the cranium, this foramen has a rather large diameter. In KINOSTERNOIDS, the foramen stapedio-temporale is significantly reduced in size and resembles a nerve foramen in size. The stapedial artery, together with the associated canal and foramina, is absent in *Baptemys wyomingensis* (Leidy) and *Dermatemys mawii* Gray. There is no disagreement regarding the distribution of this character.

Character evolution. This character with two derived states requires two character steps in the preferred hypothesis (Figure 18; CI = 1.00). A reduced foramen stapedio-temporale unambiguously unites Kinosternidae and may be the ancestral condition of KINOSTERNOIDEA. The absence of a foramen stapedio-temporale is an unambiguous synapomorphy of the clade formed by *Baptemys wyomingensis* + *Dermatemys mawii.*

Jugular Foramina

CHARACTER 55: JUGULAR FORAMINA A

Character definition. Anterior and posterior jugular foramina defined by bone (Rougier et al. 1995, 27, 28): 0 = absent, 1 = present.

Morphology and distribution. The posterior basicranium of *Proganochelys quenstedti, Australochelys africanus,* and

Palaeochersis talampayensis is poorly ossified. As a result, the anterior jugular foramen (i.e., the anterior opening to the canal that contains the vagus and accessory nerves) has a comparatively large diameter and the posterior jugular foramen (i.e., the posterior opening to the same canal) is not developed at all. In contrast, in all other turtles this region of the skull is more completely ossified (Figure 5g). Both the anterior and posterior jugular foramina are thus developed as small foramina. This character complex was originally conceived by Rougier et al. (1995) as two different characters, but because both seem correlated by necessity, they are treated as one in this analysis.

Character evolution. The presence of defined jugular foramina is an unambiguous synapomorphy of the clade that arises from the common ancestor of *Kayentachelys aprix* + *Testudines* (Figure 18; CI = 1.00).

Canalis caroticum

The carotid arterial system has been a major source of information in the attempt to resolve turtle relationships (Dryden 1988, 10; Meylan and Gaffney 1989, 2–3; Gaffney et al. 1991, 12–14, 16; Gaffney 1996, 9–14; Shaffer et al. 1997, 64, 91; Brinkman and Wu 1999, 9–14, 54, 56; Hirayama et al. 2000, 30–31). Although this character complex has been discretized in many different ways, this analysis follows the character definition offered by Hirayama et al. (2000). Additional characters could be added in the future; however, given that recent work is revealing difficulties with the primary homology of many characters pertaining to the carotid system (Jamniczky 2003), this analysis refrains from incorporating additional carotid characters.

Character 56: Canalis caroticum A

Character definition. Foramen posterius canalis caroticum internus: 0 = formed by basisphenoid only; 1 = formed by both basisphenoid and pterygoid halfway along the basisphenoid–pterygoid suture; 2 = formed by prootic only; 3 = formed mostly or fully by pterygoid, foramen positioned near the posterior end of the basisphenoid.

Morphology and distribution. The foramen posterius canalis caroticum internus, the entry point of the internal carotid artery, has a variable position among turtles. In many basal turtles, such as *Proganochelys quenstedti* and *Kayentachelys aprix,* this foramen is positioned fully within the basisphenoid (Figure 6a–b). In *Glyptops plicatulus, Pleurosternon bullockii,* and baenids the internal carotid enters the skull in the foramen, which is situated halfway along the basisphenoid pterygoid suture (Figure 6c). In many PLEURODIRES the foramen is formed entirely by the prootic. Finally, in *Meiolania platyceps* and most PANCRYPTODIRES the foramen posterius canalis caroticum internus is positioned near the posterior rim of the skull and is formed by the pterygoid only (Figure 6e–f).

Character evolution. According to the preferred phylogenetic hypothesis, this character optimizes to have five evolutionary steps for three derived character states (Figure 18; CI = 0.60). A foramen posterius canalis caroticum internus that is positioned halfway along the basisphenoid–pterygoid suture is an unambiguous synapomorphy for Paracryptodira + *Dorsetochelys delairi* Evans and Kemp. In contrast, the formation of the foramen posterius canalis caroticum internus by the prootic only is an autapomorphy for *Pelomedusa subrufa* and a synapomorphy of CHELIDAE. Finally, the formation of this foramen by the pterygoid is an autapomorphy for *Meiolania platyceps* and a synapomorphy of PANCRYPTODIRA. Interestingly, all five evolutionary steps are independent acquisitions of the three derived states from the primitive condition.

Fenestra perilymphatica

Character 57: Fenestra perilymphatica A

Character definition. Fenestra perilymphatica (Gaffney 1996, 15; Brinkman and Wu 1999, 15; Hirayama et al. 2000, 29): 0 = large; 1 = reduced in size to that of a small foramen.

Morphology and distribution. The fenestra perilymphatica is an opening that connects the cavum labyrinthicum and the recessus scalae tympani within the middle ear. In most turtles, including *Proganochelys quenstedti,* this opening is rather large allowing optimal communication between the two cavities. In contrast, the fenestra perilymphatica of *Pleurosternon bullockii* and baenids is reduced in size to a small foramen. There is no disagreement on the distribution of this character, although this analysis cautiously scores *Glyptops plicatulus* and *Dinochelys whitei* as uncertain.

Character evolution. A small perilymphatic fenestra is an unambiguous synapomorphy of Paracryptodira, to the possible exception of *Dorsetochelys delairi*, for which the condition is unknown (Figure 18; CI = 1.00).

Trigeminal Foramen

Presence of trigeminal foramen

See character 12.

Dentary

Character 58: Dentary A

Character definition. Medial contact of dentaries (Shaffer et al. 1997, 50): 0 = fused; 1 = sutured only (symphysis).

Morphology and distribution. The rami of the lower jaw of most turtles, including *Proganochelys quenstedti,* are tightly fused along the midline (Figure 7a). This condition is reversed to the primitive condition seen in most tetrapods (Romer 1956) in some representatives of CHELIDAE. In these taxa, the rami of the lower jaw are only in sutural contact with one another along the midline and thus easily disarticulate in skeletal specimens. There is no disagreement on the distribution of this character.

Character evolution. The loss of a medially fused dentary is an unambiguous synapomorphy that unites *Phrynops geoffroanus* and *Chelodina siebenrocki* (Figure 18; CI = 1.00).

Splenial

Character 59: Splenial A

Character definition. Splenial (Dryden 1988, 34; Shaffer et al. 1997, 40; Hirayama et al. 2000, 33): 0 = present; 1 = absent.

Morphology and distribution. The splenial is a flat bone that

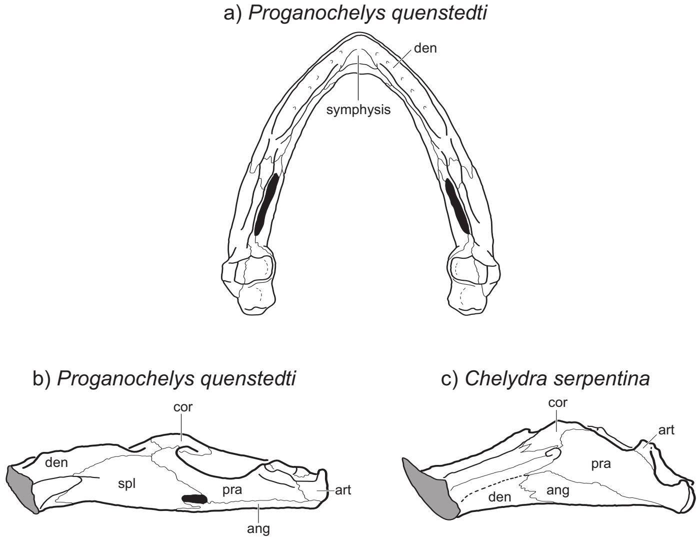


Figure 7. Dorsal and medial views of mandibles of select *Testudinata.* **a, b.** *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **c.** *Chelydra* (orig. *Testudo*) *serpentina* (Linnaeus 1758), redrawn from Gaffney (1972a). *Abbreviations:* art, articular; ang, angular; cor, coronoid; den, dentary; pra, prearticular; spl, splenial.

forms part of the medial wall of the lower jaw of numerous basal turtles, including *Proganochelys quenstedti, Kayentachelys aprix, Meiolania platyceps,* and *Mongolochelys efremovi* (Figure 7b). A splenial is also present in some Chelidae and in most basal pancryptodires. Splenials are lost in Pelomedusoides, derived baenids, and all cryptodires (Figure 7c). The distribution of this character is not controversial.

Character evolution. The loss of splenials serves as a synapomorphy for three different clades (Figure 18; CI = 0.33): Pelomedusoides, Cryptodira, and the clade formed by *Baena arenosa* + *Chisternon undatum.* No reversals occur within those clades.

Carapace

Character 60: Carapace A

Character definition. Carapacial scutes (Meylan and Gaffney 1989, 46a; Shaffer et al. 1997, 78a): 0 = present; 1 = partially present, 2 = absent.

Morphology and distribution. The carapace of *Proganochelys quenstedti* and most other turtles is completely covered by keratinous scutes that provide mechanical protection to the underlying epidermis and bony shell. Actual scutes are extremely rare in the fossil record, but their former presence can nevertheless be inferred confidently based on the presence of sulci, which are grooves in the underlying bone that outline the shape of the overlying scutes (Figure 8a–h). Scutes are limited to the central parts of the carapace in derived representatives of Pancarettochelys and taxa situated along the phylogenetic stem of *Dermochelys coriacea. Dermochelys coriacea* and all trionychids completely lack scutes (Figure 8i).

Character evolution. According to the preferred phylogenetic hypothesis, this character requires four evolutionary steps for two derived character states (Figure 18; CI = 0.50). Scutes were reduced partially twice along the phylogenetic stems of Pandermochelys and Trionychia. Within those clades, scutes were fully reduced in *Dermochelys coriacea* and Trionychidae, respectively.

Character 61: Carapace B

Character definition. Tricarinate carapace (Meylan and Gaffney 1989, 19; Shaffer et al. 1997, 93): 0 = absent; 1 = present, but only poorly developed, 2 = present and pronounced.

Morphology and distribution. The carapaces of *Proganochelys quenstedti, Kayentachelys aprix,* and most other turtles are smooth and show no sculpturing to their dorsal surfaces. In contrast, most pankinosternoids and some testudinoids have a carapace with three continuous, longitudinal keels that run the full length of the costals and neurals. These keels are particularly pronounced in *Staurotypus triporcatus* and *Hoplochelys.* Chelydrids, *Chelus fimbriatus* (Schneider), and *Platychelys oberndorferi* Wagner also have a three-keeled carapace. This ornamentation, however, is not considered homologous with that seen in pankinosternoids, because it does not represent continuous keels but rather rows of protuberances. This analysis differs from that of Meylan and Gaffney (1989) by acknowledging the presence of poorly developed keels in *Baptemys wyomingensis* and *Emarginachelys cretacea* Whetstone.

Character evolution. The evolution of this character is rather complex, with five internested steps for two derived states (Figure 18; CI = 0.4). The presence of slight tricarination is an autapomorphy for *Geoclemys hamiltonii.* This feature is also a synapomorphy for KINOSTERNOIDEA, but tricarination is lost within that clade along the phylogenetic stem of *Dermatemys mawii* and, using DELTRAN optimization, enhanced twice along the phylogenetic stem of *Hoplochelys crassa* (Cope) and *Staurotypus triporcatus,* respectively.

Nuchal

CHARACTER 62: NUCHAL A

Character definition. Articulation of nuchal with neural spine of eighth cervical vertebra (Shaffer et al. 1997, 62; Brinkman and Wu 1999, 55; Hirayama et al. 2000, 58): 0 = cervical articulates with nuchal along a blunt facet; 1 = articulation absent; 2 = cervical articulates with nuchal along a raised pedestal.

Morphology and distribution. The nuchal of *Kayentachelys aprix* is characterized by a posteriorly located single facet along its visceral side for loose articulation with the enlarged neural spine of the eighth cervical vertebra. Such an articulation is also known from *Proganochelys quenstedti* (Figure 9a) and is even sutural in some individuals. The fusion of the eighth cervical vertebra of *Proganochelys quenstedti* is functionally correlated with the absence of clearly developed central and zygapophyseal articular surfaces between the cervical and dorsal vertebral column. An articulation between the neural spine of the eighth cervical vertebra and the nuchal is also present in *Mongolochelys efremovi,* whereas *Meiolania platyceps* is even known to have an articulation with cervical VII, in addition to VIII (Gaffney 1996). In representatives of CHELONIOIDEA, the eighth cervical also articulates with the nuchal. However, the articular site is not a blunt facet, but rather a similarly located, but raised, pedestal (Figure 9c). All remaining turtles show no evidence of an osseous articulation between the cervical column and the nuchal (Figure 9b, d–e). Articulation sites between the eighth cervical vertebra and the nuchal have been reported for *Carettochelys insculpta* and *Peltochelys duchastelli* (Meylan 1987). These are not considered homologous herein with those seen in *Proganochelys quenstedti,* however, because they are not the result of articulations between the neural spines of the cervical column and the nuchal bone, but rather seem to be crests for muscular attachment.

The observed character state distribution differs from Hirayama et al. (2000) in scoring *Proganochelys quenstedti, Palaeochersis talampayensis,* and *Kallokibotion bajazidi* as 0 and not 2. As a result, the presence of an articulation is considered primitive for TESTUDINATA.

Character evolution. According to the preferred phylogenetic hypothesis, this character requires two evolutionary steps (Figure 18; CI = 1.00). The absence of cervical articulation with the nuchal through a blunt facet is an unambiguous synapomorphy for TESTUDINES. Within that clade, the acquisition of a nuchal pedestal for a regained osseous contact of the cervical column with the nuchal is an unambiguous synapomorphy of PANCHELONIOIDEA. This distribution confirms that the nuchal pedestal of PANCHELONIOIDS is not homologous with the articular site seen in *Proganochelys quenstedti.*

CHARACTER 63: NUCHAL B

Character definition. Elongate costiform processes of nuchal (Shaffer et al. 1997, 56): 0 = absent; 1 = present, process crosses peripheral I to contact peripheral II and sometimes even peripheral III.

Morphology and distribution. The nuchal of most turtles, including *Proganochelys quenstedti, Kayentachelys aprix, Mongolochelys efremovi,* and *Meiolania platyceps* is a trapezoidal element with straight lateral edges (Figure 9a–d). In representatives of CHELYDRIDAE and *Pankinosternoidae*, the nuchal produces long lateral processes that run parallel to the skin-scute sulcus along the visceral side of the carapace and cross peripheral I to contact peripheral II, and sometimes even peripheral III (Figure 9e). Because the process runs along the visceral side of the carapace, it is only visible in ventral view, making it difficult to observe in many fossils. This character is polymorphic for *Dermatemys mawii.*

These observations differ from those of Shaffer et al. (1997) by considering this process clearly present in all living kinosternoids. Conversely, no evidence can be found of a costiform process in any of the many specimens of *Platysternon megacephalum* available for this study.

Character evolution. Using DELTRAN optimization, this character requires three evolutionary steps (Figure 18; CI = 0.33) as an autapomorphy for *Emarginachelys cretacea* and as a synapomorphy of KINOSTERNIDAE on the one hand, and CHELYDRIDAE on the other. Using DELTRAN optimization, this character is acquired independently for CHELYDRIDAE and PANKINOSTERNOIDEA, but subsequently lost in *Baptemys wyomingensis* within the latter taxon.

Neural

CHARACTER 64:
NEURAL A

Character definition. Neural formula 6>4<6<6<6<6 (Meylan and Gaffney 1989, 0): 0 = absent; 1 = present.

Morphology and distribution. The neurals of turtles vary widely in number, size, and form. The most common shapes are square, rectangular, octagonal, and stretched hexagons with the short anterior or posterior sides. The neural column of representatives of Adocidae and Nanhsiungchelyidae (e.g., *Zangerlia neimongolensis* and *Basilemys beatus*) is unique among turtles by exhibiting a pattern commonly depicted as "6>4<6<6<6<6." In particular, the first neural is hexagonal with short posterior sides, the second neural is squarish and smaller than the first and third neural, and the remaining neurals are hexagonal, with short anterior sides that decrease in size towards the posterior (Figure 8g). All other turtles lack this neural configuration (Figure 8a–f, h–i).

Polarity. The neural configuration of *Proganochelys quenstedti* is unclear. However, because all other Triassic and Jurassic turtles with neural pattern do not have the neural formula seen in adocids and nanhsiungchelyids, its presence is considered derived.

Character evolution. The presence of the neural formula 6>4<6<6<6<6 is an unambiguous synapomorphy for the clade formed by *Basilemys variolosa* (Cope) + *Zangerlia neimongolensis* + *Adocus beatus* (Figure 18; CI = 1.00).

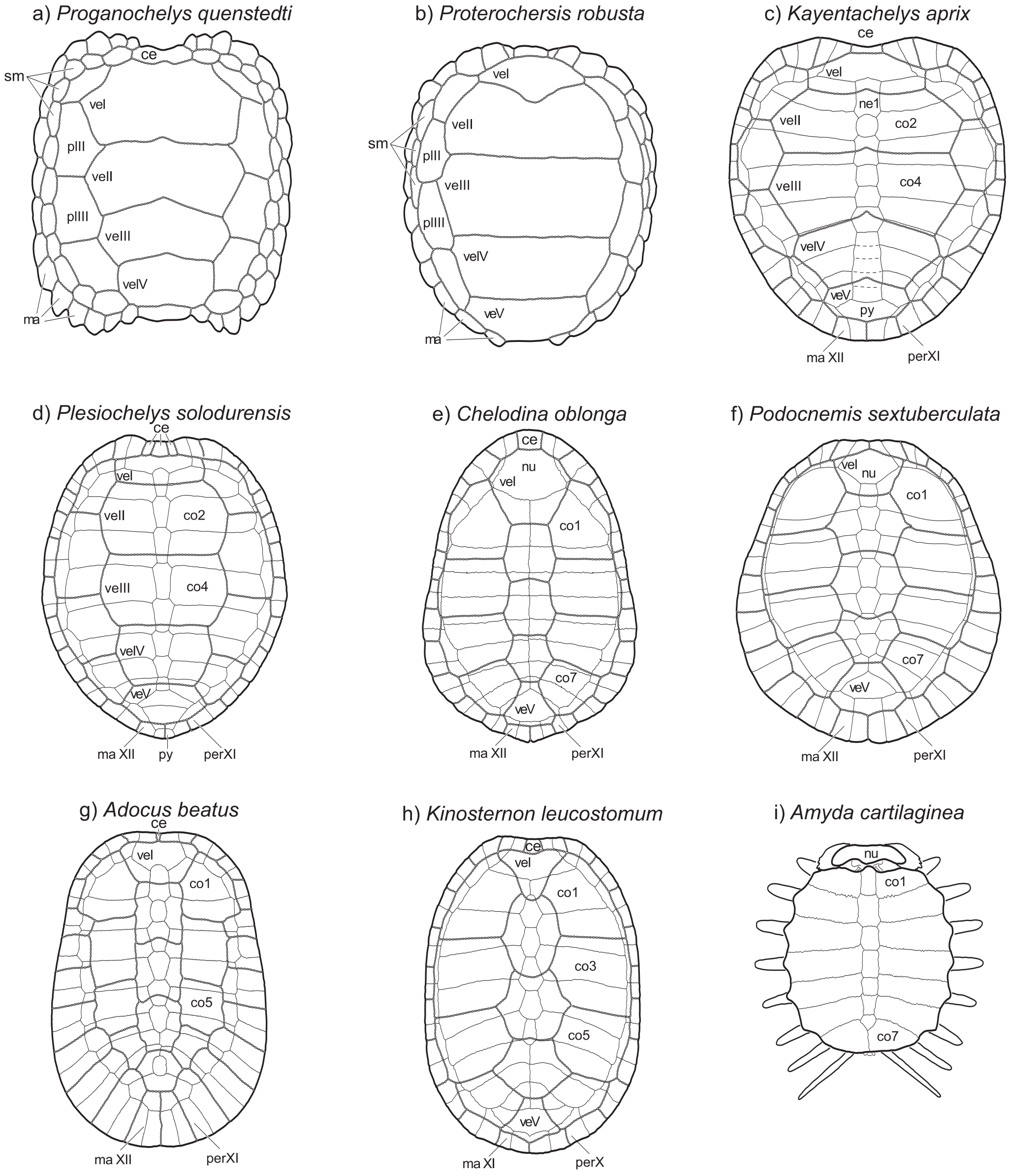


FIGURE 8. Dorsal views of carapaces of select *Testudinata*. **a.** *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **b.** *Proterochersis robusta* Fraas 1913, redrawn from Gaffney (1990). **c.** *Kayentachelys aprix* Gaffney et al. 1987. **d.** *Plesiochelys solodurensis* Rütimeyer 1873, redrawn from Bräm (1965). **e.** *Chelodina oblonga* Gray 1841, redrawn from Boulenger (1889). **f.** *Podocnemis sextuberculata* Cornalia 1849, redrawn from Boulenger (1889). **g.** *Adocus* (orig. *Emys*) *beatus* (Leidy 1865), redrawn from Marsh (1890). **h.** *Kinosternon* (orig. *Cinosternon*) *leucostomum* (Duméril and Bibron 1851), redrawn from Boulenger (1889). **i.** *Apalone* (orig. *Testudo*) *ferox* (Schneider 1783), redrawn from Meylan (1987). *Abbreviations:* ce, cervical scute; co, costal bone; ma, marginal scute; ne, neural bone; nu, nuchal bone; pl, pleural scute; per, peripheral bone; py, pygal bone; sm, supramarginal scute; ve, vertebral scute.

NUMBER OF DORSALLY EXPOSED NEURALS

See character 67.

Peripheral

CHARACTER 65: PERIPHERAL A

Character definition. Number of peripherals (Meylan and Gaffney 1989, 22, 45; Gaffney et al. 1991, 28; Rougier et al. 1995, 40; Shaffer et al. 1997, 83, 95): 0 = more than 11 pairs of peripherals present; 1 = 11 pairs of peripherals present; 2 = 10 pairs of peripherals present; 3 = less than 10 pairs of peripherals present.

Morphology and distribution. The exact number of peripherals is not clear in *Proganochelys quenstedti,* because the peripheral sutures are concealed in all currently known specimens. However, 16 to 17 pairs of marginals were present in this taxon (Gaffney 1990). In all turtles in which the number of peripherals and marginals is known, a tight relationship exists between the two, because marginals typically overlap two adjacent peripherals. As such, turtles have one pair of peripherals less than marginals, which allows the speculation that *Proganochelys quenstedti* could have had 15 to 16 pairs of peripherals. Even if this relationship does not hold true for *Proganochelys quenstedti,* it is reasonable to assume that it had more than 11 pairs of peripherals (Figure 8a). More than 11 pairs of peripherals are also present in some derived CHELONIID turtles, such as Caretta caretta (L.). In *Kayentachelys aprix, Meiolania platyceps, Mongolochelys efremovi,* PANPLEURODIRA, and most PANCRYPTODIRES, only 11 pairs of peripherals are present (Figure 8c–g). This number is further reduced in CARETTOCHELYIDAE and KINOSTERNIDAE (Figure 8h). Formed peripherals are absent in *Dermochelys coriacea* and TRIONYCHIDAE (Figure 8i).

Given how straightforward it is to determine the number of peripherals in turtles with well-developed bony sutures, it is not surprising that there is consensus on the distribution of this character. Using the method described above, however, the poorly preserved taxon *Proterochersis robusta* also shows more than 11 pairs of peripherals (Figure 8b). This contrasts with Gaffney et al. (1991), who coded this taxon as having 11 pairs or less.

Character evolution. This character of three derived character states requires six evolutionary steps (Figure 18; CI = 0.5). The reduction of peripheral elements to 11 pairs or less is an unambiguous synapomorphy of a highly inclusive clade of turtles that include *Kayentachelys aprix* + *Mongolochelys efremovi* + *Meiolania platyceps* + *Kallokibotion bajazidi* + TESTUDINES. Within that clade, the presence of only 10 pairs of peripherals is a synapomorphy for KINOSTERNIDS and a synapomorphy of the clade formed by TRIONYCHIA + *Peltochelys durlstonensis*. Peripherals are lost along the phylogenetic stem of TRIONYCHIDAE, through the reduced state of 10 pairs, and along the phylogenetic stem of *Dermochelys coriacea*, through the reduced state of 11 pairs.

CHARACTER 66: PERIPHERAL B

Character definition. Anterior peripherals incised by musk ducts (Shaffer et al. 1997, 100): 0 = absent; 1 = present.

Morphology and distribution. Most turtles have musk glands that are situated along the contact of the plastron with the carapace. These glands excrete an odorous substance that reaches the surface of the animal through ducts. In taxa with highly ossified bridges, such as *Kayentachelys aprix,* BATAGURIDAE, and PANPLEURODIRA, these musk ducts are visible as small foramina that puncture the bridge region (e.g., Figure 9d). Representatives of KINOSTERNIDAE, in contrast, are unique in having long musk ducts that produce a distinct groove along the visceral side of the anterior peripherals (Figure 9e). Because this feature is so distinct, there is no disagreement on its distribution.

Character evolution. Musk duct grooves are an unambiguous synapomorphy of KINOSTERNIDAE (Figure 18; CI = 1.00).

Costal

CHARACTER 67: COSTAL A

Character definition. Medial contact of costal I: 0 = absent, 1 = present.

Morphology and distribution. In *Proganochelys quenstedti, Kayentachelys aprix,* and most other turtles, the carapace has a complete row of neurals, which prohibit a medial contact of the costals on the dorsal carapacial surface (Figure 8a–g, i). In contrast, *Kinosternon flavescens* (Agassiz) and *Sternotherus odoratus* L. still have a complete set of neurals that separate most costals, but the first pair of costals has a medial contact anterior to the first neural and posterior to the nuchal (Figure 8h). The first costals of some CHELIDS also contact one another medially; however, this condition is not considered homologous because these taxa lack the dorsal exposure to all neurals (see character 68).

Character evolution. A medial contact of the first pair of costals is an unambiguous synapomorphy of the clade formed by *Kinosternon scorpioides* (L.) and *Sternotherus odoratus* (Figure 18; CI = 1.00).

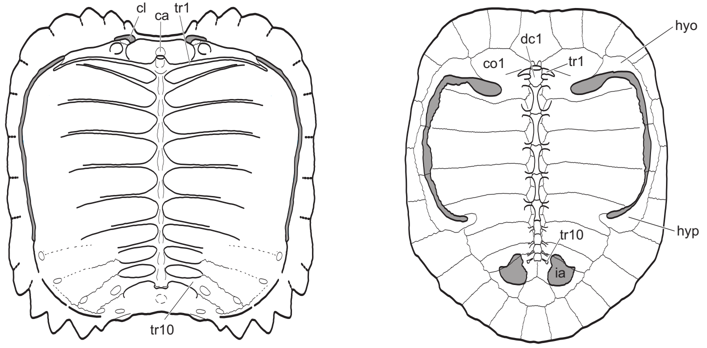
CHARACTER 68: COSTAL B

Character definition. Medial contact of posterior costals (Meylan and Gaffney 1989, 21): 0 = absent, 1 = medial contact of up to three posterior costals present; 2 = medial contact of all costals present.

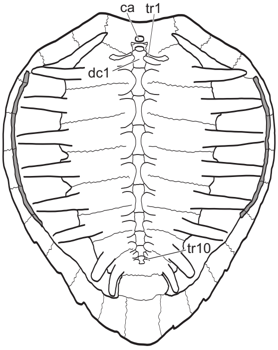
Morphology and distribution. In *Proganochelys quenstedti, Kayentachelys aprix, Mongolochelys efremovi, Meiolania platyceps,* and most basal PANPLEURODIRES and PANCRYPTODIRES, a complete series of neurals fully hinders any medial contact of the costals along the dorsal surface of the carapace (Figure 8a–d). This is in contrast to the situation in some derived CRYPTODIRES and PLEURODIRES, which have a reduction or loss of one to several posterior neurals, allowing a medial contact of as many as three posterior costals (Figure 8f–i). Some representatives of CHELIDAE have a complete reduction of the neurals on the dorsal surface of the carapace, resulting in a medial contact of all eight pair of costals (Figure 8e). The coding of this character is not controversial.

Character evolution. With seven evolutionary steps for two derived character states, this character is relatively homo-

a) *Proganochelys quenstedti* b) *Erymnochelys madagascariensis*



c) *Eretmochelys imbricata*



d) *Geoclemys hamiltonii* e) *Sternotherus odoratus*

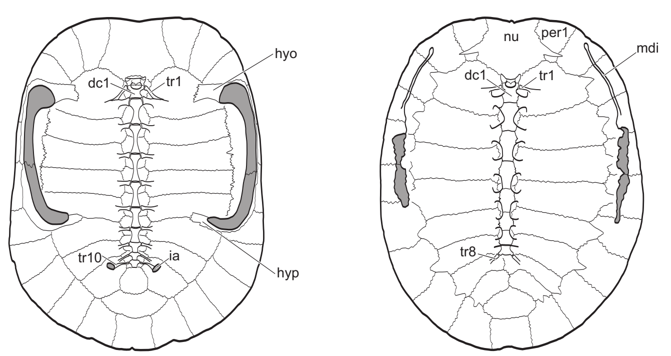


FIGURE 9. Ventral view of carapaces of select *Testudinata*. **a.** *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **b.** *Erymnochelys* (orig. *Dumerilia*) *madagascariensis* (Grandidier 1867), based on YPM R 10884. **c.** *Eretmochelys* (orig. *Testudo*) *imbricata* (Linnaeus 1766), based on YPM R 10569. **d.** *Geoclemys* (orig. *Emys*) *hamiltonii* (Gray 1831b), based on YPM R 10399. **e.** *Sternotherus* (orig. *Testudo*) *odoratus* (Latreille 1801), based on YPM R 13622. *Abbreviations:* ca, cervical articulation; cl, cleithrum; co, costal; dc, dorsal centrum; hyo, hyoplastron; hyp, hypoplastron; ia, iliac articulation; mdi, musk duct incision; nu, nuchal bone; per, peripheral bone; tr, thoracic rib.

plastic (Figure 18; CI = 0.29). A medial contact of the posterior costals is a synapomorphy for PLEURODIRA. Within that clade, the acquisition of a medial contact of all costals must be interpreted as having been acquired twice as autapomorphies for *Elseya dentata* (Gray) and *Chelodina siebenrocki* when using DELTRAN, or as a synapomorphy of CHELIDAE with a reversal for *Phrynops geoffroanus* when using ACCTRAN. Within TRIONYCHOIDEA a medial contact of the posterior costals is acquired independently four times: as separate autapomorphies to *Dermatemys mawii* and *Adocus beatus* and as separate synapomorphies to the clade formed by *Kinosternon flavescens* + *Sternotherus odoratus* and to the clade formed by *Peltochelys durlstonensis* Dollo + TRIONYCHIA.

CHARACTER 69: COSTAL C

Character definition. Reduction of costal ossification (Hirayama and Chitoku 1996, 112): 0 = absent, costals fully or almost fully ossified, costal fontanelles small or absent; 1 = present, costals ossified only two thirds the length of the costal ribs, costal fontanelles well developed.

Morphology and distribution. The costals of turtles are composite structures formed by the dorsal ribs and overlying dermal bone. In *Proganochelys quenstedti* and most other turtles, the dermal ossification covers the full length of the ribs. Costal fontanelles are absent or only poorly developed (Figures 8a–h and 9a–b, d–e). In contrast, in numerous turtles adapted to the marine environment, such as CHELONIOIDS and protostegids, the dermal ossification of the costal is poor and typically covers less than two thirds of the costal length, even in adults (Figure 9c). The distribution of this character is not controversial.

Character evolution. The presence of poorly ossified costals is an autapomorphy for *Santanachelys gaffneyi* and a synapomorphy for PANCHELONIOIDEA (Figure 18; CI = 0.5).

NUMBER OF COSTALS

See character 114.

Cervical

CHARACTER 70: CERVICAL A

Character definition. Cervical (Shaffer et al. 1997, 41): 0 = one cervical present; 1 = cervicals absent, carapacial scutes otherwise present; 2 = more than one cervical present.

Morphology and distribution. Cervicals are defined herein as scutes that only cover the anterior margin of the nuchal. One or more centrally located cervicals characterize the anterior carapacial margin of *Proganochelys quenstedti, Kayentachelys aprix,* and other turtles (Figure 8a–c, e, g–h). Cervicals are absent in *Sinemys lens* and numerous representatives of PLEURODIRA and TESTUDINIDAE (Figure 8f). In contrast, *Plesiochelys solodurensis* and numerous baenids have more than one pair of cervicals (Figure 8d).

Cervical scutes are also absent in *Dermochelys coriacea* and all representatives of TRIONYCHIA. However, because all or almost all other scutes are also missing in these taxa, and because the fossil record of these groups does not sufficiently document the succession of the loss of these elements, this character has been reworded to only include the loss of cervicals with the retention of other scutes, to avoid weighting a potentially homoplastic character complex (see Carapace A).

Character evolution. The number of cervical scutes optimizes as a relatively homoplastic character on the preferred tree (Figure 18; CI = 0.20). Cervical scutes are lost as an autapomorphy to *Elseya dentata* and *Sinemys lens* and as a synapomorphy to PELOMEDUSOIDES. In contrast, additional cervical scutes are gained as an autapomorphy to Plesiochelys solodurensis and as a synapomorphy to the clade consisting of *Baena arenosa* + *Chisternon undatum* + *Boremys pulchra.*

Supramarginal

CHARACTER 71: SUPRAMARGINAL A

Character definition. Supramarginals (Gaffney et al. 1991, 29; Rougier et al. 1995, 41; Gaffney 1996, 36; Brinkman and Wu 1999, 36; Hirayama et al. 2000, 57): 0 = complete row present, fully separating marginals from pleurals; 1 = partial row present, incompletely separating marginals from pleurals; 2 = absent.

Morphology and distribution. The pattern of scutes on the carapace of *Proganochelys quenstedti* differs from that of most other turtles in having a row of supramarginals that completely separates the marginals from the pleurals (Figure 8a). A complete row of supramarginals also seems to be present in *Palaeochersis talampayensis.* The supramarginal row is reduced to three elements in *Proterochersis robusta,* allowing only separation of the anterior marginal and pleurals (Figure 8b). A partial row of supramarginals is also known from *Platychelys oberndorferi* and *Macroclemys temminckii.* All remaining turtles show no supramarginals (Figure 8c–h). Some fossil and living taxa, such as *Palaeomedusa testa* von Meyer or *Caretta caretta,* have a single, additional scute anterior to the first pleural, which is commonly referred to as a "supramarginal" (Joyce 2003). Given that all of these taxa are highly derived relative to *Proganochelys quenstedti* and not closely related to one another, herein this additional scute is considered nonhomologous with "true" supramarginals.

Character evolution. The reduction and loss of supramarginals requires four evolutionary steps for two derived character states (Figure 18; CI = 0.50), but the evolutionary pathway is not unambiguous for basal turtles. A reduction in the number of supramarginal scutes is a synapomorphy for the clade that originates from the common ancestor of *Proterochersis robusta* and TESTUDINES (Clade 3). Within that clade, *Kayentachelys aprix* and TESTUDINES (Clade 4) are united by the complete loss of these scutes. Supramarginals are later reacquired independently along the phylogenetic stems of *Platychelys oberndorferi* and *Macroclemys temminckii.*

Marginal

NUMBER OF MARGINALS

See character 65.

Vertebral

CHARACTER 72: VERTEBRAL A

Character definition. Number of vertebrals (Dryden 1988, 39; Rougier et al. 1995, 39): 0 = four present; 1 = five or more present.

Morphology and distribution. *Proganochelys quenstedti* is unique among turtles in having only four vertebral scutes (Figure 8a). Most other turtles with a keratinous shell have five vertebrals (Figure 8b–h). *Chisternon undatum* has six vertebrals, but in the context of this analysis this characteristic is uninformative. The condition is unknown for *Palaeochersis talampayensis.* The coding of this character is not controversial.

Character evolution. The presence of five vertebrals is an unambiguous synapomorphy that unites the clade that originates from the common ancestor of *Proterochersis robusta* and TESTUDINES (Figure 18; CI = 1.00). Given that the condition is unclear for *Palaeochersis talampayensis* and *Australochelys africanus,* this character may unite a more inclusive clade.

CHARACTER 73: VERTEBRAL B

Character definition. Shape of vertebrals (Dryden 1988, 40; Hirayama et al. 2000, 59): 0 = vertebrals II to IV significantly broader than pleurals; 1 = vertebrals II to IV as narrow or narrower than pleurals.

Morphology and distribution. The carapaces of numerous basal turtles, such as *Proganochelys quenstedti, Proterochersis robusta,* and *Kayentachelys aprix,* are characterized by the presence of vertebrals that are significantly wider than they are long, and several times wider than are the adjacent pleurals (Figure 8a–d). In contrast, the vertebrals of most derived PANPLEURODIRES and PANCRYPTODIRES are as narrow or narrower than the pleurals and may even be longer than they are wide (Figure 8e–h). Unfortunately, among fossils almost every relative vertebral width seems to be present in some taxon, documenting that this is a truly continuous character. Furthermore, among living turtles there is an ontogenetic tendency toward reduction of the relative width of the vertebrals. To minimize the effects associated with ontogenetically variable continuous characters, this analysis uses one derived character state instead of two (Hirayama et al. 2000). The resulting differences in scoring are minimal. The reproducibility of this character is nevertheless considered problematic.

Character evolution. The acquisition of narrow vertebrals occurs four times in the preferred cladogram (Figure 18; CI = 0.25) as an autapomorphy for *Glyptops plicatulus* and as a synapomorphy for PLEURODIRA, Baenidae, and the clade arising from the common ancestor of *Xinjiangchelys latimarginalis* and CRYPTODIRA. No reversals are present.

CHARACTER 74: VERTEBRAL C

Character definition. Position of vertebral II–III sulcus in taxa with five vertebrals: 0 = sulcus positioned on neural VI; 1 = sulcus positioned on neural V.

Morphology and distribution. Among those turtles that have five vertebral scutes, there is systematic variation of the position of the vertebral II–III sulcus relative to the neurals. In *Kayentachelys aprix* and all unambiguous stem-pleurodires, this sulcus is positioned on neural VI (Figure 8c). In contrast, the vertebral II–III sulcus of all remaining turtles crosses neural V (Figure 8d–h). This character is not applicable to turtles that have more or less than five vertebrals, such as is the case in *Chisternon undatum* and *Proganochelys quenstedti.* This character cannot be scored for taxa that lack vertebrals, such as *Dermochelys coriacea* and TRIONYCHIA, or those that lack a dorsal exposure of the neurals (i.e., some CHELIDAE).

Polarity. The position of the vertebral II–III sulcus cannot be scored for *Proganochelys quenstedti* because the neurals of this taxon cannot be observed on the dorsal carapacial surface in the available material. Furthermore, it is questionable weather or not any condition observable in *Proganochelys quenstedti* is homologous with that seen in all other turtles, because this taxon only has four vertebral scutes. Given that the vertebral II–III sulcus crosses the fifth vertebral in all living turtles, but the sixth in many primitive turtles, this analysis concludes that the position on the sixth vertebral is primitive for TESTUDINATA.

Character evolution. Shifting the position of the vertebral II–III scute sulcus from the sixth to the fifth neural occurs as an autapomorphy for *Mongolochelys efremovi.* It furthermore occurs as an independent synapomorphy for PLEURODIRA and PANCRYPTODIRA. Within PANCRYPTODIRA the position of this sulcus shifts back to the original condition as independently acquired autapomorphies to *Santanachelys gaffneyi* and *Peltochelys durlstonensis* (Figure 18; CI = 0.20).

Plastron

CHARACTER 75: PLASTRON A

Character definition. Connection between carapace and plastron (Meylan and Gaffney 1989, 29; Gaffney 1996, 35; Shaffer et al. 1997, 58; Brinkman and Wu 1999, 35): 0 = osseous; 1 = ligamentous.

Morphology and distribution. Even though *Proganochelys quenstedti* is demonstrably the most basal known turtle, this taxon is characterized by a fully developed shell with an ossified bridge. The carapace and plastron meet in this region along a finely interdigitating, osseous suture (Figure 10a–f, i–k). A firm connection between the carapace and plastron is also present in most other basal turtles, all PANPLEURODIRES, and some CRYPTODIRES. In contrast, the bridge region of a diverse group of more derived turtles (e.g., *Meiolania platyceps, Solnhofia parsonsi, Sinemys lens, Xinjiangchelys latimarginalis,* macrobaenids, TRIONYCHIDS, CHELYDRIDS, and CHELONIOIDS) is less ossified. The plastron is primarily attached to the carapace by connective tissue, although peglike bony connections can occur as well (Figure 10g–h, l). As Gaffney (1996) noted, this character is truly continuous, making it difficult to score objectively in some taxa. To allow optimal overlap, this analysis closely follows his character definition. As a result, there is no disagreement on the distribution of the derived character state.

Character evolution. According to the preferred phylogeny, an osseous bridge is lost and reacquired a total of five times (Figure 18; CI = 0.20). The primary loss of the bridge is a synapomorphy that unites the clade formed by *Mongolochelys efremovi* + *Meiolania platyceps* and the clade that arises from the common ancestor of *Solnhofia parsonsi* and CRYPTODIRA. Within CRYPTODIRA an osseous bridge is regained for the clade formed by TESTUDINOIDEA + TRIONYCHOIDEA, but subsequently lost twice along the phylogenetic stem of *Emarginachelys cretacea* and TRIONYCHIA.

CHARACTER 76: PLASTRON B

Character definition. Central plastral fontanelle (Hirayama et al. 2000, 63): 0 = absent in adult individuals; 1 = present, even in adult individuals.

Morphology and distribution. After hatching, most living turtles have an incompletely ossified plastron with large, centrally located bony gaps called fontanelles. In most turtles, including *Proganochelys quenstedti* and *Kayentachelys aprix,* these fontanelles close up during ontogeny through the ossification of the surrounding bones. The plastron of the adult is fully ossified (Figure 10a–f, h–k). In contrast, the plastron of *Mongolochelys efremovi, Meiolania platyceps,* stem-pleurodires, and many aquatic CRYPTODIRES retains a central fontanelle even as an adult (Figure 10g, l). Surprisingly, even though this character requires assessing the ontogenetic stage of fossil taxa, the results of this analysis fully overlap with those of Hirayama et al. (2000). The reproducibility of this character is nevertheless considered poor.

Character evolution. The retention of a central fontanelle in adult individuals is a highly homoplastic character with seven independent acquisitions and one reversal (Figure 18; CI = 0.16). The independent acquisition of this characteristic is an autapomorphy of *Ordosemys leios.* It is furthermore a separate synapomorphy to PANPLEURODIRA, PANCHELONIOIDEA, CHELYDRIDAE, TRIONYCHIDAE, the clade formed by *Meiolania platyceps* + *Mongolochelys efremovi,* and the clade formed by *Solnhofia parsonsi* + "Thalassemys moseri" + *Santanachelys gaffneyi.* Within PANPLEURODIRA, a large central fontanelle is secondarily lost in PLEURODIRA.

CHARACTER 77: PLASTRON C

Character definition. Plastral kinesis (Meylan and Gaffney 1989, 28): 0 = absent, scute sulci and bony sutures do not overlap; 1 = present, scute sulci coincide with hyoplastral–epiplastral contact.

Morphology and distribution. The bones of the plastron of *Proganochelys quenstedti, Kayentachelys aprix,* and most other turtles are tightly sutured with one another, thus forming a solid, protective plate. The underlying scutes systematically cover all bony sutures to help support the rigidity of the plastron (Figure 10a–j, l). In KINOSTERNIDS, the anterior plastral lobe, consisting of the epiplastra only, is mobile relative to the remaining plastral elements. To help support this type of plastral kinesis, the scute sulci coincide with the hyoplastral–epiplastra contact (Figure 10k).

Well-developed plastral kinesis is also present in numerous TESTUDINOIDS and PELOMEDUSOIDS. However, that type of plastral mobility is not considered homologous herein, because it occurs along the contact of the hyoplastron and hypoplastron, or along the hypoplastron and xiphiplastron. Plastral kinesis per se also occurs in numerous other turtles, particularly in representatives of TRIONYCHIA (Figure 10l). However, this type of plastral kinesis was purposefully excluded from this character because it is difficult to score objectively for fossil taxa, as poorly sutured bones do not necessarily result in plastral kinesis. By restricting the definition of plastral kinesis to cases where the plastral sulci coincide with the bony contacts, the reproducibility of this character is greatly enhanced. All living representatives of TRIONYCHIA are consequently scored as uncertain because they do not have scute sulci.

Character evolution. A hinge between the epiplastra and hyoplastra is an unambiguous synapomorphy of KINOSTERNIDAE (Figure 18; CI = 1.00).

Entoplastron

CHARACTER 78: ENTOPLASTRON A

Character definition. Anterior entoplastral process (Dryden 1988, 43; Gaffney 1996, 38; Shaffer et al. 1997, 113; Brinkman and Wu 1999, 38; Hirayama et al. 2000, 71): 0 = present, medial contact of epiplastra absent; 1 = absent, medial contact of epiplastra present.

Morphology and distribution. The entoplastron (interclavicle) of several primitive turtles, such as *Proganochelys quenstedti, Proterochersis robusta, Palaeochersis talampayensis,* and *Kayentachelys aprix,* forms an anterior process that extends to the anterior plastral rim and hinders a medial contact of the epiplastra (Figure 10a–b). The derived condition is seen in all other turtles in which the epiplastron does not have an anterior process, thus allowing the epiplastra to contact one another medially and to form the entire anterior plastral rim (Figure 10c–k). This medial contact is only poorly developed in *Meiolania platyceps* and *Platychelys oberndorferi.* Although representatives of TRIONYCHIDAE lack a medial contact of the epiplastra, this condition is not considered homologous with that seen in basal turtles given the highly derived nature of their plastron and the absence of an anterior entoplastral process (Figure 10l). The observed distribution of character states overlaps with that of other authors, with the exception of Gaffney (1996), who scored his composite taxon "Pleurodira" as lacking the medial epiplastral contact. It is likely that this was done in allusion to the condition seen in the putative PANPLEURODIRE *Proterochersis robusta.*

Character evolution. A medial epiplastral contact is an unambiguous synapomorphy that unites Meiolania platyceps + *Mongolochelys efremovi* + *Kallokibotion bajazidi* + TESTUDINES (Figure 18; CI = 1.00).

CHARACTER 79: ENTOPLASTRON B

Character definition. Size of posterior entoplastral process (Rougier et al. 1995, 46; Hirayama et al. 2000, 73): 0 = posterior process long; 1 = posterior process reduced in length.

Morphology and distribution. The entoplastron (interclavicle) of *Proganochelys quenstedti, Proterochersis robusta, Palaeochersis talampayensis, Kayentachelys aprix, Meiolania platyceps,* and *Mongolochelys efremovi* has a long, rod-like neural spine that may extend as far posteriorly as the mesoplastron, being significantly longer than the main body of the entoplastron (Figure 11a–b). The entoplastron of all remaining turtles still has a posterior process, but it is greatly reduced to a thin splint (Figure 11c). The condition is unclear for numerous fossil taxa, because the visceral side of the entoplastron is commonly covered by sediment or at least not figured in the literature. Unlike Rougier et al. (1995) and Hirayama et al. (2000), this analysis considers the posterior entoplastral process of *Kayentachelys aprix, Mongolochelys efremovi,* and *Meiolania platyceps* to have the long condition.

Character evolution. A reduced posterior entoplastral process is an unambiguous synapomorphy of TESTUDINES (Figure 18; CI = 1.00).

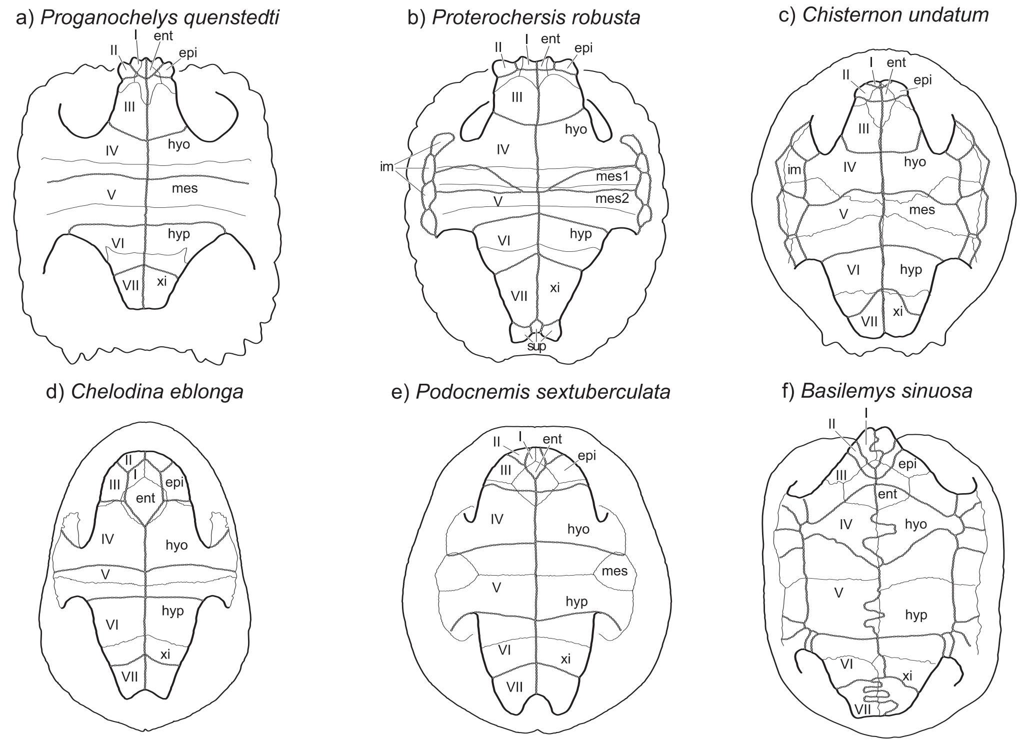


FIGURE 10. Ventral views of plastra of select *Testudinata.* **a.** *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **b.** *Proterochersis robusta* Fraas 1913, redrawn from Gaffney (1990). **c.** *Chisternon* (orig. *Baena*) *undatum* (Leidy 1871), redrawn from Gaffney (1972b). **d.** *Chelodina oblonga* Gray 1841, redrawn from Boulenger (1889). **e.** *Podocnemis sextuberculata* Cornalia 1849, redrawn from Boulenger (1889). **f.** *Basilemys sinuosa* Riggs 1906, redrawn from Langston (1956). *Abbreviations:* ent, entoplastron; epi, epiplastron; hyo, hyoplastron; hyp, hypoplastron; im, inframarginal; mes, mesoplastron; sup, supernumerary scutes; xi, xiphiplastron. Roman numerals refer to the system developed by Hutchison and Bramble (1981).

CHARACTER 80: ENTOPLASTRON C

Character definition. Distinct posterolateral entoplastral processes: 0 = present; 1 = absent.

Morphology and distribution. The entoplastron (interclavicle) of *Proganochelys quenstedti* is unique in forming distinct posterolateral processes along the visceral side of the plastron that nearly extend to the lateral rim of the anterior plastral lobe (Gaffney 1990). The entoplastron of this taxon greatly resembles the primitive reptilian interclavicle in being cross-shaped (Romer 1956; Figure 11a). Although all other turtles also have laterally expanded entoplastra, none have the distinct processes developed by *Proganochelys quenstedti* (Figure 11b–c). Unfortunately, this feature cannot be scored for many fossil taxa, because the visceral side of the plastron is typically not prepared, described, or figured in the literature.

Character evolution. The absence of a posterolateral entoplastral process is a synapomorphy that unites all turtles to the exclusion of *Proganochelys quenstedti* (Figure 18; CI = 1.00).

CHARACTER 81: ENTOPLASTRON D

Character definition. Entoplastron (Shaffer et al. 1997, 83, 85): 0 = massive and cross- to diamond-shaped; 1 = strap like and V-shaped.

Morphology and distribution. Most turtles with a complete set of plastral bones, the entoplastron (interclavicle) is a solid, cross- to diamond-shaped dermal element (Figure 10a–j). In contrast, all living members of TRIONYCHIDAE have a slender entoplastron in the shape of an upside-down "V" (Figure 10l). Given that the character states are clearly discernable, there is a consensus on their distribution.

Character evolution. The presence of a V-shaped entoplastron is an unambiguous synapomorphy of TRIONYCHIDAE (Figure 18; CI = 1.00).

CHARACTER 82: ENTOPLASTRON E

Character definition. Entoplastron: 0 = present; 1 = absent.

Morphology and distribution. Among turtles, representatives of *Kinosternon* and *Sternotherus* are unique in lacking

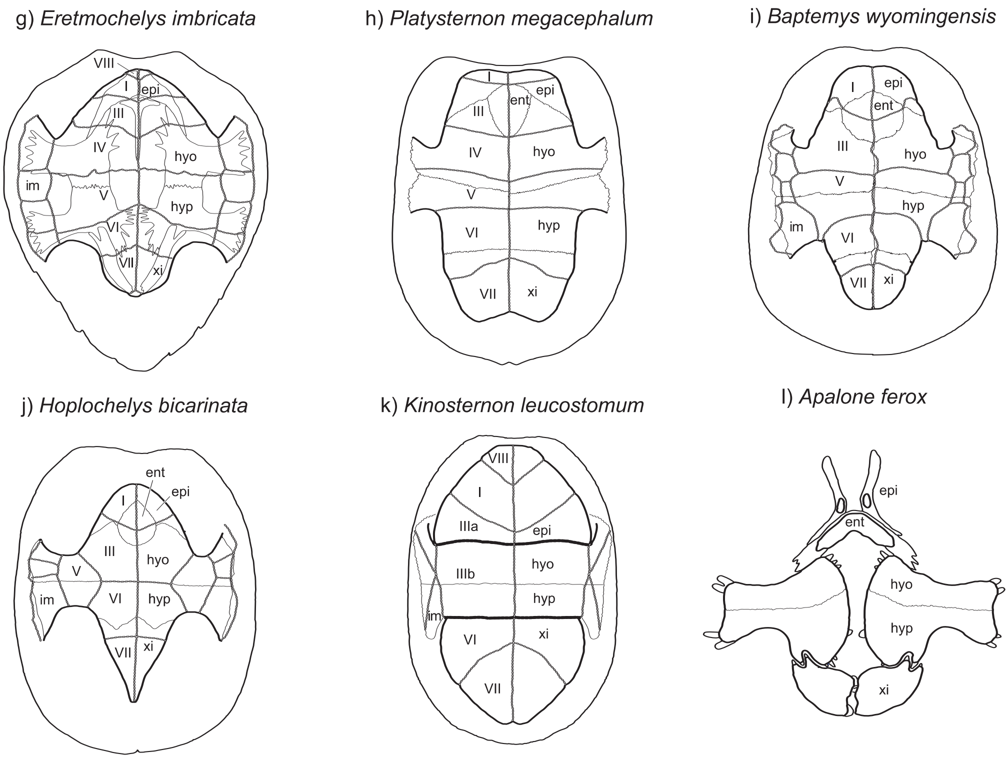

g) *Eretmochelys imbricata*
h) *Platysternon megacephalum*
i) *Baptemys wyomingensis*
j) *Hoplochelys bicarinata*
k) *Kinosternon leucostomum*
l) *Apalone ferox*

Figure 10 continued. Ventral views of plastra of select *Testudinata.* **g.** *Eretmochelys* (orig. *Testudo*) *imbricata* (Linnaeus 1766), based on YPM R10569. **h.** *Platysternon megacephalum* Gray 1831a, redrawn from Boulenger (1889). **i.** *Baptemys wyomingensis* Leidy 1869, redrawn from Hay (1908). **j.** *Hoplochelys bicarinata* Hay 1911, redrawn from Gilmore (1919). **k.** *Kinosternon* (orig. *Cinosternon*) *leucostomum* (Dumèril and Bibron 1851), redrawn from Boulenger (1889). **l.** *Apalone* (orig. *Testudo*) ferox (Schneider 1783), redrawn from Meylan (1987). *Abbreviations:* ent, entoplastron; epi, epiplastron; hyo, hyoplastron; hyp, hypoplastron; im, inframarginal; mes, mesoplastron; sup, supernumerary scutes; xi, xiphiplastron. Roman numerals refer to the system developed by Hutchison and Bramble (1981).

any trace of an entoplastron (interclavicle) (Figure 10a–j, l). All other turtles, including *Proganochelys quenstedti*, have well-developed, or at least clear, traces of an entoplastron (Figure 10k).

Character evolution. Loss of the entoplastron is an unambiguous synapomorphy of the clade formed by *Kinosternon flavescens* + *Sternotherus odoratus* (Figure 18; CI = 1.00).

ENTOPLASTRON NARROW

See character 83.

Epiplastron

CHARACTER 83:
EPIPLASTRON A

Character definition. Shape and contacts of epiplastra (Gaffney 1996, 39; Hirayama et al. 2000, 70, 72): 0 = epiplastra squarish in shape, minor posterior contact with hyoplastra; 1 = epiplastra elongate in shape, long posteromedial contact with hyoplastra.

Morphology and distribution. The epiplastra (clavicle) of *Proganochelys quenstedti*, *Kayentachelys aprix*, and most other turtles are somewhat squarish elements that are mostly situated anterior to the hyoplastra (Figure 10a–f, h–k). In *Meiolania platyceps*, *Mongolochelys efremovi*, CHELYDRIDS, CHELONIOIDS, and "macrobaenids" the epiplastra are elongate, narrow elements that also form much of the anterior plastral rim. Unlike other turtles, significant portions of the epiplastra thus cover the anterolateral portions of the hyoplastra (Figure 10g).

Characters developed in previous analyses that pertain to this morphology (Gaffney 1996; Brinkman and Wu 1999; Hirayama et al. 2000) differ from this one only by distinguishing wide from narrow plastral elements. Adding the posteromedial contact of the epiplastra with the hyoplastron to the character definition renders this character discrete and allows better reproducibility.

Character evolution. According to the preferred phylogenetic hypothesis, this character requires three evolutionary events

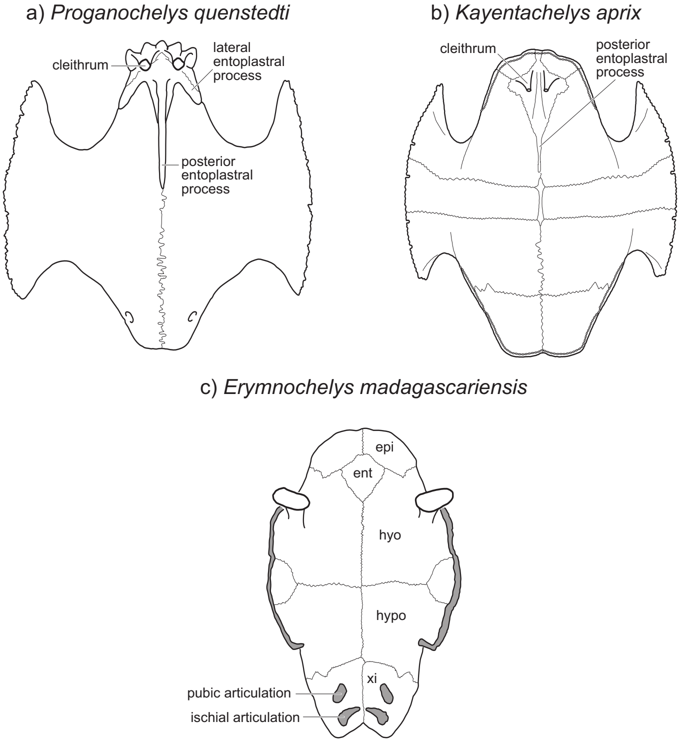


Figure 11. Dorsal views of plastra of select *Testudinata*. **a.** *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **b.** *Kayentachelys aprix* Gaffney et al. 1987. **c.** *Erymnochelys* (orig. *Dumerilia*) *madagascariensis* (Grandidier 1867), based on YPM R 10884. *Abbreviations:* ent, entoplastron; epi, epiplastron; hyo, hyoplastron; hypo, hypoplastron; xi, xiphiplastron.

(Figure 18; CI = 0.33) as a synapomorphy of the clade formed by *Meiolania platyceps* + *Mongolochelys efremovi* and as a synapomorphy of the clade that originates from the common ancestor of *Hangaiemys hoburensis* + Cryptodira. Within Cryptodira the epiplastra are secondarily enlarged along the phylogenetic stem of the clade formed by *Platysternon megacephalum* + Testudinoidea + Trionychoidea.

Hyoplastron

Character 84: Hyoplastron A

Character definition. Contacts of axillary buttresses (Dryden 1988, 47; Meylan and Gaffney 1989, 24): 0 = peripherals only; 1 = peripherals and first costal.

Morphology and distribution. The bridge region of many turtles shows axillary and inguinal buttresses that provide additional support to the shell. In most early turtles, such as *Proganochelys quenstedti* or *Kayentachelys aprix,* the axillary buttresses are poorly developed and only in contact with peripherals laterally (Figure 9a, c, e). The axillary buttresses of most pleurodires, paracryptodires, and testudinoids, in contrast, are well developed and extend anteriorly along the visceral side of the carapace to contact the first costal bone (Figure 9b, d). This contact can be easily inferred even in disarticulated specimens, because the first costal has a rough articular surface. Contrary to Sukhanov (2000), *Mongolochelys efremovi* is scored here as lacking a contact between the axillary buttresses and the costals.

Character evolution. According to the preferred phylogenetic hypothesis, this character requires five evolutionary steps (Figure 18; CI = 0.20) with one primary acquisition of a hyoplastral costal contact along the phylogenetic stem of the clade formed by *Kallokibotion bajazidi* + Testudines, a reversal along the phylogenetic stem of the clade that originated from the common ancestor of *Solnhofia parsonsi* and Cryptodira, and the subsequent reacquisition as an autapomorphy for "Thalassemys moseri," a synapomorphy of *Baptemys wyomingensis* + *Dermatemys mawii,* and as a synapomorphy of Pantestudinoidea.

Mesoplastron

Character 85: Mesoplastron A

Character definition. Number and size of mesoplastra (Dryden 1988, 44; Gaffney et al. 1991, 30–31; Gaffney 1996, 34; Brinkman and Wu 1999, 34; Hirayama et al. 2000, 74): 0 = one or two pair of mesoplastra present that fully hinder any contact between the hyoplastra and hypoplastra; 1 = one reduced pair of mesoplastra present that allows partial contact between the hyoplastra and hypoplastra; 2 = mesoplastra absent.

Morphology and distribution. Mesoplastra are dermal bones that developed between the hyoplastra and hypoplastra of many turtles. All basal turtles have one pair of mesoplastra, which fully separate the hyoplastra from the hypoplastra (Figure 10a–c). A medial contact between the mesoplastra may nevertheless be absent, due to the development of a central plastral fontanelle. Among basal turtles, *Proterochersis robusta* may be unique in having two parallel sets of mesoplastra that contact one another along the midline (Gaffney 1990). In many derived turtles, including many PANPLEURODIRES, one pair of mesoplastra is present, but they do not contact one another medially. This allows limited contact between the hyoplastra and the hypoplastra (Figure 19e). Mesoplastra are absent in all remaining turtles, including all CRYPTODIRES (Figure 10d, f–l). The distribution of this character is not controversial.

Character evolution. This character with two derived character states requires five evolutionary steps (Figure 18; CI = 0.40). Using DELTRAN optimization, mesoplastra are reduced independently as autapomorphies for *Kallokibotion bajazidi* and *Baena arenosa* and as a synapomorphy for PANPLEURODIRA. Mesoplastra are completely lost as a synapomorphy of CHELIDAE through the intermediate character state and as a synapomorphy of PANCRYPTODIRA directly from the nonreduced character state. If ACCTRAN optimization is used, the absence of mesoplastra, seen in CRYPTODIRES, could have originated from the reduced state.

Hypoplastron

CHARACTER 86: HYPOPLASTRON A

Character definition. Contacts of axillary buttresses (Dryden 1988, 47; Shaffer et al. 1997, 55; Hirayama et al. 2000, 66): 0 = peripherals only; 1 = peripherals and costal V; 2 = peripherals, costal V, and costal VI.

Morphology and distribution. The axillary buttresses of *Proganochelys quenstedti*, *Proterochersis robusta, Kayentachelys aprix,* and many other basal turtles are poorly developed and only contact the peripherals laterally (Figure 9a, c, e). The axillary buttresses of numerous derived turtles, in contrast, are well developed and ascend along the visceral side of the carapace to contact either the fifth or sixth costals, or both (Figure 9b, d). A contact between the axillary buttresses and the costals could not be observed for *Mongolochelys efremovi* (Sukhanov 2000). The development of the axillary buttresses is scored independently from the development of the inguinal buttresses (see character 84) because both characters are not correlated, as shown by the asymmetrically developed buttresses of *Chelodina siebenrocki* and *Dermatemys mawii.*

Character evolution. The CI of this character is 0.20 (Figure 18) with one acquisition (synapomorphy of the clade formed by *Kallokibotion bajazidi* + TESTUDINES), two reversals (autapomorphy of *Chelodina siebenrocki,* synapomorphy of the clade that originates from the common ancestor of *Solnhofia parsonsi* + CRYPTODIRA), and two subsequent reacquisitions (*Baptemys wyomingensis* + PANTESTUDINOIDEA).

Xiphiplastron

CHARACTER 87: XIPHIPLASTRON A

Character definition. Distinct anal notch (Hirayama et al. 2000, 76): 0 = absent; 1 = present.

Morphology and distribution. The posterior plastral rim of *Proganochelys quenstedti*, *Kayentachelys aprix*, *Mongolochelys efremovi, Meiolania platyceps,* and most derived turtles displays at most a modest anal notch (Figure 10a, c, f–g, i–l). This contrasts with the condition seen in *Proterochersis robusta,* PANPLEURODIRES, and PANTESTUDINOIDS, in which both xiphiplastra form distinct processes that frame an anal notch (Figure 10b, d–e, h). The distribution of this character is not controversial.

Character evolution. Using DELTRAN optimization, an anal notch is acquired five times within the preferred phylogeny (Figure 18; CI = 0.20) as autapomorphies to *Proterochersis robusta, Dermatemys mawii,* and *Platysternon megacephalum,* and as synapomorphies to PANPLEURODIRA and TESTUDINOIDEA. No reversals occur.

CHARACTER 88: XIPHIPLASTRON B

Character definition. Xiphiplastral shape (Hirayama et al. 2000, 5): 0 = elongate rectangles; 1 = narrow struts that frame a xiphiplastral fontanelle.

Morphology and distribution. The xiphiplastra of most turtles are elongate rectangular elements that form much of the posterior plastral lobe (Figure 10a–f, h–l). In CHELONIOIDS, the xiphiplastra still form much of the posterior plastral lobe, but their ossification is mostly limited to the rims. Therefore, these elements are narrow and frame a xiphiplastral fontanelle (Figure 10g).

At first this character seems to be correlated with the presence of a narrow epiplastra and a narrow entoplastron; however, the presence of a narrow epiplastra but broad xiphiplastra in “macrobaenids” clearly contradicts this assertion.

Character evolution. Narrow xiphiplastra that surround a medial fontanelle are an unambiguous synapomorphy of PANCHELONIOIDEA (Figure 18; CI = 1.00).

Plastral Scutes

In contrast to the keratinous scutes of the carapace, those of the plastron vary extensively among turtles in number, size, and distribution. As a result, the homology of plastral scutes remains somewhat of an enigma and their terminology is often difficult to comprehend. Fortunately, these problems are primarily associated with derived representatives of PANCRYPTODIRA, which have undergone considerable evolutionary change. The number and distribution of plastral scutes in all remaining turtles is for the most part constant. For simplicity, this analysis follows the primary homology statements and terminology of Hutchison and Bramble (1981), which is the most comprehensive and intuitive analysis of plastral scute homology to date.

CHARACTER 89: PLASTRAL SCUTES A

Character definition. Plastral scutes (Meylan and Gaffney 1989, 46b; Shaffer et al. 1997, 78b): 0 = present; 1 = absent.

Morphology and distribution. The plastron of *Proganochelys quenstedti* and most other turtles is completely covered by keratinous scutes that provide mechanical protection to the underlying epidermis and bony shell. Actual scutes are extremely rare in the fossil record, but their former presence can nevertheless be inferred confidently based on the presence of sulci, which are grooves in the underlying bone that outline the shape of the overlying scutes (Figure 10a–k). Plastral scutes are completely absent in all representatives of TRIONYCHIA and *Dermochelys coriacea* (Figure 10l).

This character was conceived as a single character pertaining to plastral scute loss in an effort to avoid weighting the absence of scutes. Taxa that lack plastral scutes altogether are scored as nonapplicable in all plastral scute characters below.

Character evolution. The loss of plastral scutes is a synapomorphy of TRIONYCHIA and an independently acquired autapomorphy of *Dermochelys coriacea* (Figure 18; CI = 0.50). There is no evidence to date of a gradual loss of plastral scutes in these taxa.

CHARACTER 90: PLASTRAL SCUTES B

Character definition. Midline sulcus (Meylan and Gaffney 1989, 30): 0 = straight; 1 = distinctly sinuous.

Morphology and distribution. The plastral scutes of most turtles, including *Proganochelys quenstedti*, are typically paired structures that meet along the midline of the plastron in a straight or slightly sinuous suture (Figure 10a–e, g–k). In contrast, the midline plastral sulcus of adocids and nanhsiungchelyids (*Zangerlia neimongolensis* and *Adocus beatus*) are strongly sinuous (Figure 10f). There is no disagreement on the distribution of this character.

Character evolution. The presence of a markedly sinuous medial plastral sulcus is an unambiguous synapomorphy of the clade formed by *Adocus beatus* + *Zangerlia neimongolensis* + *Basilemys variolosa* (Figure 18; CI = 1.00).

Gular

CHARACTER 91: GULAR A

Character definition. Plastral scale set 1, gulars (Dryden 1988, 45a): 0 = one, medially situated pair of scutes present; 1 = one, medially situated scute present.

Morphology and distribution. The anterior plastral lobe of *Proganochelys quenstedti*, *Kayentachelys aprix*, and most primitive pancryptodires has a set of gular scales that cover the entoplastron or parts of the epiplastra, or both (Figure 10a–c, f–k). In contrast, numerous derived turtles, including *Pleurosternon bullockii, Peltochelys durlstonensis,* and all known PANPLEURODIRES, only have one centrally positioned gular (Figure 10d–e).

Character evolution. A medial fusion of the gulars is an independently acquired autapomorphy for *Pleurosternon bullockii* and *Peltochelys durlstonensis.* Medially fused gulars are also a synapomorphy for the clade that originates from the common ancestor of *Platychelys oberndorferi* and PLEURODIRA (Figure 18; CI = 0.33).

Extragular

CHARACTER 92: EXTRAGULAR A

Character definition. Plastral scale set 2, extragulars (Dryden 1988, 45b; Meylan and Gaffney 1989, 31; Gaffney 1996, 40; Shaffer et al. 1997, 90; Brinkman and Wu 1999, 40; Hirayama et al. 2000, 67): 0 = present; 1 = absent.

Morphology and distribution. In addition to one pair of gulars (see character 91), the anterior plastral lobe of *Proganochelys quenstedti*, *Kayentachelys aprix*, PANPLEURODIRES, and basal PANCRYPTODIRES has an additional pair of scutes termed extragulars (Figure 10a–f). Extragulars are lost in all living CRYPTODIRES (Figure 10g–k), but still occur in some taxa thought to be basal representatives of crown CRYPTODIRA, such as *Adocus beatus* and *Peltochelys durlstonensis.* Unlike some previous analyses (Gaffney 1996, 40; Brinkman and Wu 1999, 40), this analysis follows Hutchison and Bramble (1981) by considering those scutes that are lost along the anterior plastral rim to be the extragulars and not the gulars.

Character evolution. According to the preferred phylogenetic hypothesis, extragular scutes are lost along the phylogenetic stem of the clade that originates from the common ancestor of *Hangaiemys hoburensis* and CRYPTODIRA, but subsequently homoplastically reappeared in PANTRIONYCHIA. As such, the extragulars seen in PANTRIONYCHIANS are nonhomologous to those seen in *Proganochelys quenstedti* (Figure 18; CI = 0.50).

CHARACTER 93: EXTRAGULAR B

Character definition. Medial contact of plastral scale set 2, extragulars: 0 = absent; 1 = present, contacting one another anterior to gular(s); 1 = present, contacting one another posterior to gular(s).

Morphology and distribution. The extragulars of most basal turtles, including *Proganochelys quenstedti* and *Kayentachelys aprix*, do not contact one another medially because of a contact between the gulars with the humerals. As a result, both the gulars and the extragulars participate in the anterior plastral rim (Figure 10a–b, e). In CHELODINA, the extragulars contact one another anterior to the gular, prohibiting contribution of the gular to the anterior plastral rim (Figure 10d). In contrast, the extragulars of some baenids contact one another posterior to the extragulars, thus interrupting the contact between the extragulars and the humerals (Figure 10c, f).

Character evolution. A medial contact of the extragular anterior to the gulars is a unique autapomorphy for *Chelodina siebenrocki.* In contrast, a medial contact of the gulars posterior to the gulars occurs twice as an autapomorphy of *Zangerlia neimongolensis* and as a synapomorphy of the clade formed by *Baena arenosa* + *Plesiobaena antiqua* (Lambe) + *Chisternon undatum* + *Boremys pulchra* (Figure 18; CI = 0.33).

CHARACTER 94: EXTRAGULAR C

Character definition. Anterior plastral tuberosities (Rougier et al. 1995, 44): 0 = present; 1 = absent.

Morphology and distribution. The plastra of *Proganochelys quenstedti* and *Proterochersis robusta* are heavily sculptured along their anterior margin by five distinct tuberosities, which are capped by the gulars, extragulars, and the "medial tubercle" (Figure 10a–b). In *Kayentachelys aprix* and all other remaining turtles, these tuberosities are absent and the anterior plastral rim is smooth (Figure 10c–k).

Character evolution. The absence of anterior plastral tuberosities is an unambiguous synapomorphy of the clade that arises from the common ancestor of *Kayentachelys aprix* and TESTUDINES (Figure 18; CI = 1.00).

Intergular

CHARACTER 95: INTERGULAR A

Character definition. Plastral scale set 8, intergulars: 0 = absent; 1 = present.

Morphology and distribution. According to Hutchison and Bramble (1981), KINOSTERNIDS and *Dermatemys mawii* have intergulars, which are neomorphic scutes situated between the gulars along the anterior plastral rim (Figure 10k). Although not specifically stated, their assessment of homologies to the plastron of the CHELONIIDAE implies the presence of intergulars in this taxon as well (Figure 10g). All other turtles lack intergulars (Figure 10a–f, h–j).

Character evolution. According to the preferred phylogenetic hypothesis, intergulars are acquired independently along the phylogenetic stems of *Dermatemys mawii,* CHELONIIDAE, and that of the clade that arises from the common ancestor of *Kinosternon flavescens* + *Sternotherus odoratus* (Figure 18; CI = 0.33).

Humeral

CHARACTER 96: HUMERAL A

Character definition. Plastral scale set 3, humerals: 0 = one pair present; 1 = two pair present, subdivided by a plastral hinge.

Morphology and distribution. As was convincingly argued by Hutchison and Bramble (1981), *Kinosternon* and *Sternotherus* are unique among turtles in having two pairs of humeral scutes that are separated by a plastral hinge between the epiplastra and the hyoplastra (Figure 10k). All other turtles have only one pair of humerals (Figure 10a–j, l).

Character evolution. The division of the humeral scute by an anterior plastral hinge is a unique synapomorphy that unites the clade that arises from the common ancestor of *Kinosternon flavescens* + *Sternotherus odoratus* (Figure 18; CI = 1.00) and seems to be related to the acquisition of a plastral hinge.

Pectoral

CHARACTER 97: PECTORAL A

Character definition. Plastral scale set 4, pectorals (Meylan and Gaffney 1989, 32; Shaffer et al. 1997, 104): 0 = present; 1 = absent.

Morphology and distribution. The abdominals of basal turtles cover the hyoplastral–mesoplastral suture (Figure 10a–d), but become dispensable after the loss of the mesoplastra because they only cover the hyoplastra, and thus do not provide any stability to a bony suture (Figure 10e–k). Pectorals are lost in all representatives of KINOSTERNOIDEA (Figure 10i–k).

Character evolution. The absence of pectorals is an unambiguous synapomorphy of KINOSTERNOIDEA (Figure 18; CI = 1.00).

Abdominal

CHARACTER 98: ABDOMINAL A

Character definition. Plastral scale set 5, abdominals (Meylan and Gaffney 1989, 34; Shaffer et al. 1997, 94; Brinkman and Wu 1999, 41): 0 = present, in medial contact with one another; 1 = present, medial contact absent; 2 = absent.

Morphology and distribution. The abdominal scutes cover the mesoplastral–hyoplastral suture in basal turtles (Figure 10a–c), and the hyoplastral–hypoplastral suture in turtles that lack mesoplastra (Figure 10d–j). In *Hoplochelys* and CHELYDRIDS, abdominal are still present, but they do not contact one another anymore along the midline (Figure 10j). Abdominals are lost in all representatives of KINOSTERNIDAE (Figure 10k).

Character evolution. This character with two derived character states requires three evolutionary steps (Figure 18; CI = 0.66). The lack of a medial contact of the abdominals is a synapomorphy of PANCHELYDRIDAE. It also is absent in *Hoplochelys crassa* and thus may either be interpreted as an autapomorphy of *Hoplochelys crassa* or as a synapomorphy of PANKINOSTERNIDAE. Abdominal scutes are completely lost as a synapomorphy of *Kinosternidae.*

Anal

CHARACTER 99: ANAL A

Character definition. Plastral scale set 7, anals (Hirayama et al. 2000, 68): 0 = only cover parts of the xiphiplastra; 1 = anteromedially overlap onto hypoplastra.

Morphology and distribution. The anals of *Proganochelys quenstedti*, *Kayentachelys aprix*, and other basal turtles are small scutes that only cover the posterior portions of the xiphiplastra (Figure 10a–b, d–k). In contrast, the anals of an eclectic group of turtles, including numerous baenids and primitive PANCRYPTODIRES, are relatively larger and cross the hypoplastral–xiphiplastra suture to partially cover the posteromedial portions of the hypoplastra (Figure 10c). Unfortunately, even though the use of this character for reconstructing phylogenetic relationships is not in doubt, reproducibility is currently suboptimal because truly discrete character states are absent.

Character evolution. According to the preferred phylogentic hypothesis, an overlap of the anals onto the hypoplastra is acquired twice as a synapomorphy of *Plesiobaena antiqua* + *Boremys pulchra* + *Baena arenosa* + *Chisternon undatum,* and as a synapomorphy to the clade that originates from the common ancestor of *Xinjiangchelys latimarginalis* and CRYPTODIRA. Within the latter clade, this overlap is lost twice as a synapomorphy of CHELONIIDAE and the clade formed by *Platysternon megacephalum* + TESTUDINOIDEA + TRIONYCHOIDEA (Figure 18; CI = 0.25).

Inframarginal

CHARACTER 100: INFRAMARGINAL A

Character definition. Inframarginal scutes (Dryden 1988, 46; Meylan and Gaffney 1989, 35; Shaffer et al. 1997, 101; Hirayama et al. 2000, 65): 0 = more than two pair present, plastral scutes do not contact marginals; 1 = two pair present (axillaries and inguinals), limited contact between plastral scutes and marginals present; 2 = absent, unrestricted contact between plastral scutes and marginals present.

Morphology and distribution. The bridge region of many basal turtles, including *Kayentachelys aprix* and *Mongolochelys efremovi,* is covered by more than two pair of inframarginals that completely block any contact between the carapacial and plastral scutes (Figure 10b–c, f–k). The bridge region of *Proganochelys quenstedti*, *Palaeochersis talampayensis,* and *Meiolania platyceps* is not sufficiently preserved to allow determination of the number of inframarginals present in these taxa. There are only two inframarginals in TESTUDINOIDS, allowing limited contact between plastral scutes and marginals. Inframarginals are completely absent in all known PANPLEURODIRES, thus allowing full contact between the plastral scutes and the marginals (Figure 10d–e).

Polarity. The number, or even the presence, of inframarginal scutes is unclear for *Proganochelys quenstedti*. However, given that all turtles earlier than the Tertiary have a complete set of inframarginals, it is reasonable to assume that the presence of inframarginals is primitive for TESTUDINATA.

Character evolution. The presence of a limited contact between the plastral and carapacial scutes due to the partial reduction of the inframarginals is an unambiguous synapomorphy of TESTUDINOIDEA. Conversely, the full absence of inframarginals is an unambiguous synapomorphy of the clade that originates from the common ancestor of *Platychelys oberndorferi* and PLEURODIRA (Figure 18; CI = 1.00).

Cervical Rib

CHARACTER 101: CERVICAL RIB A

Character definition. Cervical ribs (Dryden 1988, 59; Gaffney et al. 1991, 38; Rougier et al. 1995, 48; Gaffney 1996, 23, 27; Brinkman and Wu 1999, 23, 57; Hirayama et al. 2000, 34–35): 0 = large cervical ribs present; 1 = cervical ribs reduced or absent.

Morphology and distribution. The presence or absence of cervical ribs is difficult to score rigorously because the cervicals of most fossil turtles are rarely preserved, and because the cervical ribs easily disarticulate. It is thus seldom possible to conclusively show the loss of the cervical ribs. Additionally, it seems that cervical ribs were lost gradually, resulting in a paucity of clearly observable discrete character states.

These difficulties are shown by the many inconsistencies of this character that can be observed among previous analyses of basal turtle relationships. To maximize reproducibility, this analysis follows the character definition of Hirayama et al. (2000); that is, only the presence of large cervical ribs is considered primitive, thus lumping all taxa that have reduced or no cervical ribs into a second character state. New finds of fossil material may allow better resolution of this character in the future, but the reproducibility of this character is currently considered poor.

Well-developed cervical ribs are only known from *Proganochelys quenstedti, Palaeochersis talampayensis,* and *Meiolania platyceps* (Figure 12a). In contrast, all living turtles lack cervical ribs (Figure 12b–c). The presence or absence of well-developed cervical ribs has to be inferred for all other taxa. The presence of well-developed cervical ribs is inferred for *Mongolochelys efremovi* from the clear development of diapophyses and parapophyses on most of the cervical vertebrae. Similar arguments were used to infer the presence of cervical ribs for *Pleurosternon bullockii* (Gaffney 1985), and *Xinjiangchelys latimarginalis* (Peng and Brinkman 1993). However, given that these taxa are known from isolated cervicals only, it is not clear if all cervicals havae ribs. These taxa are thus scored as unknown. Personal observations also reveal clear diapophyses and parapophyses for *Chisternon undatum,* but actual cervical ribs were not found.

All currently known cervicals of stem-pleurodires do not have parapophyses, but because these taxa are only known from isolated vertebrae, they are also scored as unknown. Among others, the cervical column is also poorly understood and thus scored as unknown for *Kallokibotion bajazidi, Glyptops plicatulus, Plesiochelys solodurensis,* and *Sinemys lens.* Single and small cervical ribs are known from *Dinochelys whitei* and *Ordosemys leios,* and cervical ribs are either greatly reduced or absent in *Plesiobaena antiqua, Solnhofia parsonsi,* and *Adocus beatus.*

The presence of parapophyses in addition to diapophyses (commonly referred to as "double transverse processes") has been used previously to infer phylogenetic relationships among turtles. Given that to date not a single turtle has been conclusively shown to have cervical ribs and not parapophyses, this character is herein considered redundant with the presence of cervical ribs. This redundancy occurs by definition in several previous analyses because the presence of cervical ribs is diagnosed based on the presence of parapophyses (e.g., Gaffney 1996).

Character evolution. The loss of large cervical ribs is an unambiguous synapomorphy of TESTUDINES (Figure 18; CI = 1.00). However, *Kallokibotion bajazidi* is the sister group of TESTUDINES and currently scores as unknown. Additional data may reveal that the loss of large cervical ribs unites a more inclusive clade.

Cervical Vertebra

CHARACTER 102: CERVICAL VERTEBRA A

Character definition. Position of transverse processes (Dryden 1988, 58; Gaffney 1996, 21; Shaffer et al. 1997, 107; Brinkman and Wu 1999, 21; Hirayama et al. 2000, 36): 0 = middle of the centrum; 1 = anterior end of the centrum.

Morphology and distribution. The cervical transverse processes of primitive turtles and all PANPLEURODIRES are typically well developed, positioned along the middle of

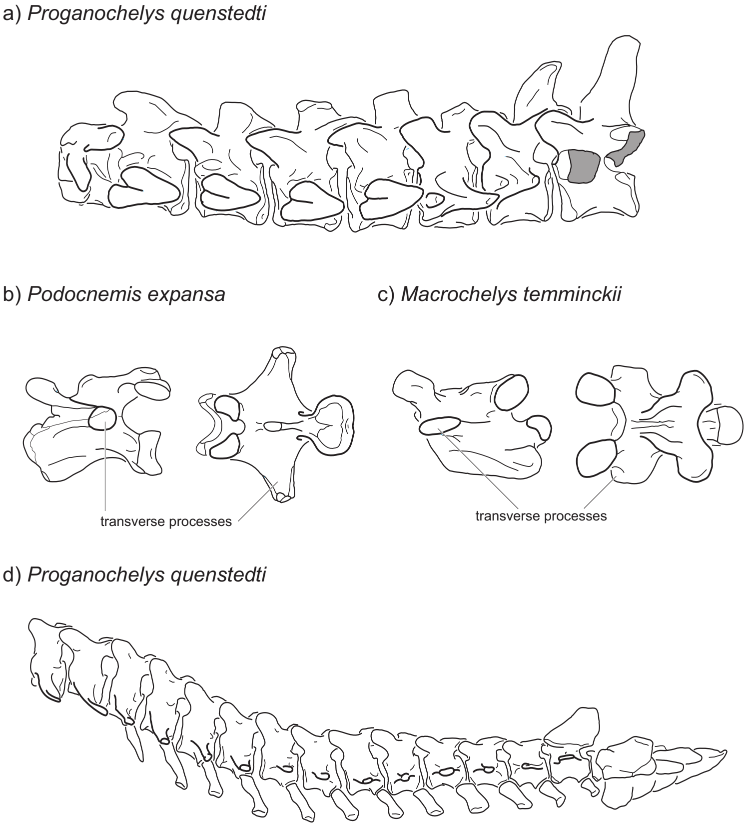


Figure 12. Vertebrae of select *Testudinata.* **a.** Cervical column of *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **b.** Fifth cervical vertebra of *Podocnemis* (orig. *Emys*) *expansa* (Schweigger 1812), redrawn from Gaffney (1990). **c.** Fifth cervical vertebra of *Macrochelys* (orig. *Chelonura*) *temminckii* (Troost 1835), redrawn from Gaffney (1990). **d.** Caudal column of *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990).

the centrum, and point laterally (Figure 12a–b). In contrast, the cervical vertebrae of all CRYPTODIRES have less prominent transverse processes, which are situated along the anterior end of the centrum and point anterolaterally (Figure 12c). Unlike Gaffney (1996), Schaffer et al. (1997), and Hirayama et al. (2000), this analysis scores both *Xinjiangchelys latimarginalis* and *Sinemys lens* as unknown, due to conflicting or insufficient data provided in the literature for these taxa.

Character evolution. The anterior location of the transverse processes is an unambiguous synapomorphy of PANCRYPTODIRA (Figure 18; CI = 1.00).

CHARACTER 103: CERVICAL VERTEBRA B

Character definition. Posterior cervicals with strongly developed ventral keels (Dryden 1988, 57; Shaffer et al. 1997, 108; Gaffney 1996, 22; Brinkman and Wu 1999, 22; Hirayama et al. 2000, 38): 0 = absent; 1 = present.

Morphology and distribution. The posterior cervicals of primitive turtles, PANPLEURODIRES, and stem-cryptodires typically lack well-developed keels, or are characterized by low keels that span the full length of the centrum. In contrast, the posterior cervicals of most CRYPTODIRES, particularly cervical VIII, have keels that form distinct posteriorly directed processes. In contrast, no evidence of keels can be found in representatives of TRIONYCHIA (contra Shaffer et al. 1997).

Character evolution. This character has a CI of 0.50 (Figure 18) with one acquisition as a synapomorphy of the clade that originates from the common ancestor of *Hangaiemys hoburensis* and TESTUDINES and one subsequent reversal along the phylogenetic stem of TRIONYCHIA.

CHARACTER 104: CERVICAL VERTEBRA C

Character definition. Cervical centrum VIII significantly shorter than VII (Brinkman and Wu 1999, 53; Hirayama et al. 2000, 40): 0 = absent; 1 = present.

Morphology and distribution. Cervical centra VII and VIII of primitive turtles, PANPLEURODIRES, and stem-cryptodires are roughly equal in length (Figure 12a). This condition differs from that seen in most CRYPTODIRES, in which cervical centrum VIII is significantly shorter than cervical centrum VII. Unfortunately, the posterior cervical region of many fossil turtles cannot be observed, because it lies within the animal's shell. Among fossil PANCRYPTODIRES, this analysis is only able to score this character for *Plesiobaena antiqua* and *Adocus beatus* from the primary literature. The scorings of *Xinjiangchelys latimarginalis, Sinemys lens,* and *Ordosemys leios* were taken from Brinkman and Wu (1999). Other taxa, particularly *Plesiochelys solodurensis, Pleurosternon bullockii,* and numerous baenids, were purposefully left as unknown, because no described cervical material is unambiguously associated with these taxa.

Character evolution. The presence of a shortened eighth cervical vertebra is a synapomorphy of TESTUDINES, but one reversal occurs as an autapomorphy of *Mesodermochelys undulatus* Hirayama and Chidoku (Figure 18; CI = 0.50).

ARTICULATION OF EIGHTH CERVICAL WITH NUCHAL

See character 62.

Cervical Articulation

The central articulations of turtle cervical vertebrae show an enormous amount of variation. Primitively, turtles are characterized by unformed amphicoelous or platycoelous vertebrae, but all living turtles have formed articular surfaces. The articular surfaces can be convex, concave, and even doubled. Especially among CRYPTODIRES, any possible combination of articular surfaces seems to exist (Williams 1950). Previous workers (Dryden 1988, 49–50; Meylan and Gaffney 1989, 38–39; Gaffney 1996, 24–26; Shaffer et al. 1997, 42, 48, 72, 86, 102, 110; Brinkman and Wu 1999, 24–26, 50; Hirayama et al. 2000, 41–43) focused their efforts on scoring characteristic cervical formulas (i.e., certain sequences of articular types), or identifying the position of characteristic vertebrae (i.e., with double convex or double concave centra). Unfortunately, these scoring methods cannot capture the full amount of variation that occurs through TESTUDINATA. For this analysis, each articular site was initially scored separately. This preliminary review of all ingroup taxa revealed that cervical articulations are either present in all cervicals or in none. To avoid weighting the acquisition of cervical articulations, this evolutionary step is formulated as a single character (105), as was done in many previous analyses (Dryden 1988, 51; Gaffney et al. 1991, 33; Rougier et al. 1995, 47; Gaffney 1996, 20; Brinkman and Wu 1999, 20; Hirayama et al. 2000, 39). The preliminary review revealed that the articulation between centrum I and II of all turtles with formed central articulations is always convex and thus uninformative (also see Williams 1950). The configuration of each remaining central articulation, including the articulation between cervical VIII and dorsal I, is herein scored as a separate character (106 to 112).

CHARACTER 105:
CERVICAL ARTICULATION A

Character definition. Cervical central articulations (Dryden 1988, 51; Gaffney et al. 1991, 33; Rougier et al. 1995, 47; Gaffney 1996, 20; Brinkman and Wu 1999, 20; Hirayama et al. 2000, 39): 0 = articulations not formed; 1 = articulations formed.

Morphology and distribution. All eight cervical vertebrae of numerous primitive turtles, including *Proganochelys quenstedti*, are truly amphicoelous, lacking any formed cervical central articulations. This is in contrast to the condition seen in *Meiolania platyceps, Mongolochelys efremovi,* PANPLEURODIRES, some baenids, and all CRYPTODIRES. The codings used in this analysis are identical to those of previous analyses.

Character evolution. According to the preferred phylogenetic hypothesis, the acquisition of cervical central articulations is surprisingly homoplastic with five independent acquisitions (Figure 18; CI = 0.20). Using DELTRAN optimization, formed cervical central articulations are independent autapomorphies of *Plesiobaena antiqua* and *Chisternon undatum* and independent synapomorphies of PANPLEURODIRA, the clade formed by *Meiolania platyceps* + *Mongolochelys efremovi,* and the clade that originated from the common ancestor of *Hangaiemys hoburensis* and CRYPTODIRA. Using ACCTRAN optimization, the evolution of this character remains similar; however, within Baenidae formed cervical articulations are considered a synapomorphy of the clade that includes *Plesiobaena antiqua* + *Chisternon undatum* + *Boremys pulchra* + *Baena arenosa* and subsequently lost in the last of these four taxa.

CHARACTERS 106 TO 111:
CERVICAL ARTICULATION B–H

All articular arrangements given below follow the notation of Walther (1922), by imitating the shape of the articular surfaces between the cervical vertebrae of interest.

Character definition. Character 106, Cervical Articulation B. Articulation between cervical II and III: 0 = 2(3; 1 = 2)3.

Character definition. Character 107, Cervical Articulation C. Articulation between cervical III and IV: 0 = 3(4; 1 = 3)4.

Character definition. Character 108, Cervical Articulation D. Articulation between cervical IV and V: 0 = 4(5; 1 = 4)5.

Character definition. Character 109, Cervical Articulation E. Articulation between cervical V and VI: 0 = 5(6; 1 = 5)6.

Character definition. Character 110, Cervical Articulation F. Articulation between cervical VI and VII: 0 = 6(7; 1 = 6)7.

Character definition. Character 111, Cervical Articulation G. Articulation between cervical VII and VIII: 0 = 7(8; 1 = 7)8.

Character definition. Character 112, Cervical Articulation H. Articulation between cervical VIII and the first dorsal: 0 = 8(dorsal; 1 = 8)dorsal; 2 = none, vertebrae only meet at zygapophyses.

Morphology and distribution. Once present, the cervical central articulations of all turtles are normally developed as either convex or concave. Because it is not possible to polarize these characters in the context of this analysis, the zero state was randomly assigned to the convex morphology. Alternative morphologies are possible among derived groups of turtles. In particular, the articular surfaces of some PODOCNEMIDS are saddle-shaped, the articulations of many TESTUDINOIDS are doubled, and the articular surfaces between cervicals VI and VII of most CHELONIOIDS tend to be flattened (Williams 1950). Within the context of this analysis, however, these morphologies are noninformative and were thus omitted. The exception is the secondarily reduced contact between cervical VIII and dorsal I, seen in all representatives of TRIONYCHIDAE.

Polarity. Polarity cannot be established for these characters because *Proganochelys quenstedti* does not have formed articular centra. More importantly, because it seems that articular centra have been formed independently multiple times within TESTUDINATA (see character 105), it is implausible to postulate that either procoelous or opisthocoelous articulations must have occurred primitively in all of these groups. The polarity of each of these characters can thus only be inferred after parsimony analysis.

Homoplasy, Character 106, Cervical Articulation B. The articular arrangement 2)3 optimizes as an autapomorphy of *Dermatemys mawii* and a synapomorphy of PELOMEDUSOIDES (Figure 18; CI = 0.50).

Homoplasy, Character 107, Cervical Articulation C. The articular arrangement 3)4 optimizes as an autapomorphy of *Mongolochelys efremovi* and a synapomorphy of PELOMEDUSOIDES and KINOSTERNOIDEA (Figure 18; CI = 0.33).

Homoplasy, Character 108, Cervical Articulation D. The presence of the articular arrangement 4(5 optimizes as an independently derived synapomorphy of CHELIDAE and TRIONYCHOIDEA (Figure 18; CI = 0.50).

Homoplasy, Character 109, Cervical Articulation E. The articular arrangement 5(6 is an unambiguous synapomorphy of TRIONYCHOIDEA (Figure 18; CI = 1.00).

Homoplasy, Character 110, Cervical Articulation F. The articular arrangement 6(7 is an autapomorphy of *Mongolochelys efremovi* and an independently derived synapomorphy of TRIONYCHOIDEA (Figure 18; CI = 0.50).

Homoplasy, Character 111, Cervical Articulation G. The acquisition of the articular arrangement 7)8 is relatively homoplastic by requiring five evolutionary steps (Figure 18; CI = 0.20). This type of articulation is an autapomorphy of *Mongolochelys efremovi*, and *Ordosemys leios* and a synapomorphy of CHELIDAE. Furthermore, this character is a synapomorphy of the clade formed by *Platysternon megacephalum* + TESTUDINOIDEA + TRIONYCHOIDEA; however, this character is subsequently reversed as a synapomorphy of PANKINOSTERNOIDEA.

Homoplasy, Character 112, Cervical Articulation H. This character, with two derived character states, requires only two evolutionary steps (Figure 18; CI = 1.00). The secondary loss of any direct articulation between the eighth cervical centrum and the first dorsal centrum is an unambiguous synapomorphy of TRIONYCHIDAE. Conversely, the articular arrangement 8(dorsal is an autapomorphy for *Adocus beatus*.

Dorsal Rib

CHARACTER 113: DORSAL RIB

Character definition. Length of first dorsal rib (Dryden 1988, 37; Gaffney et al. 1991, 35; Rougier et al. 1995, 49; Gaffney 1996, 32; Brinkman and Wu 1999, 32; Hirayama et al. 2000, 45): 0 = long, extends full length of first costal and may even contact peripherals distally; 1 = intermediate, in contact with well-developed anterior bridge buttresses; 2 = intermediate to short, extends less than halfway across first costal.

Morphology and distribution. The first thoracic ribs of all turtles contribute to the formation of the shell, but do not fuse with the overlaying costals. In basal turtles, such as *Proganochelys quenstedti*, *Kayentachelys aprix*, and *Meiolania platyceps*, the first thoracic ribs are similar in length to the remaining thoracic ribs, extending the full width of the first costal to the peripherals (Figure 9a). In *Platychelys oberndorferi* and some baenids, the first thoracic ribs are also well developed, but the plastral buttresses are so large that the ribs are unable to span the full width of the costals. In all living PLEURODIRES and CRYPTODIRES, the first thoracic ribs are greatly reduced in length and cover, at most, half the width of the first costals (Figure 9b–e).

The internal carapacial morphology of many fossil taxa is not accessible, making it impossible to score these taxa. There is an additional problem with fossil material in which the first thoracic ribs have disarticulated from the carapace. In these cases, it is reasonable to infer the length of the first thoracic ribs based on the length of the articular scar left on the visceral side of the first costals. A recent discovery of a well-preserved turtle from the Middle Jurassic of Russia, *Heckerochelys romani* Sukhanov (2006), indicates that this line of reasoning is specious. In this basal taxon, the first thoracic ribs are well developed, but only articulate with the costals for less than one third of their length, leaving behind greatly reduced articular scars. Consequently, fossil taxa that are represented by material that lacks first thoracic ribs, but reveals short scars, are coded as unknown.

The codings of this analysis generally match with those of previous studies, with the sole exception of Rougier et al. (1995), who only observed long first thoracic ribs in *Proganochelys quenstedti.* The scoring for *Kallokibotion bajazidi* and *Sinemys lens* were taken from Gaffney (1996) and Hirayama et al. (2000).

Character evolution. The reduction of the first thoracic rib requires six evolutionary steps for two derived character states (Figure 18; CI = 0.33). The acquisition of a contact of the first thoracic rib of the axillary buttresses is an autapomorphy for "Thalassemys moseri" and a synapomorphy for Baenidae. Short first thoracic ribs are a synapomorphy of PANPLEURODIRA and of the clade that arises from the common ancestor of *Xinjiangchelys latimarginalis* and CRYPTODIRA. However, a contact of the first thoracic rib is reacquired as an autapomorphy of *Platychelys oberndorferi* within PANPLEURODIRA and long thoracic ribs are reacquired in the clade formed by *Sinemys lens* + *Ordosemys leios* within PANCRYPTODIRA.

CHARACTER 114: DORSAL RIB B

Character definition. Contact of dorsal ribs IX and X with costals (Meylan and Gaffney 1989, 23): 0 = present, 1 = absent.

Morphology and distribution. The shell of a turtle is a composite structure formed, among others, by ribs and overlying dermal bones. The rib component can be observed in most turtles, because each costal has a rib head that articulates medially with the dorsal vertebrae (Figure 9a–d). This contrasts the condition seen in KINOSTERNIDS, in which the osseous rib heads of dorsal ribs IX and X are reduced. The eighth pair of costals thus has no trace of rib heads (Figure 9e). There is no disagreement regarding the distribution of this character.

Character evolution. The reduction of dorsal ribs IX and X is an unambiguous synapomorphy of KINOSTERNIDAE (Figure 18; CI = 1.00).

CHARACTER 115: DORSAL RIB C

Character definition. Dorsal rib X (Dryden 1988, 36; Gaffney et al. 1991, 39; Rougier et al. 1995, 50; Shaffer et al. 1997, 69, 96; Hirayama et al. 2000, 46–47, 60): 0 = dorsal rib X long, spanning full length of costals and contacting peripherals distally; 1 = dorsal rib X short, not spanning farther distally than pelvis.

Morphology and distribution. In basal turtles, such as *Proganochelys quenstedti*, *Kayentachelys aprix*, and *Mongolochelys efremovi*, the posterior nine pair of thoracic ribs are associated with their own, separate costal bones (costals I to IX) and insert distally into separate peripherals (peripherals III to XI; Figure 9a). This condition differs from that seen in all PLEURODIRES and CRYPTODIRES, in which the ninth pair of costals is absent. Furthermore, the tenth thoracic ribs are so greatly reduced in length that they come to terminate near the ilial attachment on costal VIII (Figure 9b–e). Numerous previous analyses accommodated this morphology by counting the number of costals only. However, it appears that the eighth and ninth costals fuse during ontogeny in some primitive turtles, resulting in conflicting observations. At least for all taxa used in this study, this conflict is solved by focusing on the morphology of the underlying ribs. Previous authors have noted that many extant turtles, particularly *Chelydra serpentina,* regularly have nine pair of costals. However, observations of material at hand reveal that these individuals do not display the primitive morphology seen in *Proganochelys quenstedti* with nine costals and ten dorsal ribs. Instead, such individuals have a pair of supernumerary ribs and costals, resulting in a total of nine costals and eleven pair of ribs.

Character evolution. A shortened dorsal rib X is an unambiguous synapomorphy of TESTUDINES (Figure 18; CI = 1.00).

Dorsal Vertebra

CHARACTER 116: DORSAL VERTEBRA A

Character definition. Anterior articulation of first dorsal centrum (Dryden 1988, 38, 48; Gaffney et al. 1991, 34, 48; Gaffney 1996, 33; Brinkman and Wu 1999, 33; Hirayama et al. 2000, 44): 0 = faces at most slightly anteroventrally; 1 = faces strongly anteroventrally.

Morphology and distribution. The anterior central articulation of the first thoracic vertebra with the last cervical vertebra of all primitive turtles, PANPLEURODIRES, and basal PANCRYPTODIRES faces anteriorly or slightly anteroventrally (Figure 9a–b). In contrast, this articular surface faces strongly anteroventrally in most CRYPTODIRES, allowing for the more efficient retraction of the neck (Figure 9c–e). This morphology seems to be tightly correlated with the presence of elongate and curved postzygapophyses of the eighth cervical vertebra. There is no disagreement on the distribution of this character.

Character evolution. According to the preferred phylogenetic hypothesis, an anteroventrally facing first thoracic centrum is independently acquired in CHELONIIDAE and the clade formed by CHELYDRIDAE + TESTUDINOIDEA + TRIONYCHOIDEA (Figure 18; CI = 0.50).

Chevron

CHARACTER 117: CHEVRON A

Character definition. Chevrons (Gaffney et al. 1991, 36; Gaffney 1996, 31; Brinkman and Wu 1999, 31; Hirayama et al. 2000, 48): 0 = present on nearly all caudals; 1 = absent, or only poorly developed, along the posterior caudals.

Morphology and distribution. The tails of *Proganochelys quenstedti*, *Meiolania platyceps,* and *Mongolochelys efremovi* are known to have had well-developed chevrons along their full length (Figure 12d). Although actual chevrons are not preserved for some fossil taxa, such as *Kayentachelys aprix*, they can nevertheless be inferred to have been present based on the presence of paired articular sites along the posteroventral rim of the caudal centra. Among extant turtles, chevrons are only known from CHELYDRIDS and *Platysternon megacephalum.* Tiny chevrons can also be found at the posterior tip of the tail of many TESTUDINOIDS. All remaining living turtles lack chevrons. Numerous fossil taxa are known to lack chevrons, because they have tails that are preserved well enough to document their absence along the entire tail.

Unlike previous analyses (Gaffney et al. 1991; Gaffney 1996; Hirayama et al. 2000), *Pleurosternon bullockii, Plesiochelys solodurensis,* and *Sinemys lens* are scored as unknown, due to the lack of caudal material associated with these taxa. In addition, *Xinjiangchelys latimarginalis* is scored as having chevrons, whereas *Judithemys sukhanovi* is scored as lacking these structures.

Character evolution. According to the preferred phylogenetic hypothesis, chevrons are independently lost four times (Figure 18; CI = 0.50). These losses occur as separate synapomorphies for PANPLEURODIRA, CHELONIOIDEA + TESTUDINOIDEA, TRIONYCHOIDEA, and the clade formed by *Judithemys sukhanovi* + *Sinemys lens* + *Dracochelys bicuspis* + *Ordosemys leios.* This distribution suggests that the presence of chevrons in *Platysternon megacephalum* and CHELYDRIDAE is not a synapomorphy, but rather a symplesiomorphy.

Caudal

CHARACTER 118: CAUDAL A

Character definition. Tail club (Dryden 1988, 56): 0 = present; 1 = absent.

Morphology and distribution. The primitive turtles *Proganochelys quenstedti* and *Meiolania platyceps* are unique in having massive tail clubs. These structures are comprised of the distal caudal vertebrae and numerous dermal ossicles (Figure 12d). Tail clubs are absent in all other fossil turtles with sufficiently preserved tails. No living turtle has a tail club. There is no disagreement on the distribution of this character.

Character evolution. Tail clubs may either be interpreted as independently derived autapomorphies to *Proganochelys quenstedti* and *Meiolania platyceps* or their absence may be considered a synapomorphy to the clade of turtles that includes all but *Proganochelys quenstedti* with a subsequent reversal for *Meiolania platyceps* (Figure 18; CI = 0.50).

CHARACTER 119: CAUDAL B

Character definition. Caudal centra (Dryden 1988, 55; Gaffney et al. 1991, 37; Gaffney 1996, 29–30; Shaffer et al. 1997, 57; Brinkman and Wu 1999, 29–30; Hirayama et al. 2000, 49–50): 0 = all centra amphicoelous; 1 = all centra more or less pronounced procoelous; 2 = all centra more or less pronounced opisthocoelous; 3 = anterior few centra procoelous, posterior centra predominantly opisthocoelous.

Morphology and distribution. The articular surfaces of the caudal centra are developed in various ways among turtles, but four basic patterns can be discerned. In *Proganochelys quenstedti*, all caudal centra are amphicoelous. This is in contrast to the condition seen in all PLEURODIRES and most CRYPTODIRES in which all caudal centra are procoelous, a condition that is typically more pronounced in the anterior comparaed with the posterior vertebrae. Finally, some stem-cryptodires, CHELYDRIDS, and *Platysternon megacephalum* have a single biconvex caudal that separates the anterior procoelous column from the posterior opisthocoelous column.

No turtle in this analysis is known to have a fully opisthocoelous caudal column. However, the caudal column of *Meiolania platyceps* is only known from a few opisthocoelous anterior vertebrae, because the posterior vertebrae are not known. As such, this taxon is scored as being either fully opisthocoelous, or as being opisthocoelous anteriorly and procoelous posteriorly. A similar argument can be made for *Platychelys oberndorferi,* from which only a single, procoelous caudal is known.

n contrast to Gaffney (1996) and Shaffer et al. (1997), this analysis scored *Sinemys lens* as unknown, because not a single caudal column in known for this taxon. In addition, this analysis scores *Australochelys africanus* and *Plesiochelys solodurensis* as unknown, as opposed to Hirayama et al. (2000).

Character evolution. This character with three derived states had a complex evolutionary history that requires seven evolutionary events (Figure 18; CI = 0.43). The acquisition of a procoelous caudal column is a synapomorphy of PLEURODIRA and an opisthocoelous column a synapomorphy of the clade formed by *Baena arenosa* + *Chisternon undatum* + *Boremys pulchra.* The anteriorly procoelous and posteriorly opisthocoelous arrangement, in contrast, is an autapomorphy of *Mongolochelys efremovi* and unites the clade that originated from the common ancestor of *Xinjiangchelys latimarginalis* + CRYPTODIRA. Within CRYPTODIRA, PANCHELONIOIDEA and the clade consisting of TESTUDINOIDEA + TRIONYCHOIDEA secondarily acquire procoelous caudal vertebrae from the biconvex condition, but this arrangement is then again reversed along the phylogenetic stem of *Baptemys wyomingensis.*

Cleithrum

CHARACTER 120: CLEITHRUM A

Character definition. Cleithra (Dryden 1988, 42, 53; Rougier et al. 1995, 45; Gaffney 1996, 37; Shaffer et al. 1997, 112; Brinkman and Wu 1999, 37; Hirayama et al. 2000, 69): 0 = present and in contact with the carapace; 1 = present, osseous contact with carapace absent; 2 = absent.

Morphology and distribution. In *Proganochelys quenstedti*, *Palaeochersis talampayensis,* and *Proterochersis robusta* the cleithra (also called epiplastral processes, Joyce et al. 2006) are massive elements that arise from the anterior rim of the plastron and contact the carapace near the nuchal–peripheral contact (Figures 9a and 11a). In many more derived turtles, such as *Kayentachelys aprix* and *Mongolochelys efremovi,* cleithra are still clearly present, but they are reduced in thickness and do not contact the carapace (Figure 11b). All PLEURODIRES and all CRYPTODIRES lack cleithra (Figure 11c). Unfortunately, although cleithra often fused with the anterior plastral elements in many taxa, they are nevertheless separate elements in other taxa at younger ontogenetic stages and commonly disarticulate. The presence or absence of articular scars, however, is seldom reported in the literature. As such, the absence of cleithra cannot be assumed for most fossil turtles and must be scored as unknown. This analysis consequently disagrees substantially with some previous analyses regarding the distribution of this character.

Character evolution. The primary reduction of the cleithra is an unambiguous synapomorphy that unites the clade comprised of *Kayentachelys aprix* + *Mongolochelys efremovi* + *Meiolania platyceps* + *Kallokibotion bajazidi* + TESTUDINES. Within that clade, cleithra are fully lost at least three times as a synapomorphy of PLEURODIRA, CRYPTODIRA, and the clade formed by *Baena arenosa* + *Boremys pulchra* + *Chisternon undatum* (Figure 18; CI = 0.50).

Scapula

CHARACTER 121: SCAPULA A

Character definition. Length of acromial process (Rougier et al. 1995, 51; Hirayama et al. 2000, 52): 0 = less than one half length of scapular process; 1 = more than one half length of scapular process.

Morphology and distribution. The acromial process is a short and sturdy flange that protrudes from the anteroventral edge of the scapula in *Proganochelys quenstedti*. The length of the acromion process is less than one half the length of the scapular process (Figure 13a). A short acromial process has also been reported for *Palaeochersis talampayensis* (Rougier et al. 1995). In all other turtles, the acromion process is more rod-like, being longer than half the length of the scapular process (Figure 13b). There is no disagreement on the distribution of this character.

Character evolution. A long acromial process is an unambiguous synapomorphy of the clade that originates from the common ancestor of *Kayentachelys aprix* + TESTUDINES (Figure 18; CI = 1.00).

CHARACTER 122: SCAPULA B

Character definition. Acromial ridge: 0 = present, contacts the glenoid proximally; 1 = absent.

Morphology and distribution. The acromial process of numerous basal turtles, including *Proganochelys quenstedti*, *Kayentachelys aprix*, *Mongolochelys efremovi,* and *Meiolania platyceps*, is characterized by a distinct anteromedial ridge that runs the full length of the process, giving the acromion its distinct triradiate appearance in cross section. Proximally, the acromial ridge contacts the glenoid (Figure 13a). In all other turtles, the acromial ridge is absent. The acromion process is rod-like and round in cross section (Figure 13b).

Character evolution. The absence of an acromial ridge is an unambiguous synapomorphy of TESTUDINES (Figure 18; CI = 1.00).

CHARACTER 123: SCAPULA C

Character definition. Glenoid neck present on scapula (Shaffer et al. 1997, 115): 0 = absent; 1 = present.

Morphology and distribution. The glenoid of some derived turtles is set on a distinct pedestal, commonly termed a "neck," which was hypothesized by Bräm (1965) to be an adaptation for aquatic habitats. The glenoid neck seems to be distributed unevenly among turtles, being present in some PLEURODIRES, some basal PANCRYPTODIRES, and CHELONIOIDS. This structure is absent in all other turtles, including *Proganochelys quenstedti* and *Kayentachelys aprix*.

Character evolution. The presence of a glenoid neck is a synapomorphy of TESTUDINES, but this structure is secondarily lost in the clade formed by *Erymnochelys madagascariensis* + *Pelomedusa subrufa* and the clade formed by CHELYDRIDAE + TESTUDINOIDEA + KINOSTERNOIDAE (Figure 18; CI = 0.33).

Coracoid

CHARACTER 124: CORACOID A

Character definition. Coracoid foramen (Rougier et al. 1995, 52–53; Hirayama et al. 2000, 51): 0 = present; 1 = absent.

Morphology and distribution. The scapulacoracoid of *Proganochelys quenstedti* is perforated by a large foramen, the coracoid foramen, which is situated medial to the glenoid along the broad scapula–coracoid contact (Figure 13a). Such a coracoid foramen is also reported to be present in *Palaeochersis talampayensis.* A coracoid foramen is absent in all other known turtles, predominantly because the scapula and coracoid only meet at the glenoid (Figure 13b). This character seems to be correlated with the presence of a slim coracoid. The distribution of this character is not controversial.

Character evolution. The loss of a coracoid foramen is an unambiguous synapomorphy that unites the clade that originated from the common ancestor of *Kayentachelys aprix* and TESTUDINES (Figure 18; CI = 1.00).

Pelvis

CHARACTER 125: PELVIS A

Character definition. Sutural articulation of pelvis to shell (Dryden 1988, 41; Gaffney et al. 1991, 32; Rougier et al. 1995, 57; Hirayama et al. 2000, 53): 0 = absent; 1 = present.

Morphology and distribution. The pelvis of all unambiguous panpleurodires is unique among turtles in being sutured to the shell. All three elements of the pelvis contribute to this osseous connection by forming extensive interdigitating sutures with the costals, pygals, and suprapygals above and with the xiphiplastron below (Figures 9a, c–e and 11a–b). In all other turtles, including *Proganochelys quenstedti* and *Kayentachelys aprix*, the pelvis is flexibly attached to the shell by way of the sacrum and connective tissue (Figures 9b, 11c and 13d).

Sutured pelves have also been reported for the primitive turtles *Proterochersis robusta* (Fraas 1913) and *Palaeochersis talampayensis* (Rougier et al. 1995). However, the *Proterochersis robusta* material is not sufficiently prepared to allow unambiguous determination of whether or not the pelvis is indeed attached to the shell, or if the distal end of the ilium is simply expanded as in *Proganochelys quenstedti.* The presence of a fused pelvis in *Palaeochersis talampayensis* is also unclear (Gaffney, pers. comm. 2000). Until the condition can be clarified unambiguously for these taxa, both are scored as uncertain.

Character evolution. The presence of a sutured pelvis is an unambiguous synapomorphy of PANPLEURODIRA (Figure 18; CI = 1.00).

Ilium

CHARACTER 126: ILIUM A

Character definition. Elongated iliac neck (Rougier et al. 1995, 54): 0 = absent; 1 = present.

Morphology and distribution. The ilium of *Proganochelys quenstedti* is a short and stout element characterized by a large dorsal expansion for articulation with the sacrum, an expanded ventral portion that contributes to the acetabulum, and a short shaft (Figure 13c). An ilium with a short shaft has also been reported for *Palaeochersis talampayensis* (Rougier et al. 1995). The ilium of all other turtles retains the dorsal and ventral expansions to varying degrees, but all show a well-developed slender central shaft (Figure 13d–e).

Character evolution. An elongate ilial neck is an unambiguous synapomorphy that unites all turtles to the exclusion of *Proganochelys quenstedti* and *Palaeochersis talampayensis* (Figure 18; CI = 1.00).

CHARACTER 127: ILIUM B

Character definition. Iliac scar (Fuente and Iturralde-Vinent 2001, 11–12): 0 = extends from costals onto the peripherals and pygal; 1 = positioned on costals only.

Morphology and distribution. Among those PANPLEURODIRES that have their pelves fused to the shell, there is variation in regard to the elements of the carapace with which the pelves articulate. In *Platychelys oberndorferi* the articulation site is rather large and includes parts of the costals, peripherals,

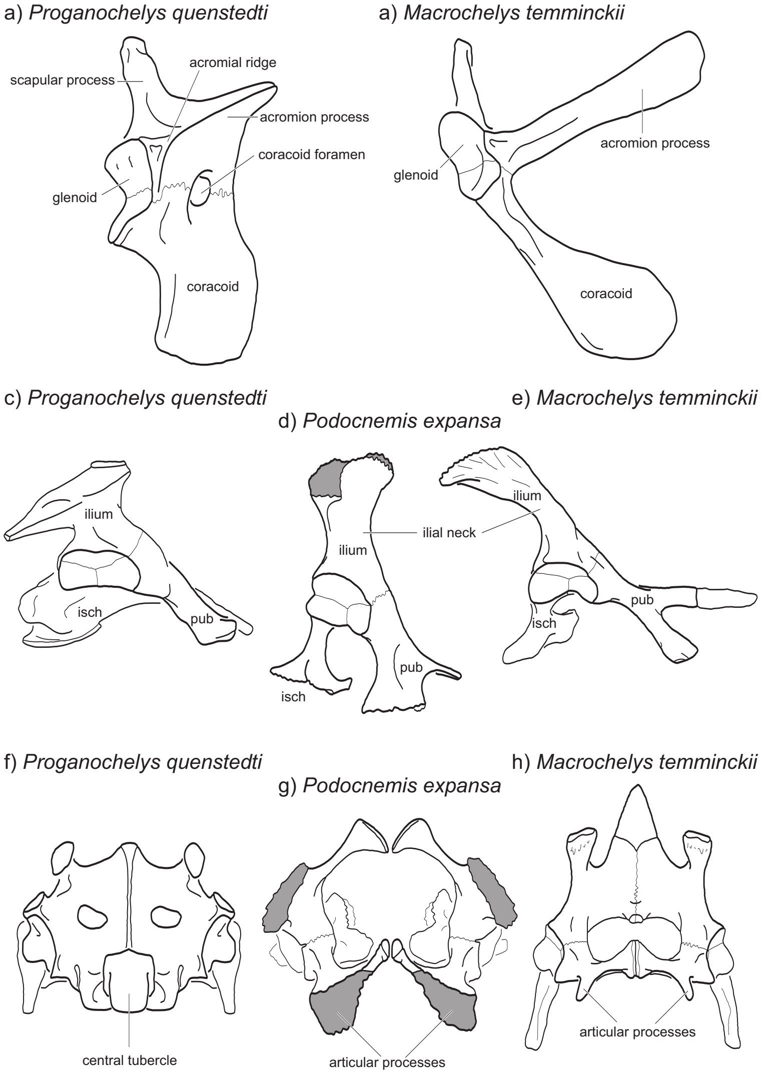


FIGURE 13. Pectoral and pelvic girdles of select *Testudinata.* **a.** Scapulacoracoid of *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **b.** Scapulacoracoid of *Macrochelys* (orig. *Chelonura*) *temminckii* (Troost 1835), redrawn from Gaffney (1990). **c.** Lateral view of pelvis of *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **d.** Lateral view of pelvis of *Podocnemis* (orig. *Emys*) *expansa* (Schweigger 1812), redrawn from Gaffney (1990). **e.** Lateral view of pelvis of *Macrochelys* (orig. *Chelonura*) *temminckii* (Troost 1835), redrawn from Gaffney (1990). **f.** Ventral view of pelvis of *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **g.** Ventral view of pelvis of *Podocnemis* (orig. *Emys*) *expansa* (Schweigger 1812), redrawn from Gaffney (1990). **h.** Ventral view of pelvis of *Macrochelys* (orig. *Chelonura*) *temminckii* (Troost 1835), redrawn from Gaffney (1990). *Abbreviations:* isch, ischium; pub, pubes.

and the pygal. In all other PANPLEURODIRES, the articulation site is limited to the costals only (Figure 9b). There is no disagreement on the distribution of this character.

Polarity. The pelvis of *Proganochelys quenstedti* and most other turtles is not fused to the shell, making it difficult to assess the primitive condition of this character. The distal part of the ilium of all nonpleurodiran turtles, however, is expanded parallel to the long-axis of the body, making it more plausible that the elongate articular morphology seen in *Platychelys oberndorferi* is indeed the primitive condition for PANPLEURODIRES. This assertion is further supported by the fact that *Platychelys oberndorferi* is stratigraphically the oldest unambiguous PANPLEURODIRAN turtle.

Character evolution. According to the preferred phylogenetic hypothesis, the restriction of the ilial scar to the costals is a synapomorphy of the clade that originates from the common ancestor of *Caribemys oxfordiensis* Fuente and Iturralde-Vinent and PLEURODIRA (Figure 18; CI = 1.00).

CHARACTER 128: ILIUM C

Character definition. Shape of ilium articular site (Fuente and Iturralde-Vinent 2001, 12): 0 = narrow and pointed posteriorly; 1 = oval.

Morphology and distribution. The shape of the articular site of the ilium with the carapace varies among PANPLEURODIRAN turtles. In *Platychelys oberndorferi* and *Caribemys oxfordiensis* the articular site is elongate and points posteriorly. In contrast, this articular site is oval in all remaining PANPLEURODIRES. The distribution of this character is unambiguous.

Polarity. See character 127.

Character evolution. An oval ilial scar is an unambiguous synapomorphy of the clade that originates from the common ancestor of *Notoemys laticentralis* Cattoi and Freiberg and PLEURODIRA (Figure 18; CI = 0.50).

CHARACTER 129: ILIUM D

Character definition. Posterior notch in acetabulum (Shaffer et al. 1997, 61): 0 = absent; 1 = present.

Morphology and distribution. The acetabulum of most turtles, including *Proganochelys quenstedti*, is a round depression formed by the ilium, ischium, and pubis. The rim of this structure is even. In contrast, the acetabulum of most KINOSTERNOIDS has a deep posterior notch just behind the ascending process of the ilium. The distribution of this character is not controversial.

Character evolution. The acquisition of the posterior ilial notch is a synapomorphy of Kinosternoidea, but is subsequently reversed along the phylogenetic stem of *Dermatemys mawii* (Figure 18; CI = 0.50).

Ischium

CHARACTER 130: ISCHIUM A

Character definition. Ischial contacts with plastron (Rougier et al. 1995, 55): 0 = contact by way of a large central tubercle; 1 = contact by way of two separate ischial processes.

Morphology and distribution. The pubis of *Proganochelys quenstedti* contacts the plastron at three points, much like a tripod. The lateral processes of the right and left pubes form the two anterior contacts. The third posterior contact is a large medially positioned tubercle that is formed jointly by the ischia only (Figure 13f). Observations of the *Proterochersis robusta* material reveal what seems to be a similar arrangement. In all other known turtles, the central tubercle is absent and the ischia contact the plastron by means of separate processes (Figure 13g–h).

Character evolution. The presence of two separate ischial contacts is an unambiguous synapomorphy of all taxa excluding *Proganochelys quenstedti* and *Proterochersis robusta* (Figure 18; CI = 1.00).

Hypoischium

CHARACTER 131: HYPOISCHIUM A

Character definition. Hypoischium (Rougier et al. 1995, 56; Hirayama et al. 2000, 55): 0 = present; 1 = absent.

Morphology and distribution. Hypoischia are distinctive bony structures that are positioned posterior to the pelvis and known from several groups of reptiles (Romer 1956; Gaffney 1990). Among turtles, hypoischia are only known from *Proganochelys quenstedti* and *Palaeochersis talampayensis.* The distribution of this character is not controversial.

Character evolution. The absence of hypoischia is a synapomorphy of the clade that originates from the common ancestor of *Kayentachelys aprix* and TESTUDINES (Figure 18; CI = 1.00).

Manus

CHARACTER 132: MANUS A

Character definition. Phalangeal formula of manus and pes (Meylan and Gaffney 1989, 40; Rougier et al. 1995, 60; Shaffer et al. 1997, 61; Hirayama et al. 2000, 56): 0 = most digits with three elongate phalanges; 1 = most digits with two short phalanges.

Morphology and distribution. The phalangeal formula of the manus and pes of turtles varies widely; however, two types are apparent. In most turtles, the digits of the hands and feet are elongate and typically have three phalanges or more (Figure 14a–e, g). This morphology is correlated with aquatic habitats (see Joyce and Gauthier 2004). In *Proganochelys quenstedti, Palaeochersis talampayensis, Meiolania platyceps,* nanhsiungchelyids, and TESTUDINIDS the digits of the hands and feet are short and typically have only two or fewer phalanges (Figure 14f). Given the presence of this morphology in *Proganochelys quenstedti* and other basal turtles, this terrestrial adaptation is considered primitive for TESTUDINATA, unlike in most other analyses (see Joyce and Gauthier 2004).

Character evolution. According to the preferred phylogenetic hypothesis, this character requires four evolutionary events (Figure 18; CI = 0.25). A nonreduced digital formula is an autapomorphy of *Mongolochelys efremovi* and a synapomorphy of TESTUDINES. Within the latter taxon, a reduced digital formula is reacquired as a synapomorphy of *Zangerlia neimongolensis + Basilemys variolosa* and as an autapomorphy of *Gopherus polyphemus* (Daudin).

CHARACTERS 133, 134: MANUS B–C

Character definition. Character 133, Manus B, paddles (Brinkman and Wu 1999, 51): 0 = absent; 1 = short paddles present; 2 = elongate paddles present.

Character definition. Character 134, Manus C, flippers: 0 = absent; 1 = short flippers present; 2 = elongate flippers present.

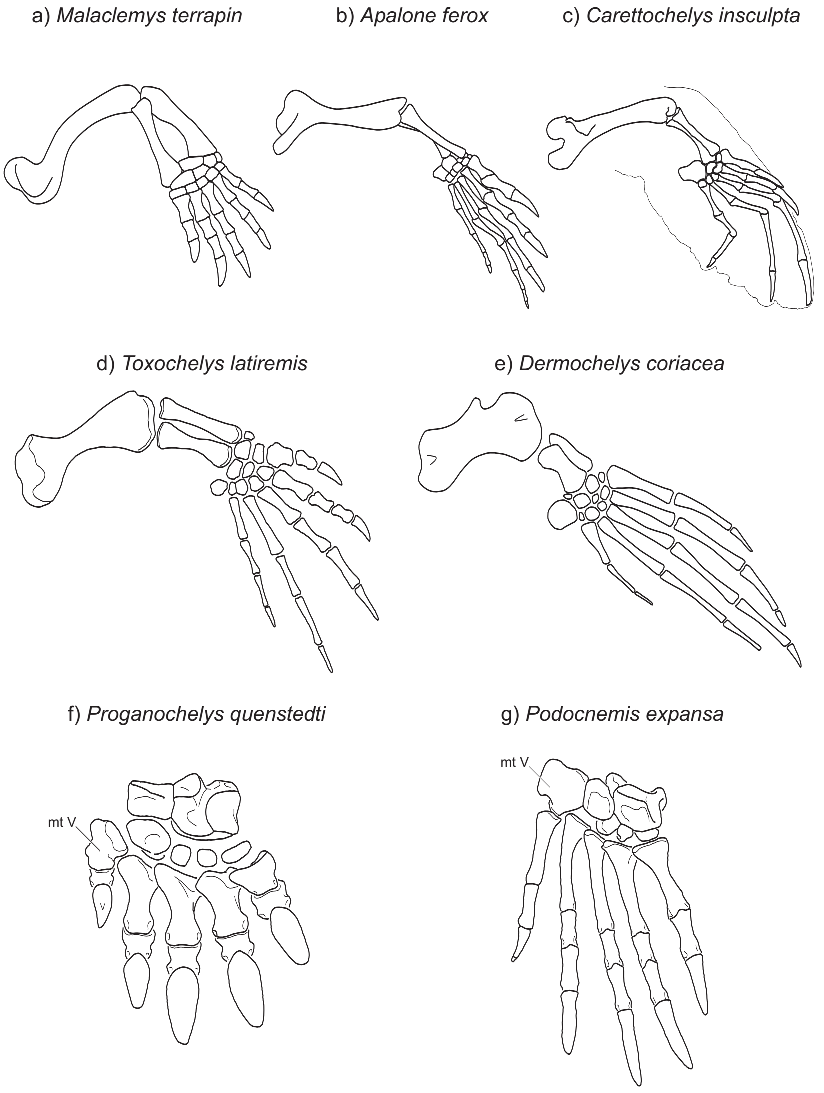


FIGURE 14. Hands and feet of select *Testudinata.* **a.** Forearm of *Malaclemys* (orig. *Testudo*) *terrapin* (Schoepff 1793), based on YPM R 15450. **b.** Forearm of *Apalone* (orig. *Testudo*) *ferox* (Schneider 1783), based on YPM R 10564. **c.** Forearm of *Carettochelys insculpta* Ramsay 1887, redrawn from Walther (1922). **d.** Forearm *Toxochelys latiremis* Cope 1872b, redrawn from Wieland (1902). **e.** Forearm of *Dermochelys* (orig. *Testudo*) *coriacea* (Linnaeus 1766), based on YPM R 5924. **f.** Hind foot of *Proganochelys quenstedti* Baur 1887, redrawn from Gaffney (1990). **g.** Hind foot of *Podocnemis* (orig. *Emys*) *expansa* (Schweigger 1812), redrawn from Gaffney (1990). *Abbreviations:* mt, metatarsal.

Morphology and distribution. The limbs are the sole means of propulsion in TESTUDINATES, because the trunk is fully encased in a ridged shell. Consequently, turtles always have well-developed limbs that closely reflect the habitat to which they are adapted (Joyce and Gauthier 2004).

The hands of most terrestrial and aquatic turtles, including *Proganochelys quenstedti,* reveal their amniotic ancestry by their five elongate digits. These digits are rather mobile, being able to flex, extend, and move relative to one another (Figure 14a). In representatives of TRIONYCHIA, the hand is developed into a flipper that greatly resembles the forelimbs of pinnipeds (i.e., seals, sea lions, and walruses). Even though the hand remains five fingered, this feature is not fully apparent externally because the fingers are completely encased in skin. The entire flipper is highly mobile, as can be seen by the well-developed articular surfaces on the metacarpals and phalanges. This type of flipper is moderately long in TRIONYCHIDS (Figure 14b) and extremely long is CARET-

TOCHELYIDS (Figure 14c). In contrast, the forelimbs of marine turtles are developed into paddles like those seen in cetaceans, plesiosaurs, and ichthyosaurs. Like the hands of TRIONYCHIANS, the fingers that form the paddles are fully encased by skin as well, but they are tightly bound to one another with connective tissue, resulting in a stiffened paddle. This paddle is relatively short in *Santanachelys gaffneyi* and *Toxochelys latiremis* (Figure 14d) and greatly elongated in protostegids and CHELONIOIDS (Figure 14e). The distribution of this character is not controversial.

Homoplasy, character 133, Manus B. The acquisition of short paddles is an autapomorphy of *Santanachelys gaffneyi* and a synapomorphy of PANCHELONIOIDEA. Within PANCHELONIOIDEA, elongate paddles occur as a synapomorphy of CHELONIOIDEA (Figure 18; CI = 0.66).

Homoplasy, character 134, Manus C. Short flippers are a synapomorphy of TRIONYCHIA, whereas long flippers are a synapomorphy of CARETTOCHELYIDAE (Figure 18; CI = 1.00). No reversals are apparent.

Pes

CHARACTERS 135, 136:
PES A–B

Character definition. Character 135, Pes A, claw of fifth digit: 0 = present; 1 = absent.

Character definition. Character 136, Pes B, metatarsal V and "functional metatarsal V": 0 = metatarsal V functions as true metatarsal; 1 = metatarsal V functions as a tarsal, with the first phalanx of digit V functioning as a metatarsal.

Morphology and distribution. The foot of extant turtles exhibits a number of peculiarities that distinguish it from the foot of basal turtles. The major differences all pertain to the morphology of the fifth digit. In particular, the fifth digit of all extant turtles is somewhat reduced in length and ends blind within the skin. A claw is always absent (Figure 14g). In contrast, the foot of *Proganochelys quenstedti* shows the primitive amniote condition with five fully formed and clawed digits (Figure 14f). Furthermore, in all extant turtles, the metatarsal of the fifth digit is strongly "hooked" and rotated outwards to be more closely associated topologically with the tarsals. The fifth metatarsal is thus often confused as a tarsal (see Joyce 2000 for examples). As a functional replacement for the metatarsal, the first phalanx of the fifth digit is much elongated and greatly resembles a metatarsal in being aligned with the remaining, true metatarsals (Figure 14g). The foot of *Proganochelys quenstedti* closely reflects the primitive amniotic condition with five claws and five subequal digits (Figure 14f).

Homoplasy, Pes A. The reduction of the fifth claw is an unambiguous synapomorphy of the clade formed by *Meiolania platyceps* + *Kallokibotion bajazidi* + TESTUDINES, and thus predicts the absence of a fifth claw in *Meiolania platyceps* as well (Figure 18; CI = 1.00).

Homoplasy, Pes B. Using DELTRAN optimization, the acquisition of a hooked fifth metatarsal and the elongation of the first phalange of the fifth digit to function as a metatarsal occurs as an autapomorphy of *Mongolochelys efremovi* and as a synapomorphy of TESTUDINES (Figure 18; CI = 0.50). However, given the many basal turtles currently scored as unknown, it remains possible that the formation of a hooked fifth metatarsal is a synapomorphy to a much more inclusive clade with a subsequent reversal in *Meiolania platyceps* (ACCTRAN).

Results

Three principal phylogenetic analyses were performed, and these differ primarily in the ordering of multistate characters that can be arranged in morphoclines and in the omission of rogue taxa.

For the first analysis, all characters were left unordered and equally weighted. This resulted in 5,120 most parsimonious solutions after 1,000 replicates and filtering. The shortest tree length was 366 steps. The retention index (RI) of these trees was 0.80 and the consistency index (CI) was 0.47. Given that no parsimony uninformative characters were included in the analysis, there was no need to calculate another CI. The Adams consensus and 50% majority rule consensus trees are given in Figure 15. Nodes that are supported by strict consensus methods are highlighted in both trees.

In the second analysis, all characters were left equally weighted, but the morphoclinal multistate characters were ordered. A total of 1,005 trees were retained with a length of 369 steps, a RI of 0.81, and a CI of 0.46. The consensus trees resulting from this analysis are given in Figure 16.

The third and final parsimony analysis replicates the second phylogenetic analysis by ordering the morphoclinic multistate characters; however, *Portlandemys mcdowelli* Gaffney, *Sandownia harrisi* Meylan, Moody, Walther and Chapman, and *Mongolemys elegans* Khozatsky and Mlynarski were omitted. These taxa were determined to be "rogue taxa" within the context of this analysis, due to their behavior in the first two analyses, in that these taxa had significantly different positions in the majority consensus trees relative to the Adam's consensus trees. Omission of these taxa reduced the number of optimal trees to 49. The length of these trees was 360. Their CI was 0.47 after exclusion of parsimony uninformative characters, and their RI was 0.82. The consensus trees are given in Figure 17.

Decay indices greater than 2 and bootstrap values greater than 50% are provided in Figure 18, which essentially depicts the 50% consensus cladogram obtained from the third analysis with the rogue taxa re-inserted (see Discussion).

Discussion

This paper provides the first opportunity to test the monophyly of many clades of fossil and living turtles, because only species are used as terminal taxa. Despite this methodological refinement, the analyses herein support the monophyly of most previously hypothesized clades. The monophyly of other groups, however, is not supported by this analysis and the accepted view of the basal divergence among turtles is in question, which in principle confirms the results of Dryden (1988) and Rougier et al. (1995). To allow for greater transparency, the results of these analyses will be discussed in sections and by reference to a single phylogenetic hypothesis termed the "preferred tree" (see Figure 18). This tree essentially captures the topology obtained in the 50% majority and Adam's consensus tree of the third phylogenetic analysis, but the taxa that were removed for this analysis were reinserted a posteriori. The rationale for favoring this topology and for the placement of omitted taxa is given below.

Choosing the Preferred Topology

The novel topology obtained in this study makes explicit statements about the traditionally accepted diagnostic characters of PLEURODIRES and CRYPTODIRES. In particular, the sutured pelvis seen in *Proterochersis robusta* must be considered homoplastic with that of PLEURODIRES, as was previously argued by Rougier et al. (1995). Furthermore, at least some of the features pertaining to the trochlear system and the bracing of the braincase seen in CRYPTODIRES must be considered ancestral to the condition seen in PLEURODIRES (see Character Evolution of Diagnostic Traits, below) and thus do not diagnose clades. As a logical consequence of the fact that the PLEUDORIAN condition derived from the CRYPTODIRAN condition, PLEURODIRES may be situated anywhere within that clade of turtles that is diagnosed by an at least partially braced braincase and a primitive trochlear system. This conclusion becomes obvious in the first analysis, which reveals that PLEURODIRES are situated within TESTUDINOIDEA (Figure 15). Although this analysis may seem preferable because all characters are left unordered and unweighted, the outcome is less preferable a posteriori, for two reasons.

First, according to the topology of this analysis, the oldest known PANPLEURODIRE is *Caribemys oxfordiensis* from the Late Jurassic (Oxfordian). A placement of PANPLEURODIRA with a paraphyletic "Testudinoidea" predicts that all other lineages of living turtles (such as PANCHELONIOIDEA, PANCHELYDRIDAE, PANPLATYSTERNON, PANTRIONYCHOIDEA, PANTESTUDINIDAE, PANEMYDIDAE, and PANGEOEMYDIDAE) must extend as ghost lineages into the Late Jurassic as well. Given the nature of the fossil record, these predictions cannot be falsified. However, current knowledge of the fossil record cannot corroborate them at any level either, because positive evidence reveals that most of these lineages extend only into the Late Cretaceous at most.

Second, consider the topology observable within PANPLEURODIRA. Among systematists, there is a strong consensus that many primitive turtles from the Late Jurassic (*Platychelys oberndorferi, Caribemys oxfordiensis,* and *Notoemys laticentralis*) represent the sister groups to crown PLEURODIRA (e.g., Gaffney and Meylan 1988; Lapparent de Broin and Murelaga 1999; Fuente and Iturralde-Vinent 2001). This hypothesis is supported by numerous characters and is consistent with the stratigraphic appearance of PANPLEURODIRAN taxa. According to the first analysis, however, these Late Jurassic taxa are the most derived PANPLEURODIRES, thus completely reversing the stratigraphic order in which PANPLEURODIRAN taxa appear.

These two observations (that is, the predicted presence of extensive ghost lineages and the reversal of the stratigraphic appearance of PANPLEURODIRAN taxa) suggest that the results of the first analysis are likely faulty due to extensive "morphological long-branch attraction" (systematic homoplasy that unites convergent lineages). PLEURODIRES are likely drawn into TESTUDINOIDEA by a suite of convergent characteristics that pertain particularly to the heavy ossification of the shell seen in both groups, including axillary and inguinal buttresses, an anal notch, and the reduction of inframarginals. The future inclusion of more primitive PANPLEURODIRAN taxa, particularly cranial characters, combined with the addition of CRYPTODIRAN characters will likely alleviate this situation. Within the context of this study, that aspect of the first analysis is dismissed and the topologies obtained from the second and third analyses are preferred because they are more consistent with external data.

The second analysis differs from the first only in the ordering of those characters that can be arranged into morphoclines. The topologies that result from the second analysis (Figure 16) are somewhat more intuitive relative to those obtained from the first analysis, but significant differences are apparent between the 50% majority trees and the Adams consensus tree. In particular, *Mongolemys elegans, Sandownia harrisi,* and PLEURODIRA reveal behavior associated with "rogue taxa"—they are placed significantly more basally in the Adams consensus tree than in the 50% consensus tree, indicating that their position varies wildly, whereas other taxa remain rather stable. Analysis of individual most parsimonious trees further reveals that the placement of *Portlandemys mcdowelli* varies widely as well. Considering that the placement of PLEURODIRA is of utmost importance to this analysis, the other tree taxa were isolated as rogue taxa and omitted from the third analysis.

The third analysis differs only by the three rogue taxa identified in the second analysis. The rogue nature of these three taxa is confirmed since the number of equally parsimonious trees drops drastically from 1,005 to 49. Differences between the Adams consensus and 50% consensus trees are minimal. Most nodes are supported by 100% of the most parsimonious trees, and most of the remaining nodes are found in more than 75% of most parsimonious trees.

The preferred phylogenetic tree essentially captures the topology obtained from the 50% of the third analysis, but minor adjustments are made to the topology (e.g., by placing PARACRYPTODIRES to be basal pancryptodires) and the rogue taxa are reinserted secondarily. The reasons for these changes and additions are discussed with each clade below. The stability of each node is discussed using information obtained from the consensus trees, decay indices, and bootstrap values.

Current Hypotheses of Basal Turtle Relationships

Among the most important outcomes of this study are the phylogenetic placement of *Proterochersis robusta, Kayentachelys aprix, Meiolania platyceps, Mongolochelys efremovi,* and *Kallokibotion bajazidi,* and the primary split of turtles into the PLEURODIRAN and CRYPTODIRAN lineage. This primary subdivision of all living turtles into two primary groups has been recognized by neontologists since Nopcsa (1923a), but not until Gaffney (1975a) was the putative monophyly of both crown groups established using cladistic arguments. Unlike his predecessors, Gaffney (1975a) not only compiled a list of morphological characters that diagnose these two living groups of turtles, but also used outgroup analysis in an attempt to clarify whether these characters were symplesiomorphies or synapomorphies. This approach is not only relevant for establishing the monophyly of these two clades, but is also important when assessing the placement of fossil taxa along the phylogenetic stems of both crown clades. However, even if a character complex has several derived character states that diagnose both crown clades, the possibility remains that one of the derived characters is ancestral to the other and thus does not unite a monophyletic group exclusive of the other. Gaffney (1975a) was aware of this problem and consequently focused his efforts on identifying characters that not only diagnose both crown groups, but that can also be argued to have originated independently from the ancestral condition observable in the primitive turtle *Proganochelys quenstedti.* This search led to the discovery of two character complexes: the trochlear system of the jaw closure mechanisms and the elements involved in the bracing of the basicranium.

Turtles are unique among amniotes in having a pulley mechanism (trochlea) that directs the greatly expanded adductor jaw musculature over the ear region posteriorly through the posttemporal fenestra toward the origin of the muscle (Figure 19). In CRYPTODIRES, the trochlea is mainly formed by the quadrate, whereas in PLEURODIRES is it formed by a lateral expansion of the pterygoid (Schumacher 1954). As the involved bony structures are not homologous, Gaffney (1975a) concluded that the trochlear mechanisms could not be homologous either, and must have originated independently from the primitive condition seen in *Proganochelys quenstedti.*

Conversely, the basipterygoid articulation of all living turtles is fused, but the condition seen in both crown clades differs fundamentally. In PLEURODIRES, the fusion of this joint (the sutural contact between pterygoid and basisphenoid) is supported by an articulation of the quadrate with the basisphenoid and prootic. In contrast, in CRYPTODIRES, the basipterygoid articulation is locked by an extended posterior process of the pterygoid that broadly contacts the basisphenoid medially, and that may even reach the basioccipital at the posterior end of the cranium. The cranioquadrate space (the bony gap that exists between the basicranium and the palatocranium in *Proganochelys quenstedti*) is filled with bone in both conditions, but the course of some cranial vessels and nerves within these bones differs slightly. Based on these differences, Gaffney (1975a) concluded that the fusion of the basicranium to the palatocranium occurred twice within TESTUDINES and that neither condition is ancestral to the other.

Following the arguments of Gaffney (1975a), these two cranial character complexes can be used to assess the phylogenetic placement of most fossil turtles as belonging to either PANPLEURODIRA or PANCRYPTODIRA. For instance, the primitive turtles *Meiolania platyceps* and *Kallokibotion bajazidi* have extensive posterior pterygoid processes and may thus be attributed to the phylogenetic stem of CRYPTODIRA (Gaffney and Meylan 1988, 1992). In contrast, the Early Jurassic turtle *Kayentachelys aprix* lacks the extensive bracing of the braincase seen in PLEURODIRES or CRYPTODIRES, but has vertical external pterygoid processes; it may thus be attributed to the phylogenetic stem of CRYPTODIRA because these structures are associated with the unique jaw-closure mechanisms of that clade (Gaffney et al. 1987). Finally, the Late Triassic turtle *Proterochersis robusta,* known only from shells, seems to have a sutured pelvis; this taxon may thus be attributed parsimoniously to the phylogenetic stem of PLEURODIRA, because that feature is only present in PLEURODIRES and absent in all CRYPTODIRES as in the basalmost turtle *Proganochelys quenstedti*. For simplicity, the topology obtained from these primary homology assessments will be referred to as the "traditional hypothesis."

The primary homology assessments of Gaffney (1975a) are carefully constructed and represent a milestone in advancing the study of the phylogenetic relationships among turtles. However, no matter how carefully any argument of primary homology is constructed, the ultimate test of homology must still be considered congruence (Patterson 1982, 1988). In return, any rigorous test of congruence demands sound character and taxon sampling combined with powerful computing technologies, none of which were available to Gaffney in the early to mid 1970s. This situation has changed during the last 30 years. Fueled by the adoption of cladistic methodology and catalyzed by Gaffney's work, many morphological characters have been identified and many fossil turtles described, allowing for the efficient extraction of information from the literature and compilation of an extensive data matrix. Even though the compilation of such a large data matrix may have been possible by the mid 1980s (Gaffney and Meylan 1988), only more recent advances in computing technology have made it possible to use single species only as terminal taxa and still run analyses within reasonable timespans.

An Alternative Hypothesis of Basal Turtle Relationships

Three principal analyses were performed within the context of this study, which differ in the ordering of the morphoclinic multistate characters and by the exclusion of rogue taxa. Despite all differences that exist in the resulting trees (see Figure 15), all agree that *Proterochersis robusta, Kayentachelys aprix, Meiolania platyceps, Mongolochelys efremovi,* and perhaps even *Kallokibotion bajazidi* should be considered representatives of the phylogenetic stem of TESTUDINES, in addition to the previously unquestioned stem turtles *Proganochelys quenstedti, Palaeochersis talampayensis,* and *Australochelys africanus.* This result resembles that of Dryden (1988) to a certain degree (see Figure 1a), but is much less drastic in its claims relative to the PLEURODIRE–CRYPTODIRE split because plesiochelyids, baenids, and pleurosternids are left within crown TESTUDINES.

Interestingly, all three analyses more or less obtain the traditional hypothesis of the internesting of Mesozoic turtles if PANPLEURODIRA is removed from consideration. The primary difference can thus be summarized as the placement of PANPLEURODIRA either just above *Proganochelys quenstedti* with *Palaeo-*

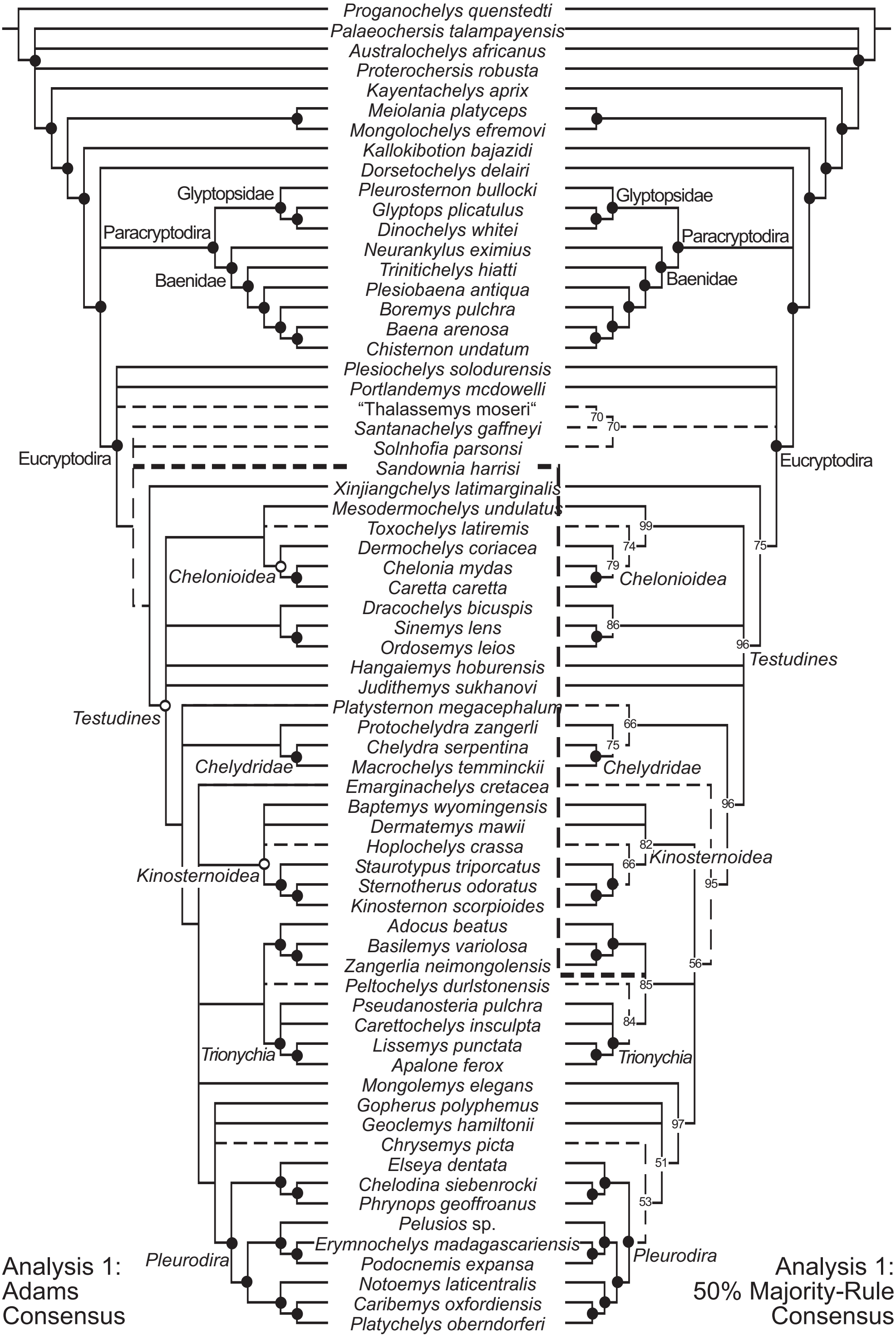


FIGURE 15. Phylogenetic hypothesis resulting from the first analysis. All characters are equally weighted and unordered. Dark circles indicate nodes that are supported even in the strict consensus trees. Thin and thick dashed lines highlight differences between the Adams Consensus and 50% Majority-Rule Consensus trees, respectively.

chersis talampayensis sister to *Proterochersis robusta,* or as sister to a more restricted clade that excludes *Kayentachelys aprix, Mongolochelys efremovi, Meiolania platyceps,* and *Kallokibotion bajazidi.*

CLADE 1: TESTUDINATA

The monophyly of TESTUDINATA (the clade of amniotes diagnosed by the presence of a turtle shell that is homologous with that seen in TESTUDINES) has never been seriously doubted (Gaffney and Meylan 1988), and its monophyly is assumed in this study. Given that all characters that unify this clade were omitted a priori because they are parsimony uninformative, no synapomorphies are apparent for this group within the context of this analysis, except, of course, the presence of a "turtle" shell.

CLADE 2: PALAEOCHERSIS NODE

Three lineages are united as a polytomy at the base of this clade. These are *Palaeochersis talampayensis, Australochelys africanus,* and the clade that originated from the common ancestor of *Proterochersis robusta* + TESTUDINES. This lack of resolution is primarily because *Australochelys africanus* is only known from a single, poorly preserved skull and because the scoring of this skull is redundant with that of *Palaeochersis talampayensis* within the context of this analysis.

The analysis of Rougier et al. (1995) was the first to establish the position of *Australochelys africanus* and *Palaeochersis talampayensis* as advanced relative to *Proganochelys quenstedti,* but primitive relative to *Proterochersis robusta.* This node is supported by a decay index of 2.6 and 100% bootstrap values. Rougier et al. (1995) went further, however, in proposing a sister group relationship between *Australochelys africanus* and *Palaeochersis talampayensis,* which they called the Australochelyidae. Unfortunately, none of the characters that unite this taxon were included in this study, because they could not be verified based on the preliminary description that Rougier et al. (1995) provided for *Palaeochersis talampayensis.* As such, this study neither corroborates nor refutes the monophyly of Australochelyidae.

Representatives of Clade 2 are united by the following: the absence of prefrontal prominences (character 8); absence of vomerine and palatine teeth (character 29); presence of a partially formed cavum tympani (character 33); formation of an incisura stapes (character 36); fusion of the basipterygoid articulation (character 39); fusion of the paroccipital process to the quadrate and squamosal (character 49); and anterior displacement of the stapedial artery (character 53).

CLADE 3: PROTEROCHERSIS NODE

The placement of *Proterochersis robusta* along the phylogenetic stem of TESTUDINES was first proposed by Rougier et al. (1995). This species is characterized by a sutured pelvis and has thus been traditionally regarded as the most basal representatives of PANPLEURODIRA (e.g., Gaffney and Meylan 1988; Lapparent de Broin and Murelaga 1999; Fuente and Iturralde-Vinent 2001). Forcing this topology in the preferred phylogenetic hypothesis requires 13 additional evolutionary steps. In contrast, forcing a sister group relationship of PANPLEURODIRA with any major clade of CRYPTODIRA (e.g., CHELONIOIDEA or CHELYDRIDAE) only requires four to nine additional steps, indicating that the basal placement of this taxon is quite solid. Naturally, the possibility remains that *Proterochersis robusta* is in fact the earliest divergence within PANPLEURODIRA. However, until additional fossil turtles are found that show that the characters currently uniting all PLEURODIRES and CRYPTODIRES relative to *Proterochersis robusta* and *Kayentachelys aprix* are indeed homoplastic, *Proterochersis robusta* should neither be considered the basalmost PANPLEURODIRE nor used when assessing ancestral states for PANPLEURODIRA (e.g., Gaffney et al. 1991; Gaffney 1996).

The clade that originates from the common ancestor of *Proterochersis robusta* and TESTUDINES is united by several derived characters. These include the reduction of the number of supramarginals (character 71), an increase in the number of vertebrals to five (character 72), the absence of distinct posterolateral entoplastral processes (character 80), and the presence of an elongate ilial neck (character 126).

CLADE 4: "KAYENTACHELYS NODE"

The basal placement of *Kayentachelys aprix* was first proposed by Dryden (1988). A large suite of characters unites the clade that originates from

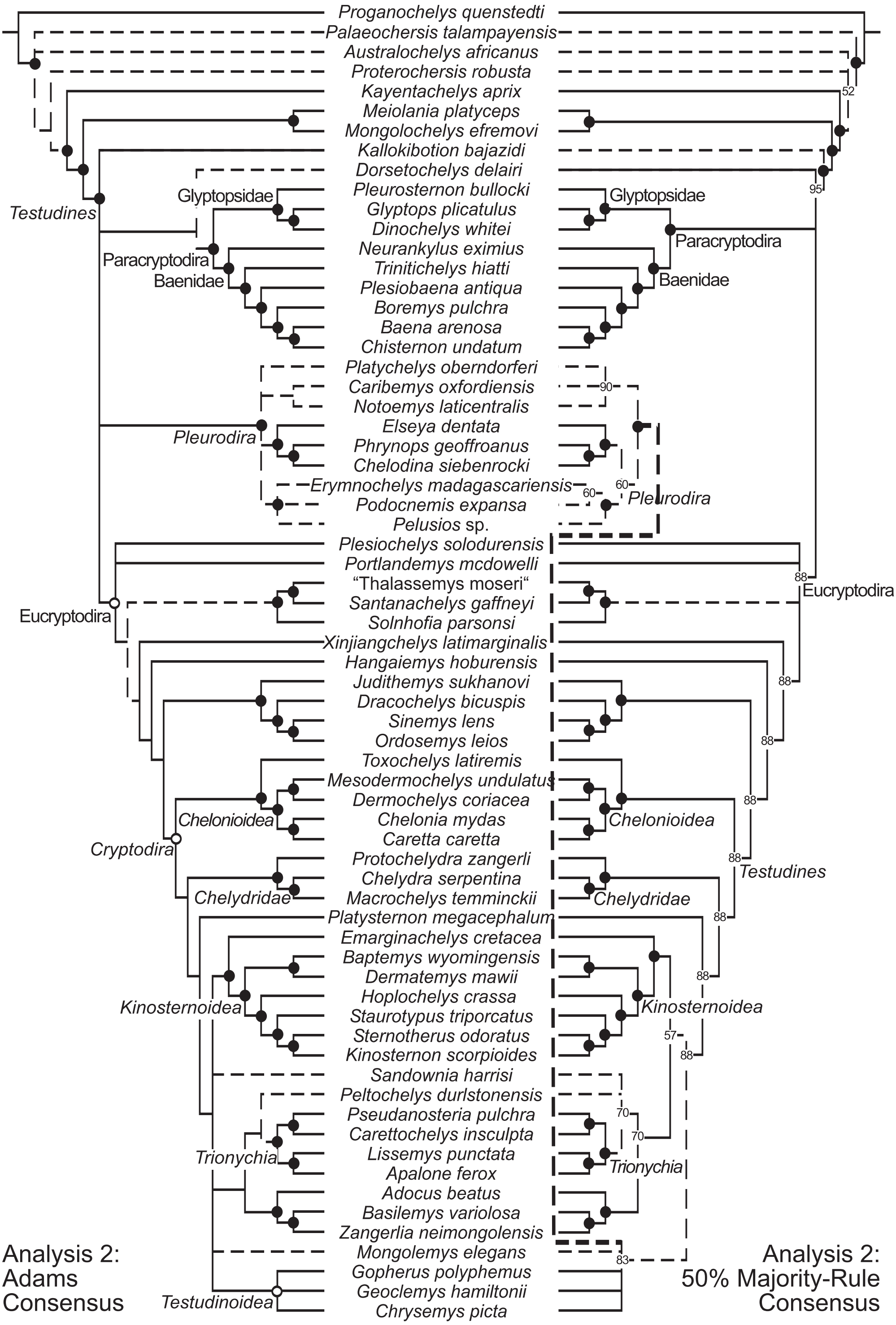


FIGURE 16. Phylogenetic hypothesis resulting from the second analysis. All characters are equally weighted, but all multistate characters that can be arranged into morphoclines are ordered. Dark circles indicate nodes that are supported even in the strict consensus trees. Thin and thick dashed lines highlight differences between the Adams Consensus and 50% Majority-Rule Consensus trees, respectively.

the common ancestor of *Kayentachelys aprix* and TESTUDINES. These include the following: the presence of a medial prefrontal contact (character 5); absence of lacrimals (character 9); loss of a jugal squamosal contact (character 14); loss of supratemporals (character 21); acquisition of fused external nares (character 22); medial fusion of the vomer (character 27); acquisition of a central constriction of the middle ear region (character 32); formation of a fully developed cavum tympani (character 33); formation of an antrum postoticum (character 35); formation of defined anterior and posterior jugular foramina (character 55); reduction of the peripherals to 11 pairs (character 65); complete loss of supramarginals (character 71); loss anterior plastral tuberosities (character 94); loss of a dorsal contact of the cleithra with the nuchal (character 120); acquisition of an elongate scapular process (character 121); and the absence of coracoid foramen (character 124). The support values are correspondingly strong with a decay index of 3.6 and bootstrap values of 100%.

If the traditionally accepted hypothesis were correct and *Kayentachelys aprix* were indeed a stem-cryptodire and *Proterochersis robusta* a stem-pleurodire, all of the above characters would have had to be acquired homoplastically in both lineages.

CLADE 5

The phylogenetic analysis of Hirayama et al. (2000) is similar to this analysis in hypothesizing that *Meiolania platyceps* and *Mongolochelys efremovi* are more derived than *Kayentachelys aprix,* but less derived than *Kallokibotion bajazidi* relative to CRYPTODIRA. This analysis progresses a step further by hypothesizing a sister group relationship between these two taxa, based on the following characters: an extensive squamosal supraoccipital contact (character 19); extensive contribution of the supraoccipital to the dorsal skull roofing (character 47); loss of an osseous bridge (character 75); retention of a central plastral fontanelle during ontogeny (character 76); acquisition of narrow epiplastra (character 83); development of formed central articulations of the cervical vertebrae (character 105); and the acquisition of anteriorly procoelous and posteriorly opisthocoelous caudal vertebrae (character 119). Forcing the paraphyly of this grouping adds four evolutionary steps to the preferred hypothesis. Interestingly, of the long list of synapomorphies that unite this clade, all but the first two occur homoplastically along the phylogenetic stem of CRYPTODIRA, providing support to the hypothesis that *Meiolania platyceps* and *Mongolochelys efremovi* may indeed be placed with PANCRYPTODIRA (Gaffney and Meylan 1988 [Figure 1b]; Gaffney 1996 [Figure 1d]). However, any placement of *Meiolania platyceps* and *Mongolochelys efremovi* along the phylogenetic stem of CRYPTODIRA increases the number of required steps by six to eleven, indicating that the number of characters that exclude these taxa from PANCRYPTODIRA far exceeds the number of characters that place them within. This clade is supported by a decay index of 3.3 and bootstrap values of 79%.

Meiolania platyceps and *Mongolochelys efremovi* diverged from another no later than the Maastrichtian (Late Cretaceous), based on the available material of *Mongolochelys efremovi.* However, fragmentary remains from the Upper Cretaceous of Argentina tentatively referrable to the phylogenetic stem of *Meiolania platyceps* extend this divergence deeper into the Cretaceous.

CLADE 6: "MEIOLANIA NODE"

The clade formed by *Meiolania platyceps, Mongolochelys efremovi,* and TESTUDINES is united by the following list of derived characters: the formation of a bony trigeminal foramen (character 12); partial flooring of the cavum acustico-jugulare and cavum labyrinthicum by the posterior process of the pterygoid (character 31); loss of pterygoid teeth (character 38); closure of the pterygoid vacuity (character 40); acquisition of a supraoccipital crest that protrudes posteriorly beyond the foramen magnum (character 46); acquisition of a medial contact of the epiplastra (character 78); and loss of the claw of the fifth pedal digit (character 135). Support for this clade is rather strong with a decay index of 3.3 and bootstrap values of 93%.

If the traditionally accepted hypothesis is correct and *Kayentachelys aprix, Meiolania platyceps,* and *Mongolochelys efremovi* are primitive PANCRYPTODIRES and *Proterochersis robusta* a primitive PANPLEURODIRE, most of the characters listed above would have had to be acquired independently along the phylogenetic stems of

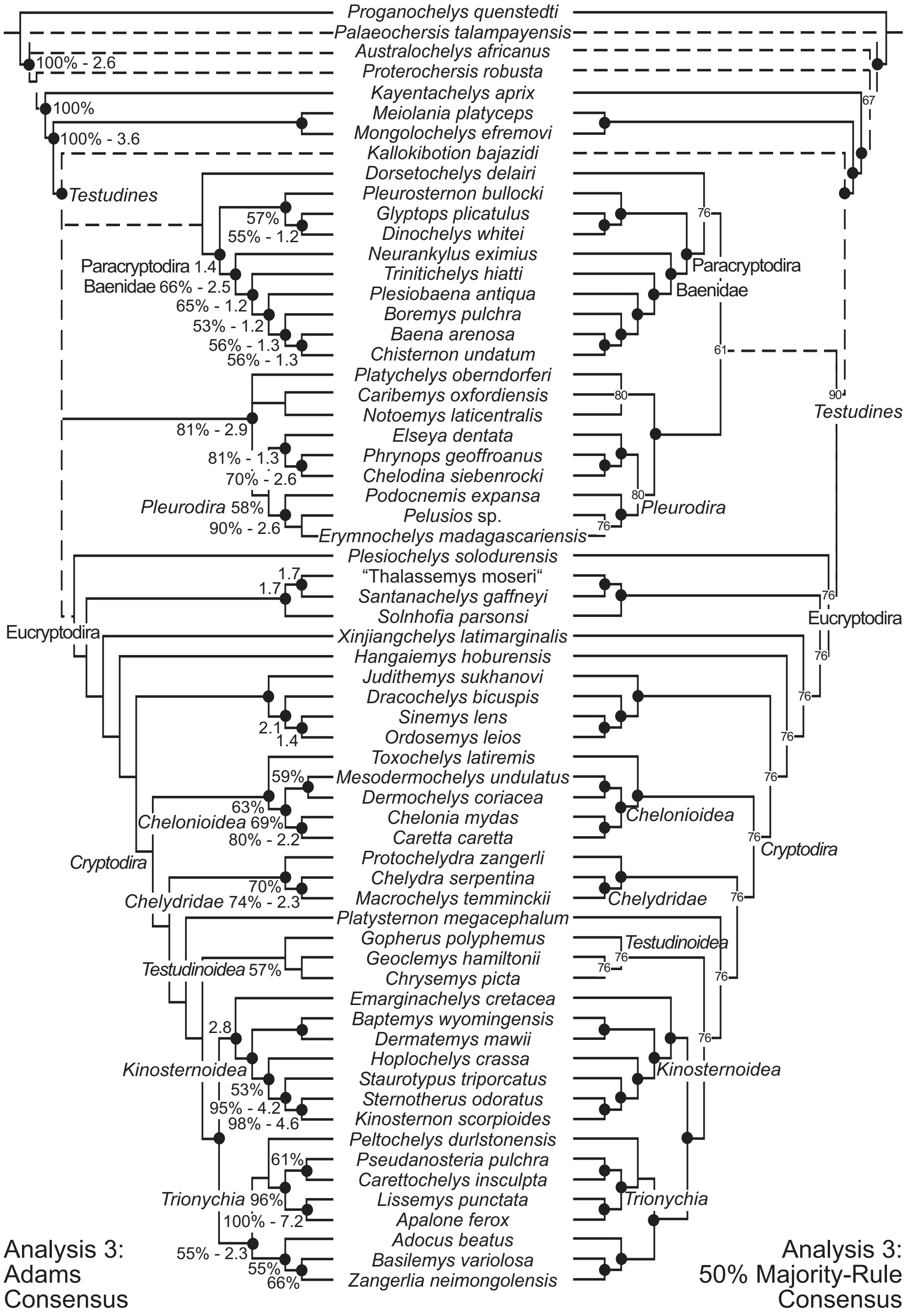


Figure 17. Phylogenetic hypothesis resulting from the third analysis. All characters are equally weighted and the morphoclinic multistate characters are ordered; however, *Portlandemys mcdowelli, Sandownia harrisi,* and *Mongolemys elegans* are omitted. Dark circles indicate nodes that are supported even in the strict consensus trees. Thin and thick dashed lines highlight differences between the Adams Consensus and 50% Majority-Rule Consensus trees, respectively.

both crown clades, in addition to the characters listed for Clade 4.

CLADE 7: "KALLOKIBOTION NODE"

Three characters unite *Kallokibotion bajazidi* with TESTUDINES relative to *Meiolania platyceps* and *Mongolochelys efremovi*: a reduction of nasal size (character 3); and the development of axillary and inguinal buttresses that contact the costals along the visceral side of the carapace (characters 84 and 86).

Again, if the traditionally accepted hypothesis were correct and *Kayentachelys aprix, Meiolania platyceps, Mongolochelys efremovi,* and *Kallokibotion bajazidi* were stem-cryptodires and *Proterochersis robusta* a stem-pleurodire, all of these characters would have had to be acquired twice along the phylogenetic stems of both crown clades, in addition to those listed for Clades 4 and 6. Despite this cumulative evidence in favor of placing *Kayentachelys aprix* and *Proterochersis robusta* basal to the crown, the basal position of *Kallokibotion bajazidi* is much less secure considering that it only requires one more step to place it within the crown.

CLADE 8: TESTUDINES

The turtle crown TESTUDINES is diagnosed by a series of characters relative to its phylogenetic stem. These include the following: the exclusion of the frontal from the orbit (character 10); loss of a contact between the eighth cervical and the nuchal (character 62); reduction of the posterior entoplastral process (character 79); loss of large cervical ribs (character 101); the reduction of the tenth thoracic rib (character 115); loss of an extensive acromial ridge (character 122); acquisition of a glenoid neck (character 123); addition of phalanges to most digits of the hands and feet (character 132); and the reorganization of the fifth pedal digit (character 136). Despite this list of synapomorphies, this clade is rather poorly supported, considering that it only requires one additional step to pull in *Kallokibotion bajazidi.*

Once again, if *Kayentachelys aprix* were a basal PANCRYPTODIRE and *Proterochersis robusta* a basal PANPLEURODIRE, most of the characters listed above, combined with those characters that unite clades Clades 4, 6, and 7, would have had to have originated independently along the phylogenetic stems of both crown clades. Although the possibility exists that the PLEURODIRAN and CRYPTODIRAN stem indeed acquired these many characters independently from one another, until fossils are found that show such a systematic accumulation of homoplasy, this must be considered less parsimonious.

This analysis reveals the presence of several characters that seem to further unite all living PLEURODIRES and CRYPTODIRES, but which demonstrably originated twice during the evolution of both clades. These seemingly synapomorphic characters include the following: the loss of a parietal squamosal contact (character 11, present in fossil PANCRYPTODIRES); the acquisition of elongate anterior extension to the lateral braincase walls (character 13, absent in primitive PANCRYPTODIRES); the development of temporal emarginations (character 18, absent in fossil PANCRYPTODIRES); the formation of an anteriorly enclose antrum postoticum (character 35, absent in primitive PANCRYPTODIRES); the presence of narrow vertebral scutes (character 73, absent in fossil PANCRYPTODIRES and PANPLEURODIRES); a shift of the vertebral II–III sulcus onto the fifth neural (character 74, absent in primitive PANPLEURODIRES); the development of formed cervical central articulations (character 105, absent in fossil PANCRYPTODIRES); the reduction of the first thoracic rib (character 113, elongate first thoracic ribs present in fossil PANCRYPTODIRES and PANPLEURODIRES); loss of chevrons (character 117, present in fossil PANCRYPTODIRES); the acquisition of procoelous caudal vertebrae (character 119, absent in fossil PANPLEURODIRES and PANCRYPTODIRES); and the loss of cleithra (character 120, present in numerous primitive PANCRYPTODIRES). This suite of demonstrably homoplastic characters illustrates the importance of integrating fossil taxa into phylogenetic analyses.

The Basal Dichotomy of TESTUDINES *and the Placement of Paracryptodira*

The crown of turtles, by definition, is comprised of the PANPLEURODIRAN and PANCRYPTODIRAN clades (Joyce et al. 2004). Based on numerous derived characters (see Clade 8), TESTUDINES also

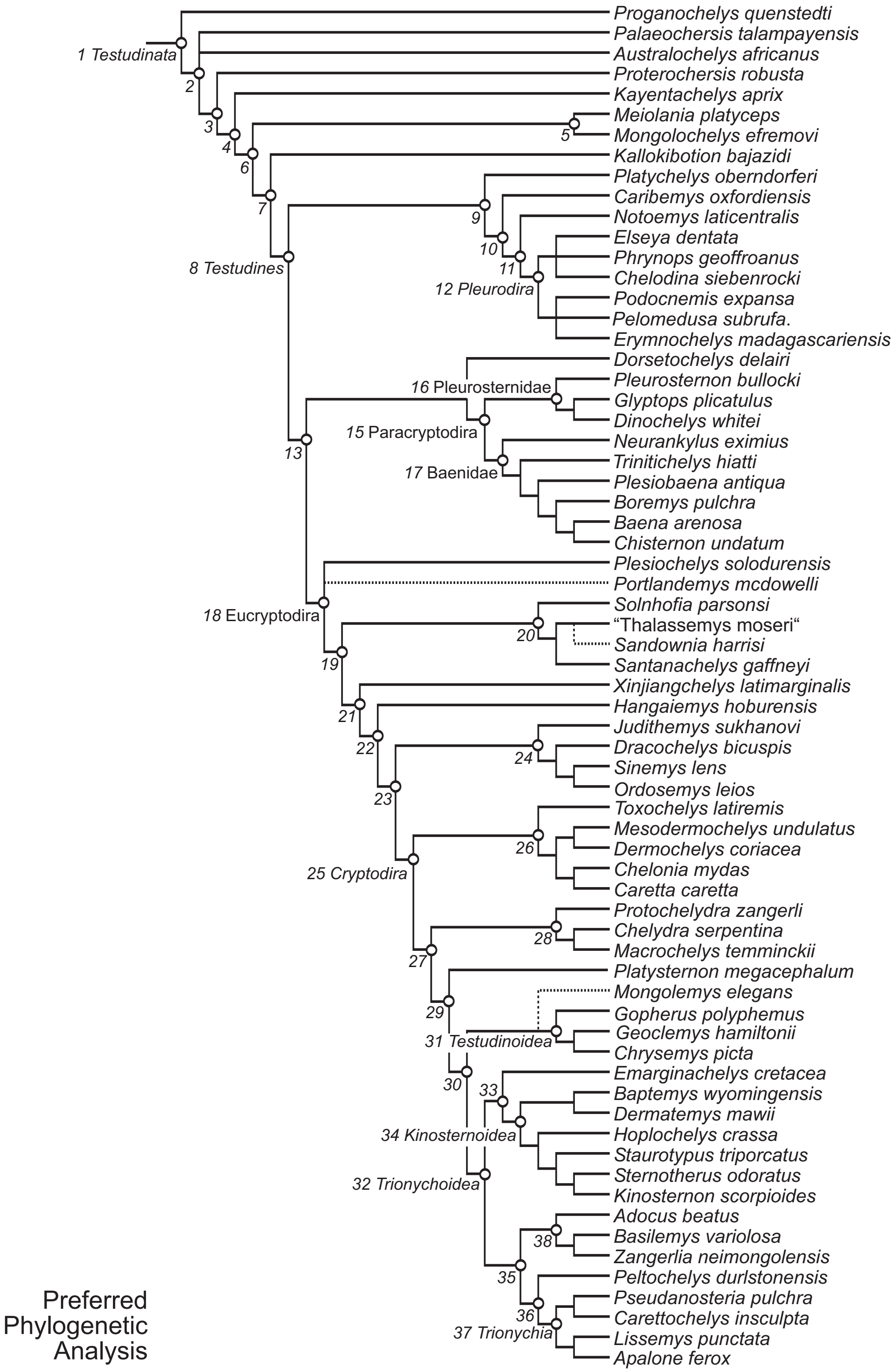


Figure 18. The preferred phylogenetic hypothesis. The cladogram is primarily based on the hypothesis obtained from the third analysis, but *Portlandemys mcdowelli, Sandownia harrisi,* and *Mongolemys elegans* are reinserted. Numbers at nodes represent boot strap values and decay indices.

comprises all paracryptodires (e.g., Pleurosternidae + Baenidae), but it is equally parsimonious to place this clade as the most basal member of PANPLEURODIRA or PANCRYPTODIRA. In contrast, the placement of Paracryptodira outside of TESTUDINES, as was hypothesized by Dryden (1988), is one step less parsimonious.

An analysis of the characters that support the placement of Paracryptodira, either along the phylogenetic stem of PLEURODIRA or CRYPTODIRA, does not provide any conclusive evidence to resolve this problem. A PANPLEURODIRAN placement of Paracryptodira is supported by the acquisition of an extensive anterior extension to the lateral braincase wall (character 13). However, this character also occurs as a synapomorphy along the phylogenetic stem of PANCRYPTODIRA, and could actually represent a synapomorphy of TESTUDINES in general. In contrast, a PANCRYPTODIRAN placement is supported by a pterygoid–basioccipital contact (character 41), and a shift of the vertebral II–III sulcus onto the fifth neural (character 74), but this placement would also require these two characters to be homoplastically acquired within PANPLEURODIRA and *Kallokibotion bajazidi,* respectively.

The most conservative solution to this problem would be to advocate a basal trichotomy for TESTUDINES. However, because the position of the foramen posterius canalis carotici interni of paracryptodires is arguably ancestral to the condition seen in more derived PANCRYPTODIRES (Evans and Kemp 1976), placing Paracryptodira within PANCRYPTODIRA is favored here, as has been traditionally accepted.

Phylogenetic Relationships of PANPLEURODIRA

CLADE 9: "PLATYCHELYS NODE"

In contrast to previous analyses (Gaffney and Meylan 1988; Lapparent de Broin and Murelaga 1999; Fuente and Iturralde-Vinent 2001), this study reveals that PANPLEURODIRA is slightly less inclusive than previously thought, in that it excludes the Upper Triassic turtle *Proterochersis robusta* (see discussion above). PANPLEURODIRA is thus restricted to the stem-pleurodires *Platychelys oberndorferi, Caribemys oxfordiensis, Notoemys laticentralis,* and crown PLEURODIRA. Unfortunately, of the available PANPLEURODIRES, only *Notoemys laticentralis* is currently known from cranial material, though this material is rather fragmentary. Nevertheless, the following list of postcranial characters gives substantial support to this clade: the retention of a medial plastral fontanelle in adults (character 76); loss of a medial contact of the mesoplastra (character 85); acquisition of a well-developed anal notch (character 87); medial fusion of the gulars (character 91); complete loss of inframarginals (character 100); acquisition of formed central articulations to the cervical vertebrae (character 105); loss of chevrons (character 117); and the sutural articulation of the pelvis with the shell (character 125). This node is well supported with a decay index of 2.9 and a bootstrap value of 81%.

CLADE 10: "*CARIBEMYS* NODE"

This analysis closely replicates the topology obtained by Fuente and Iturralde-Vinent (2001) on the basal representatives of PANPLEURODIRA. *Caribemys oxfordiensis, Notoemys laticentralis,* and PLEURODIRA are derived relative to *Platychelys oberndorferi,* based on the reduced visceral contact of the ilium with the overlying carapace (character 127). However, this node is not well supported by the decay indices and bootstrap values.

CLADE 11: "*NOTOEMYS* NODE"

Notoemys laticentralis and PLEURODIRA shared the following derived characters relative to *Platysternon oberndorferi* and *Caribemys laticentralis*: the flooring of the cavum acusticojugulare and cavum labyrinthicum by the ventral process of the quadrate or the prootic, or both (character 31); the reduction of the first thoracic rib (character 113); and the acquisition of a round visceral contact of the ilium with the carapace (character 128). This node is characterized by insignificant bootstrap values and decay indices.

CLADE 12: PLEURODIRA

Gaffney (1975a) conclusively showed the monophyly of PLEURODIRA, which has never been seriously doubted since. The following list of synapomorphies, which unites representatives of PLEURODIRA, confirms this claim: secondary loss of the prefrontal vomer contact (character 5); loss of the prefrontal palatine contact (character 6);

acquisition of an elongate extension to the lateral braincase wall (character 13); formation of a solid posterior orbital wall by contact of the postorbital with the palatine (character 20); acquisition of an anteriorly enclosed antrum postoticum (character 35); a wide closure of the incisura stapes that includes the Eustachian tube (character 36); loss of the epipterygoids (character 37); development of the processus trochlearis pterygoideus (character 42); acquisition of a separate path for the hyomandibular nerve (character 52); medial contact of the posterius costals (character 68); acquisition of narrow vertebrals (character 73); anterior movement of the vertebral II–III sulcus onto the fifth neural (character 74); reacquisition of a solidly ossified plastron (character 76); complete loss of cleithra (character 120); and acquisition of procoelous caudal vertebrae (character 119).

Given that the primary focus of this study was to resolve basal turtle relationships, only a few characters were included that addressed relationships within PLEURODIRA. The two primary clades of this taxon, CHELIDAE and PELOMEDUSOIDES, could nevertheless be recovered, although relationships are not clearly resolved within these subclades.

The following suite of characters unites all representatives of CHELIDAE: the loss of mesoplastra (character 85); loss of a medial nasal contact (character 2); loss of quadratojugals (character 16); loss of a squamosal postorbital contact due to the development of an extensive lower temporal emargination (character 18); enclosure of the foramen posterius canalis caroticum internus within the prootic only (character 56); and the acquisition of anteriorly convex articulations between cervical IV and V (character 108), and between cervical VII and VIII (character 111).

In contrast, the following unites representatives of PELOMEDUSOIDES: the loss of nasals (character 1); acquisition of a medial prefrontal contact (character 4); loss of a parietal squamosal contact (character 11); loss of a postorbital squamosal contact (character 18); reduction or complete loss of the vomer (character 27); loss of a vomer pterygoid contact in palatal view (character 28); acquisition of a deep precolumellar fossa (character 34); loss of splenials (character 59); loss of cervical scutes (character 70); and the acquisition of anteriorly concave articulations between cervical II and III (character 106), and cervical III and IV (character 107).

Basal PANCRYPTODIRES —Paracryptodira

CLADE 13: "PARACRYPTODIRE NODE"

Representatives of PANCRYPTODIRA are united by a pterygoid basioccipital contact (character 41), a shift of the vertebral II–III sulcus onto the fifth neural (character 74), and the placement of the foramen posterius canalis caroticum internus halfway along the basisphenoid–pterygoid suture (character 56). The pterygoid basioccipital contact, along with the position of the foramen posterius canalis caroticum internus, have long been thought to be among the most diagnostic PANCRYPTODIRE characters (Gaffney 1975a). According to the topology of the preferred phylogenetic hypothesis, however, a pterygoid basioccipital contact is obtained independently along the phylogenetic stem of *Meiolania platyceps* and *Kallokibotion bajazidi* and a carotid canal morphology that resembles that of extant CRYPTODIRES is obtained independently in *Meiolania platyceps.* As such, no single character is currently available that unambiguously diagnoses PANCRYPTODIRE turtles.

CLADE 14: "*DORSETOCHELYS* NODE"

This study is the first to assess the placement of *Dorsetochelys delairi* within the context of a global analysis revealing, its placement as the sister taxon to Paracryptodira. The monophyly of this clade is supported by the secondary reduction of the supraoccipital crests (character 46). A second character that seemingly unites this clade is the placement of the foramen posterius canalis carotici interni halfway along the pterygoid basisphenoid suture (character 56). However, as had been argued previously by Evans and Kemp (1976), the carotid condition seen in these taxa is likely ancestral to the condition seen in more derived PANCRYPTODIRES. This intermediate condition is thereby considered here to be a synapomorphy of PANCRYPTODIRA (see above). Overall, this node is rather poorly supported with a bootstrap value below 50%.

To some, the application of the name

"Paracryptodira" may seem more desirable for the clade comprised of Pleurosternidae, Baenidae, and *Dorsetochelys delairi*; however, to remain consistent with the usage of Gaffney (1975a), the name "Paracryptodira" is applied here to the clade formed by Pleurosternidae and Baenidae only.

CLADE 15: PARACRYPTODIRA

The clade Paracryptodira was originally hypothesized by Gaffney (1975a) based on the placement of the foramen posterius canalis carotici interni halfway along the pterygoid basisphenoid suture (character 56). This hypothesis was later dismissed because this character was thought to be a symplesiomorphy (Evans and Kemp 1976; Gaffney and Meylan 1988). Like more recent analyses (e.g., Gaffney 1996), however, this study again finds evidence in favor of Paracryptodira. In addition to the secondary reduction of the supraoccipital crest (see Clade 15), this clade is united by the reduction of the prefrontal exposure to the dorsal skull roof (character 7), and the reduction of the fenestra perilymphatica (character 57). Forcing the paraphyly of this group relative to CRYPTODIRA requires three additional steps. This clade is only supported by low bootstrap values, but also by a decay index of 1.4.

CLADE 16: PLEUROSTERNIDAE

Representatives of Pleurosternidae are united relative to other paracryptodires by the following two derived characters: loss of a medial contact of the nasals (character 2) and acquisition of a contact of the basisphenoid with the vomer that hinders the medial contact of the pterygoids (character 44). Within this clade, *Dinochelys whitei* and *Glyptops plicatulus* are hypothesized to be sister clades based on the development of a strongly hooked beak (character 26).

CLADE 17: BAENIDAE

Baenidae is a clade of exclusively North American turtles that have been analyzed extensively within a cladistic framework (Gaffney 1972b; Gaffney and Meylan 1988; Brinkman and Nicholls 1993). Not surprisingly, the present analysis also supports the monophyly of this clade. The following characters unite all baenids: absence of epipterygoids (character 37); reduction in width of the vertebrals (character 73); and acquisition of a contact between the first thoracic rib and the axillary buttresses (character 113). The monophyly of Baenidae is well supported by a bootstrap value of 66% and decay index of 2.5. Within this clade, relationships broadly agree with those proposed by previous analyses. The clade that includes all baenids to the exclusion of *Neurankylus eximius* is united by the complete or near complete reduction of the prefrontals on the dorsal skull surface (character 7) and the loss of a parietal squamosal contact (character 11). The clade that includes all baenids to the exclusion of *Neurankylus eximius* and *Trinitichelys hiatti* Gaffney is united by a medial contact of the extragulars posterior to the gulars (character 93) and an overlap of the anal onto the xiphiplastron (character 99). The clade consisting of *Boremys pulchra* + *Baena arenosa* + *Chisternon undatum* is characterized by the acquisition of supernumerary cervical scutes, an opisthocoelous caudal column (character 119), and the complete loss of cleithra, although the last characteristic is probably diagnostic for a more inclusive clade of baenids. Finally, the clade consisting of *Baena arenosa* + *Chisternon undatum* is united by the reacquisition of a parietal squamosal contact (character 11) and the loss of splenials (character 59).

Basal Eucryptodires —"Plesiochelyidae"

Many previous studies (e.g., Dryden 1988; Gaffney and Meylan 1988; Gaffney et al. 1991; Gaffney 1996; Hirayama et al. 2000) agree with the results herein by considering many Late Jurassic turtles from Western Europe to be the most basal Eucryptodires. These taxa include numerous turtles traditionally classified in the families Plesiochelyidae, Eurysternidae, and Thalassemydidae. Unfortunately, with the exception of Gaffney and Meylan (1988), all analyses combine observations from these taxa into a single terminal taxon called "Plesiochelyidae," but the exact application of this taxon name remains somewhat unclear.

Within the context of this study, it remains difficult to determine phylogenetic relationships among these basal eucryptodires. Many characters seem to be good candidates to show monophyly; however, none are ultimately resolved as synapomorphies. Until more evidence is found, this assemblage of turtles must be considered paraphyletic, in contrast to Gaffney and Meylan (1988).

CLADE 18: EUCRYPTODIRA

Two characters unite representatives of Eucryptodira relative to all other turtles: acquisition of a medial prefrontal contact (character 4) and posterior displacement of the foramen posterius canalis caroticum internus to the posterior end of the pterygoid (character 56). The latter character is homoplastically acquired in *Meiolania platyceps* as well. Bootstrap support is low for this clade.

The phylogenetic position of the rogue taxon *Portlandemys mcdowelli* is somewhat difficult to determine, because it has many equally parsimonious positions. This taxon is conservatively placed in a basal polytomy with *Plesiochelys solodurensis* in the preferred phylogenetic tree.

CLADE 19: "SOLNHOFIA NODE"

Four derived characters place the Late Jurassic *Solnhofia parsonsi* and "Thalassemys marina" closer to CRYPTODIRA than *Plesiochelys solodurensis*: loss of an osseous bridge (character 75), loss of axillary and inguinal buttresses (character 84 and character 86), and anterior placement of the cervical transverse processes (Cervical Vertebrae A).

CLADE 20: "SANTANACHELYS NODE"

One of the most surprising results of this study is the phylogenetic placement of the Early Cretaceous *Santanachelys gaffneyi* and the monophyly of "marine turtles." According to recent phylogenetic hypotheses, all Cretaceous and Tertiary PAN-CRYPTODIRAN marine turtles form a single clade called CHELONIOIDEA (e.g., Hirayama 1998; Hirayama and Hikida 1998). Two primary branches can be discerned within this clade, which ultimately lead to the extant taxa *Dermochelys coriacea* and CHELONIIDAE. Under this hypothesis, Cretaceous marine turtles of the Toxochelyidae and Osteopygidae are assigned to the phylogenetic stem of CHELONIIDAE, whereas those of the Protostegidae, including *Santanachelys gaffneyi,* are assigned to the phylogentic stem of *Dermochelys coriacea.* Although this hypothesis has great intuitive appeal, there seem to be some inconsistencies. For instance, representatives of the Protostegidae are markedly primitive in many of their characteristics, including the absence of formed cervical articulations and the presence of elongate first thoracic ribs. A placement of Protostegidae within CHELONIOIDEA thus either requires the systematic reacquisition of these primitive traits within CHELONIOIDEA, or the independent loss of these traits in numerous CRYPTODIRAN lineages.

Within the context of this analysis, *Santanachelys gaffneyi* is placed within a clade formed by *Solnhofia parsonsi* and "Thalassemys marina." The primitive characters apparent in this protostegid taxon are thus symplesiomorphies and not secondarily acquired primitive characters. *Santanachelys gaffneyi* shares with *Solnhofia parsonsi* and "Thalassemys marina" the absence of a vomer pterygoid contact in palatal view (character 28) and the retention of a central plastral fontanelle in adult individuals (character 76). *Santanachelys gaffneyi* furthermore shares with "Thalassemys marina" the secondary loss of a medial prefrontal contact (character 4) and a laterally open foramen palatinum posterius (character 43). As such, it seems that protostegids represent an independent lineage of marine turtles that originated in the Late Jurassic.

Another surprising result is the placement of the problematic Early Cretaceous *Sandownia harrisi.* This recently named species is based on an isolated cranium and interpreted as one of the oldest representatives of TRIONYCHOIDEA (Meylan et al. 2000). Within the context of this analysis, *Sandownia harrisi* displays all the characteristics of a rogue taxon having no firm affinities with any group of CRYPTODIRES. Interestingly, placement of *Sandownia harrisi* as sister to "Thalassemys marina" within Clade 20 only requires one step more than its placement as a basal representatives of TRIONYCHOIDEA. Although less parsimonious, the former placement is preferred within the context of this analysis because of stratigraphic considerations.

CLADE 21: "*XINJIANGCHELYS* NODE"

The results of this study agree with recent work by Peng and Brinkman (1993), Gaffney (1996), and Hirayama et al. (2000) by finding evidence that *Xinjiangchelys latimarginalis* is phylogenetically derived relative to *Plesiochelys solodurensis* but phylogenetically primitive relative to *Sinemys* *lens*. The following characters unite *Xinjiangchelys latimarginalis* with CRYPTODIRA: acquisition of paired pits on the ventral surface of basisphenoid (character 51); narrowing of the vertebral scutes (character 73); overlap of the anals onto the hypoplastra (character 99); reduction of the length of the first thoracic rib (character 113); and acquisition of a proximally procoelous and distally opisthocoelous caudal column (character 119). This node is not supported by any significant boot strap values or decay indices.

"Macrobaenidae" and "Sinemydidae"

"Macrobaenidae" and "Sinemydidae" are groups of primarily Asian turtles that have only recently been phylogenetically analyzed within a cladistic framework (Gaffney 1996; Brinkman and Wu 1999; Parham and Hutchison 2003). All analyses agree that these turtles are a paraphyletic grade more derived than *Xinjiangchelys latimarginalis*, but primitive relative to CRYPTODIRA. However, there is no consensus about their relationships. The results of the present study confirm that "macrobaenids" and "sinemydids" combined form a paraphyletic grade, but the results once again differ from previous studies. Until more taxa or characters, or both, are added, relationships will likely not be resolved with more confidence.

CLADE 22: "*HANGAIEMYS* NODE"

A suite of characters unites the clade that originates from the common ancestor of *Hangaiemys hoburensis* and CRYPTODIRA: the acquisition of an elongate extension to the lateral braincase wall (character 13); gain of narrow and elongate epiplastra (character 83); loss of extragulars (character 92); formation of strongly developed ventral processes along the posterior cervicals (character 103); and the acquisition of formed cervical central articulations (character 105).

CLADE 23: "*SINEMYS* NODE"

According to the preferred phylogenetic hypothesis *Judithemys sukhanovi, Dracochelys bicuspis, Ordosemys leios, Sinemys lens,* and CRYPTODIRA are more closely related with CRYPTODIRA than *Hangaiemys hoburensis,* based on the loss of a parietal postorbital contact (character 11).

CLADE 24

Judithemys sukhanovi, Dracochelys bicuspis, Ordosemys leios, and *Sinemys lens* are united by the loss of chevrons (character 117). Within that clade, all but *Judithemys sukhanovi* have a precolumellar fossa (character 34). Finally, *Ordosemys leios* and *Sinemys lens* are characterized by the secondary loss of a medial prefrontal contact (character 4) and by the secondary acquisition of an elongate first thoracic rib (character 113).

CRYPTODIRA

Relationships within CRYPTODIRA remain difficult to resolve, even though enough characters are available to provide resolution within this clade. The first cladistic analyses of CRYPTODIRAN relationships (Gaffney 1975a) tentatively concluded that all CRYPTODIRES could be arranged into a trichotomy consisting of CHELONIOIDEA, TRIONYCHOIDEA, and a clade comprised of CHELYDRIDAE + TESTUDINOIDEA. Most subsequent morphology-based hypotheses replaced this arrangement with a more explicit hypothesis in which CHELYDRIDAE (inclusive of *Platysternon megacephalum*) and CHELONIOIDEA are thought to be the successive outgroups to a clade formed by TRIONYCHOIDEA + TESTUDINOIDEA (e.g., Gaffney and Meylan 1988; Gaffney et al. 1991; Gaffney 1996; Hirayama et al. 2000; see Figure 1b–d, f). A similar topology was obtained by Brinkman and Wu (1999), but the relative positions of CHELONIOIDEA and CHELYDRIDAE were switched. Finally, the combined analysis of the available morphological and molecular data undertaken by Shaffer et al. (1997) resulted in a drastically different topology in which TRIONYCHIA, CHELYDRIDAE, and TESTUDINOIDEA were the successive outgroups to a clade formed by CHELONIOIDEA + KINOSTERNOIDEA (see Figure 1e).

The present study reveals a topology that generally agrees with that of Brinkman and Wu (1999). However, unlike all previous analyses, *Platysternon megacephalum* is neither placed within, nor as sister, to CHELYDRIDAE.

CLADE 25: CRYPTODIRA

Four characters distinguish all CRYPTODIRES from their sister groups. In particular, representatives of CRYPTODIRA are united by the following: secondary loss of paired pits on the ventral surface of basisphenoid (character 51); loss of splenials (character 59); acquisition of an eighth cervical centrum that is significantly shorter than the centrum of the seventh cervical (character 104); and loss of cleithra (character 120).

CLADE 26: "*TOXOCHELYS* NODE"

Many characters unite *Toxochelys latiremis* with CHELONIOIDEA. These include the following: the acquisition of a raised pedestal along the visceral side of the nuchal (character 62); retention of carapacial and plastral fontanelles in adults (characters 69, 76, and 88); acquisition of a procoelous caudal column (character 119); and the development of modest paddles (character 133). The following characters unite representatives of CHELONIOIDEA within this clade: the loss of nasals (character 1); reacquisition of the parietal squamosal contact (character 11); loss of the posterior palatine foramen (character 43); acquisition of a narrow and rod-like rostrum basisphenoidale (character 50); loss of chevrons (character 117); and the development of elongate paddles (character 133). CHELONIIDS share the following: reacquisition of a narrow anterior brain case wall (character 13); loss of the foramen praepalatinum (character 24); development of intergulars (character 95); secondary loss of an anal overlap onto the hypoplastra (character 99); and acquisition of an anteroventrally facing anterior articulation of the first dorsal centrum (Dorsal Vertebrae A). In contrast, representatives of PANDERMOCHELYS are united solely by the partial loss of carapacial scutes (character 60), at least within the limitations of this study.

CLADE 27.

The following synapomorphies unite the CRYPTODIRAN clade that originates from the common ancestor of CHELYDRIDAE, TESTUDINOIDEA, and TRIONYCHOIDEA: loss of nasals (character 1); enclosing of the incisura stapes (character 36); loss of the pterygoid contribution to foramen palatinum posterius (character 45); acquisition of an anteroventrally facing anterior articulation of the first dorsal centrum (Dorsal Vertebrae A); and secondary loss of a glenoid neck (character 123).

CLADE 28: "*PROTOCHELYDRA* NODE"

The results of this study differ from all previous morphological analyses by not considering *Platysternon megacephalum* to be part of PANCHELYDRIDAE (e.g., Gaffney and Meylan 1988; Shaffer et al. 1997; Brinkman and Wu 1999). Within the context of the preferred phylogenetic hypothesis, forcing the placement *Platysternon megacephalum* as a basal PANCHELYDRID adds two evolutionary steps, and placement within CHELYDRIDAE adds four evolutionary steps.

Representatives of PANCHELYDRIDAE are united by reacquisition of a frontal participation to the orbital rim (character 10), formation of an anteriorly enclosed antrum postoticum (character 35), and loss of a medial contact of the abdominals (character 98). *Chelydra serpentina* and *Macroclemys temminckii* are derived relative to *Protochelydra zangerli* based on acquisition of a distinct premaxillary hook (character 26), acquisition of costiform processes (character 63), and retention of a central plastral fontanelle in adults (character 76).

CLADE 29: "*PLATYSTERNON* NODE"

The clade that originates from the common ancestor of *Platysternon megacephalum*, TESTUDINOIDEA, and TRIONYCHOIDEA is united by reacquisition of broad epiplastra (character 83), secondary loss of an anal overlap onto the hypoplastra (character 99), and acquisition of an anteriorly convex articulation between cervicals VII and VIII (character 111).

CLADE 30

TESTUDINOIDEA and TRIONYCHOIDEA are united by a series of characters, notably: loss of a squamosal postorbital contact due to the development of an upper temporal emargination (character 18); presence of an anteriorly enclosed antrum postoticum (character 35); redevelopment of an osseous bridge region (character 75); loss of chevrons (character 117); and acquisition of a procoelous caudal vertebral column (character 119).

CLADE 31: TESTUDINOIDEA

Representatives of TESTUDINOIDEA are united by four postcranial characters: the development of extensive axillary and inguinal buttresses that contact the costals along their visceral side (characters 84 and 86); acquisition of an anal notch (character 87); and the reduction of the inframarginals from four to two pair (character 100). A single character, the reacquisition of an open incisura stapes (character 36), weakly unites *Geo-*

clemys hamiltonii and *Chrysemys picta* within this clade.

Within the context of this analysis, the placement of *Mongolemys elegans* must be considered problematic because its inclusion leads to a loss of resolution. Until additional characters and taxa are added to help resolve basal TESTUDINOID relationships, this taxon is inserted into the preferred tree as a basal representative of PAN-TESTUDINOIDEA as proposed by Sukhanov (2000) and Danilov and Sukhanov (2001).

CLADE 32: TRIONYCHOIDEA

The clade TRIONYCHOIDEA, consisting of TRIONYCHIA and KINOSTERNOIDEA, is only weakly supported in this analysis by a single character: the contribution of the palatine to the lateral brain case wall (character 30). Numerous additional characters were said to unite this clade in the past (Gaffney 1975a; Gaffney and Meylan 1988; Meylan and Gaffney 1989), but within the context of this analysis most of these characters were either dismissed a priori as problematic (see Appendix 2), or were resolved to be acquired homoplastically along the phylogenetic stems of both major crown. Until the problematic characters are critically reviewed, future analyses should avoid using TRIONYCHOIDEA as a terminal taxon.

CLADE 33:
"*EMARGINACHELYS* NODE"

The results of this study closely match the topology obtained in previous analyses of PANKINOSTERNOID relationships (Hutchison and Bramble 1981; Meylan and Gaffney 1989), particularly when the analysis is run with the morphoclinal characters ordered. This is somewhat surprising given that only a fraction of the characters known to resolve PANKINOSTERNOID relationships were included in this study.

Emarginachelys cretacea is hypothesized to be the sister of all other PANKINOSTERNOIDS, based on reacquisition of a posteriorly open incisura stapes (character 36), formation of tricarination to the carapace (character 61), and acquisition of a posteriorly convex articulation between cervicals VII and VIII (character 111).

CLADE 34: KINOSTERNOIDEA

Within the context of this analysis, crown group KINOSTERNOIDEA is diagnosed by the following three synapomorphies: a significant reduction in the size of the foramen stapedio-temporale (character 54); loss of pectoral scutes (character 97); and the acquisition of a posteriorly convex articulation between cervical III and IV (character 107). Within that clade, *Dermatemys mawii* and *Baptemys wyomingensis* are hypothesized to be sisters, based on the loss of the foramen stapedio-temporale (character 54) and the acquisition of a contact between the axillary buttress and the visceral side of the costals (character 84). In contrast, *Hoplochelys crassa* is hypothesized to be the sister group to KINOSTERNIDAE, based on the loss of a medial contact of the abdominals (character 98) and the presence of costiform processes (character 63).

Representatives of KINOSTERNIDAE are united by a suite of synapomorphies, including the following: the loss of a frontal contribution to the orbit (character 10); gain of a quadratojugal maxilla contact (character 17); reduction of the peripherals from 11 to 10 pairs (character 65); acquisition of musk duct incisions (character 66); development of plastral kinesis (character 77); loss of abdominal scutes (character 98); loss of a contact of the dorsal ribs IX and X with the costals (character 114); and the acquisition of a posterior notch to the acetabulum (character 129). Within that clade, *Kinosternon flavescens* and *Sternotherus odoratus* are hypothesized to be more closely related to one another than *Staurotypus triporcatus* because of the acquisition of a medial contact of the anterior and posterior costals (characters 67 and 68), loss of the entoplastron (character 82), acquisition of intergular scutes (character 95), and the subdivision of the humerals into two sets of scutes (character 96).

CLADE 35

Within the context of this study, *Adocus beatus, Basilemys variolosa, Zangerlia neimongolensis,* and *Peltochelys durlstonensis* are placed along the phylogenetic stem of TRIONYCHIA. The characters that unite all known PANTRIONYCHIANS include reacquisition of extragulars (character 92) and acquisition of anteriorly convex articulation between cervicals IV through VII (characters 108, 109 and 110).

CLADE 36

Peltochelys durlstonensis is united with TRIONYCHIA based on two characters: the reduction of the number of peripherals from 11 to 10 pair (character 65) and the medial contact of the posterior costals (character 68). This taxon diverged from all remaining PANTRIONYCHIANS no later than the Early Cretaceous.

CLADE 37: TRIONYCHIA

Representatives of TRIONYCHIA are united by an array of synapomorphies: the loss of a prefrontal palatine contact (character 6); fusion of the premaxillae (character 23); development of a foramen intermaxillaris (character 24); medial contact of the palatines (character 28); loss of the medial contact of the pterygoids (character 44); partial loss of carapacial scutes (character 60); secondary loss of an ossified bridge (character 75); loss of plastral scutes (character 89); loss of strongly developed ventral processes the posterior cervicals (character 103); and acquisition of flippers (character 134). Within that clade, PANCARETTOCHELYIDS are united by the acquisition of particularly elongate and flexible flippers (character 134). In contrast, representatives of TRIONYCHIDAE are united by the following: a contribution of the jugal to the upper temporal emargination (character 15); loss of a contribution of the fused premaxilla to the external nares (character 25); secondary loss of anteriorly enclosed antrum postoticum (character 35); complete absence of carapacial (character 60) and plastral scutes (character 76); reduction of peripherals to less than 10 pairs (character 65); acquisition of a V-shaped entoplastron (character 81); and loss of a central articulation between cervical vertebra VIII and dorsal vertebra I (character 112).

CLADE 38

Adocus beatus, Basilemys variolosa, and *Zangerlia neimongolensis* are united as a clade by the presence of the neural formula 6>4<6<6<6<6 (character 64) and the acquisition of a strongly sinuous midplastral scute sulcus (character 90). Within that clade, *Basilemys variolosa* and *Zangerlia neimongolensis* are united by the reduction of the manual and pedal phalangeal formula (character 132).

Character Evolution of Diagnostic Traits

The newly established topology of basal turtles indicates that the evolution of several character complexes occurred along a different pathway than previously thought. While the evolutionary scenarios of Gaffney (1975a) pertaining to the basicranial fusion and jaw muscular of primitive turtles are contradicted, most of his observations and conclusions still hold true and his evolutionary scenarios require only slight modification.

Jaw Closure Mechanism

Among amniotes, turtles uniquely solved the size limitations that an enclosed skull poses on the development of the jaw musculature by passing the adductor muscular posteriorly through the posttemporal fenestra, thus providing ample space for this muscle to expand. However, given that the otic region blocks the direct line between the origin and insertion of the adductors, a pulley mechanism called a trochlea redirects these muscles around the otic region (Schumacher 1954).

In CRYPTODIRES, as in all primitive amniotes, a lateral process of the pterygoid guides the lower jaw during closure and the trochlea is formed by the quadrate and the prootic. Consequently, the obstructing otic region itself redirects the jaw muscular (Figure 19b). In contrast, the trochlea of PLEURODIRES is formed by a large lateral expansion of the pterygoid (Figure 19d), called the processus trochlearis pterygoidei (Schumacher 1954). Given that the bony components involved are clearly nonhomologous, Gaffney (1975a) concluded that the muscular mechanisms were also nonhomologous; that is, they must have formed independently in PANPLEURODIRA and PANCRYPTODIRA from the ancestral condition seen in *Proganochelys quenstedti* (Figure 19a).

Reconstructing the precise evolution of the trochlear mechanisms is difficult because most of the structures involved in the formation of the trochlear system are formed by soft tissue that does not readily preserve in skeletal specimens and fossils. The trochlear system of living PLEURODIRES can be identified unambiguously in osteological specimens by the presence of the processus trochlearis pterygoidei, a large winglike structure that protrudes from the palate. The trochlear system of living CRYPTODIRES is coupled with the formation of a synovial capsule and the ductus angularis oralis, but these anatomical systems are not preserved in fossil taxa at all. The trochlear system of many living CRYPTODIRES is also characterized by the formation of a vertical pterygoid flange, the thickening of the anterior wall of the otic capsule, or even a process that protrudes from this area, the processus trochlearis oticum. However, of these structures, only the processus trochlearis oticum can be taken as positive evidence for a CRYPTODIRE-style trochlear mechanism, because the other two may plausibly develop for other functions as well, such as the more efficient guidance of the lower jaw during jaw closure. Unfortunately, the processus trochlearis oticum is commonly not developed, even in taxa known to possess a CRYPTODIRAN trochlear mechanism (e.g., *Dermochelys coriacea*).

Because of these intricacies, it is difficult to assess with confidence whether or not the fossils placed by this analysis along the phylogenetic stem of turtles did indeed have a trochlear mechanism. According to the arguments of Gaffney (1975a, 1990), *Proganochelys quenstedti* may have lacked a trochlear system, because it does not show any of the structures associated with the trochlear system of living turtles. A longitudinal section of the skull of this taxon generally confirms this assertion, because the otic region does not block the direct route between the most distal origination site of the temporal muscle and its insertion on the coronoid (see Figure 19a). *Kayentachelys aprix* has previously been argued to show positive signs of a CRYPTODIRE-type trochlear system based on the presence of a small vertical flange on the processus externus pterygoidei and a thickening of the anterior edge of the otic region (Gaffney et al. 1987). As discussed above, however, both morphologies are not conclusive evidence for this type of jaw closure mechanism, although they do not contradict this claim.

The most conclusive evidence for a trochlear mechanism in fossil stem turtles is provided by *Meiolania platyceps* and *Mongolochelys efremovi.* These taxa clearly lack a processus trochlearis oticum or a processus trochlearis pterygoidei, but the dorsal side of the otic region of both taxa is greatly roughened along the area where CRYPTODIRAN turtles have the processus trochlearis oticum. Furthermore, a cross section of the skull reveals that the otic region indeed blocks the direct line between the crista supraoccipitalis and the coronoid process. Given the lack of any other conclusive anatomical evidence, it is premature to postulate whether or not these taxa had the trochlear system as seen in CRYPTODIRES; that is, a trochlear system that includes a synovial capsule or even a sesamoid bone. However, it is plausible that the otic region of these taxa indeed redirected the adductor musculature in a way similar to that seen in CRYPTODIRES. As such, following the topology obtained from this phylogenetic analysis, a trochlear mechanism equivalent to that of CRYPTODIRES must be considered ancestral to TESTUDINES, and that this CRYPTODIRE-type trochlear system gave rise to the condition seen in PLEURODIRA. Although the bony structures involved are nonhomologous, the trochlear system of PLEURODIRES and CRYPTODIRES is homologous.

Even though this result may seem counterintuitive to some, a transfer of function can explain a shift from a CRYPTODIRE-type trochlear system to a PLEURODIRE-type trochlear system. Similar transfers of functions are known in other groups of vertebrates. For instance, the primitive jaw joint of amniotes is formed by the quadrate and the articular, but in mammals, the joint is formed by the squamosal and dentary (Carroll 1988). Given that the involved bony structures are nonhomologous, one may be tempted to hypothesize that the jaw articulation of mammals evolved independently from the jaw articulation of all other vertebrates. However, fossil evidence clearly reveals that the mammalian condition indeed derived from the primitive amniote condition through an intermediate stage in which both sets of bones are involved in the formation of the jaw joints. This efficiently transfers the function from one joint to the other, without sacrificing the function of the mandible during the transition.

A similar scenario is plausible for turtles. The following points summarize the sequence in which this transfer of function could have occurred:

1. Primitive jaw closure mechanism, lower jaw guided by the external pterygoid process. Condition documented by *Proganochelys quenstedti* (see Figure 19a).

2. Posterior movement of the temporal musculature. External pterygoid process retains function in guiding lower jaw during adduction; otic region forms a CRYPTODIRE-type trochlear system. Condition documented by *Mongolochelys*

efremovi and *Meiolania platyceps* (see Figure 19b).

3. External pterygoid process hypertrophies, thus transferring its function from guidance only to guidance and redirection of the adductor musculature. Both the external pterygoid process and the otic chamber share the function of redirecting the temporal musculature. This condition is not yet documented in any known fossil turtle (a hypothetical turtle with such an intermediate condition is given in Figure 19c).

4. External pterygoid process hypertrophies fully, converting to a processus trochlearis oticum. The redirecting function associated with the otic chamber is lost. This condition is seen in representatives of Pleurodira (see Figure 19d).

For the moment, it remains unclear why such a transfer of function may have taken place. However, it is possible that the pleurodiran condition has a mechanical and, as such, an adaptive advantage over the cryptodiran condition, because the temporal muscles pull the lower jaw straight upwards versus diagonally backwards. This may result in a more forceful bite with the same muscle mass or an equally forceful bite with a smaller muscle mass.

Fusion of the Basipterygoid Articulation

The evolutionary scenario for the fusion of the basipterygoid articulation demands revision, but the changes are less than those associated with the trochlear system. The basipterygoid articulation of all living turtles is fused, but the condition seen in both crown groups differs systematically. In pleurodires the fusion of the basipterygoid articulation is supported by a sutured contact between the quadrate and the basisphenoid; in cryptodires, the articulation is locked by an extended posterior process of the pterygoid that may even contact the basioccipital. Both conditions were thus postulated to have originated independently from the primitive, unfused condition seen in *Proganochelys quenstedti* (Gaffney et al. 1987).

The morphologies observable in the remaining representatives of the turtle stem form a grade. In *Australochelys africanus* and *Palaeochersis talampayensis,* the basipterygoid suture is fused, but neither the quadrate nor the pterygoid support this lock. In *Kayentachelys aprix* and *Mongolochelys efremovi,* the basipterygoid articulation is fused as well, but in these taxa the joint is locked further by a minor articulation of the pterygoid with the basisphenoid. Although these observations clearly indicate that a fused basipterygoid joint is primitive for Testudines, the condition seen in *Kayentachelys aprix* and *Mongolochelys efremovi* may plausibly have given rise to either the pleurodiran condition, through the addition of a lateral process of the quadrate, or the cryptodiran condition, through the extension of the posterior process of the pterygoid. The complete closure of the cranioquadrate space could thus have occurred independently in both lineages, as Gaffney et al. (1987) proposed. However, following the preferred phylogenetic hypothesis, *Kallokibotion bajazidi* must be interpreted as the most derived stem turtle. This taxon shows the condition seen in cryptodires, thus predicting that a long posterior pterygoid process is indeed primitive for Testudines, and that the pleurodiran condition was derived from the cryptodiran condition. *Meiolania platyceps* is another stem turtle that has the cryptodiran condition, but this is interpreted as a homoplastic acquisition within the context of this study.

Commentary

The use of cladistic methodology in phylogenetic reconstruction has been a catalyst in the understanding of relationships among fossil and living turtles. Although great progress has been achieved, any given topology must be viewed with caution, because many factors, notably poor taxon and character sampling, are known to negatively affect tree topology. The following section compares the obtained tree topology to the results obtained from other analyses.

Basal Turtle Relationships

This study provides surprising, though intuitive, results for the evolution of basal turtles, primarily because this group of organisms was sampled as densely as possible and because characters pertaining to basal turtles were included exhaustively. As such, all basal turtle clades are supported by numerous characters (ultimately an indication of poor taxon sampling) and competing hypotheses on basal turtle relationships are signifi-

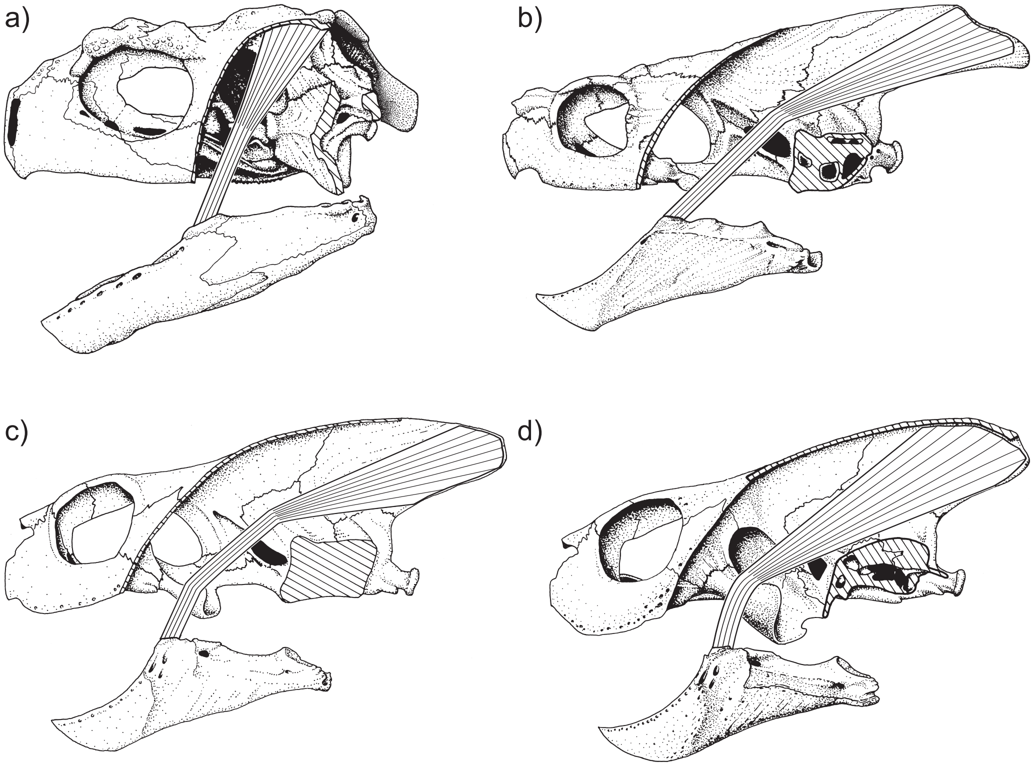


Figure 19. The trochlear system of turtles. **a.** The jaw closure system of basal turtles, as exemplified by *Proganochelys quenstedti.* **b.** The trochlear system of CRYPTODIRAN turtles, as exemplified by *Chelydra serpentia,* in which the jaw musculature is redirected posteriorly by the processus trochlearis oticum. **c.** The trochlear system of a hypothetical intermediate that has both a processus trochlearis oticum and a processus trochlearis pterygoidei. **d.** The trochlear system of PLEURODIRAN turtles, as exemplified by *Elseya dentata,* in which the jaw musculature is redirected posteriorly by the processus trochlearis pterygoidei.

cantly less parsimonious. All basal clades are well supported by the boot strap analysis and decay indices. Whereas this study does not provide definite solutions for the placement of *Kallokibotion bajazidi,* Paracryptodira, and perhaps even the clade comprised of *Meiolania platyceps* and *Mongolochelys efremovi,* the basal placement of *Palaeochersis talampayensis, Proterochersis robusta,* and *Kayentachelys aprix* is strongly supported.

Interestingly, the topology obtained herein furthers the arguments of Joyce and Gauthier (2004) for a terrestrial origin of turtles, because the entire phylogenetic stem of turtles now seems to have been decisively terrestrial in its habitat preferences. This could explain why basal turtles are far less common in the fossil record than their derived, aquatic relatives.

PANPLEURODIRAN Relationships

The fossil record of PANPLEURODIRES has always been known to be less complete that that of their sister group (e.g., Mlynarski 1976), but significant amounts of fossil diversity have recently been described that will certainly help resolve PANPLEURODIRAN relationships, once integrated into a comprehensive analysis. Particularly intriguing new finds include the long-necked *Yaminuechelys gasparinii* Fuente, Lapparent de Broin and Manera de Bianco from the Late Cretaceous of Argentina (Fuente et al. 2001).

The relationship of basal PANPLEURODIRES obtained here is highly plausible, because stratigraphically older turtles are placed basal to the crown. However, it is unfortunate that this topology was only obtained after running the analysis with the characters ordered (see above). Given that this study focused on resolving basal turtle relationships and the placement of the PANPLEURODIRAN clade, sampling of taxa and characters within PLEURODIRA is poor and resolution suffers accordingly. This study, however, may be considered a useful starting point for future, expanded studies of PANPLEURODIRAN relationships.

Pancryptodiran Relationships

The phylogenetic relationships of the major CRYPTODIRAN clades remains problematic to this day, despite an excellent fossil record (e.g., Mlynarski 1976). This is underlined by incongruent tree topologies derived from molecular and morphological analyses combined with the sequence of appearance of clades in the fossil record. In particular, several recent morphological analyses reveal that Chelydridae is to be considered the basal representatives of CRYPTODIRA (including *Platysternon megacephalum*), followed by CHELONIOIDEA, TESTUDINOIDEA, and finally a clade comprised of TRIONYCHIA and KINOSTERNOIDEA (e.g., Dryden 1988, Gaffney and Meylan 1988, Gaffney et al. 1991, Gaffney 1996, Hirayama et al. 2000). Molecular hypotheses, in contrast, commonly reveal TRIONYCHIA to be the basalmost clade of CRYPTODIRA, followed by TESTUDINOIDEA, CHELONIOIDEA, and finally KINOSTERNOIDEA (e.g., Shaffer et al. 1997; Fujita et al. 2004).

The preferred topology of the present study resembles that of many previous morphological analyses with the minor difference that CHELONIOIDEA is considered more basal than CHELYDRIDAE. When considering the fossil record, a basal placement of CHELONIOIDEA may not be surprising given that Early Cretaceous protostegids are commonly thought to be early stem representatives of this group (e.g., Hirayama 1998) and thus among the oldest known representatives of crown CRYPTODIRA. This study, however, reveals that these taxa may actually not represent stem representatives of CHELONIOIDEA, but rather those of CRYPTODIRA. If protostegids are removed from consideration, the oldest known representative of PANCHELONIOIDEA must be considered the Late Cretaceous *Toxochelys latiremis*. Similarly, the oldest known representatives of PANTESTUDINOIDEA, PANKINOSTERNOIDEA, and PANCHELYDRIDAE are all Late Cretaceous in age as well (see Joyce et al. 2004 for literature summary). In contrast, according to this analysis and others, the only clade of extant CRYPTODIRA currently hypothesized to have a lower Cretaceous representative is PANTRIONYCHIA with *Peltochelys durlstonensis*. Thus, a basal placement of this clade may thus be more plausible indeed.

Summary

The phylogenetic relationships of turtles have been subject to scrutiny within a cladistic framework for more than 30 years (Gaffney 1972b). Because of computational limitations, the initial exploratory work demanded simplifying assumptions that allowed for development of the first phylogenetic hypotheses. These assumptions pertain to the monophyly of numerous groups of turtles and the evolution of several character complexes, particularly the development of the trochlear system and the fusion of the basipterygoid articulation. Interestingly, many of these initial assumptions are still used to this day.

This study is the first morphological analysis of turtle relationships that attempts to test these initial assumptions explicitly by integrating a large number of fossil taxa, reducing a priori assumptions about the character evolution of all involved traits, and by using single species only as terminal taxa.

The results of this analysis support the monophyly of many previously hypothesized clades; however, the orthodoxy of the arrangement of crown turtles is questioned. In particular, based on a large array of characters, the primitive turtles *Proterochersis robusta, Kayentachelys aprix, Mongolochelys efremovi, Meiolania platyceps,* and *Kallokibotion bajazidi* are removed from their current position as crown turtles and placed along the phylogenetic stem of this clade. The age of the basalmost divergence in the turtle crown is consequently revised from Late Triassic to Late Jurassic.

The revised topology of basal turtles implies that the allegedly fused pelvis seen in *Proterochersis robusta* is homoplastic relative to that of PANPLEURODIRES. Furthermore, this topology also implies that a CRYPTODIRE-type trochlear system and basicranial fusion is primitive for the turtle crown (TESTUDINES), and that these morphologies gave rise to the PLEURODIRAN condition. The transition from a CRYPTODIRE-type trochlear system to a PLEURODIRE-type trochlear system likely took place through an intermediate stage, during which a hypertrophied lateral process of the pterygoid shared the function of redirecting the adductor jaw musculature with the otic region, before managing this task completely. Other noteworthy results of this study include the tentative exclusion of protostegids from CHELONIOIDEA, the placement of *Platysternon megacephalum* outside of CHELYDRIDAE, and the tentative interpretation of *Sandownia harrisi* as a basal eucryptodire.

Acknowledgments

Among others, I would like to express my gratitude to Brian Andres, Gabe Bever, Don Brinkman, Dan Brinkman, Chris Bell, Chris Brochu, Julia Clarke, Igor Danilov, Jason Downs, Marilyn Fox, Gene Gaffney, Walton Green, Jenney Hall, Pat Holroyd, Howard Hutchison, Ted Macrini, Jim Parham, Jeff Rahl, Olivier Rieppel, Robert Reisz, Tim Rowe, Phil Skemer, Krister Smith, Juliana Sterli, Vladimir Sukhanov, Takanobu Tsuihiji, and Oliver Wings for their friendship and help in improving the quality of this research through discussions and proof reading. This manuscript received additional insightful comments from Jacques Gauthier, Leo Hickey, Ren Hirayama, Karl Turekian, Elisabeth Vrba, and Jeff Wilson. Brian Roach crafted the beautiful illustrations used in Figure 19.

I particularly thank the many faculty and staff of the institutions that provided access to specimens for this study. For simplicity, only the institutional names are listed: American Museum of Natural History (New York, New York, USA), Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany), Bürgermeister Müller Museum (Solnhofen, Germany), California Academy of Sciences (San Francisco, California, USA), Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA), Cambridge University Museum of Zoology (Cambridge, England), Chernyshev's Central Museum of Geological Exploration (St. Petersburg, Russia), Dorset County Museum (Dorset, England), Field Museum of Natural History (Chicago, Illinois, USA), Jura Museum (Eichstätt, Germany), Louisiana Museum of Natural History (Baton Rouge, Louisiana, USA), Museum für Naturkunde (Berlin, Germany), Museum of Comparative Zoology (Cambridge, Massachusetts, USA), Museum of Northern Arizona (Flagstaff, Arizona, USA), Natural History Museum (London, England), Naturmuseum Solothurn (Solothurn, Switzerland), Paleontological Institute of the Russian Academy of Sciences (Moscow, Russia), Science Museum of Minnesota (St. Paul, Minnesota, USA), Sedgwick Museum (Cambridge, England), Senckenberg Museum (Frankfurt, Germany), Staatliches Museum für Naturkunde (Stuttgart, Germany), Texas Memorial Museum (Austin, Texas, USA), Tulane University Museum of Natural History (New Orleans, Louisiana, USA), United States National Museum (Washington, D.C., USA), University of California Museum of Paleontology (Berkeley, California, USA), University of Kansas Natural History Museum (Lawrence, Kansas, USA), Yale Peabody Museum of Natural History (New Haven, Connecticut, USA), and the Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia).

I am also indebted to the librarians of the following institutions for providing access to primary literature: American Museum of Natural History (New York, New York, USA), Friedrich–Alexander Universität (Erlangen, Germany), Harvard University (Cambridge, Massachusetts, USA), Natural History Museum (London, England), New York Botanical Garden (New York, New York, USA), and Yale University (New Haven, Connecticut, USA).

Funding for this project was provided by the Geological Society of America (Grant in Aid), Mid-America Paleontological Society (Student Award), Paleontological Society (Steven Jay Gould Grant, Grant in Aid), Society of Vertebrate Paleontology (Estes Prize), University of California Museum of Paleontology (Welles Research Fund), Yale University Graduate School (Enders Grant, John Perry Miller Fund, Graduate Student Fellowship), and Yale University Department of Geology and Geophysics (William and Virgie Twenhofel Fellowship, Yale Institute for Biospheric Studies Fellowship).

Received 6 June 2006; revised and accepted 23 January 2007.

Appendix 1: Turtle Species Used in This Study

Fossil Turtles

Adocus (orig. *Emys*) *beatus* (Leidy 1865); hypodigm of White (1972); as described and depicted by Meylan and Gaffney (1989) and Marsh (1890); personal observation of YPM 782 (holotype *Adocus punctatus* Marsh 1890).

Australochelys africanus Gaffney and Kitching 1994; holotype only; as described and figured by Gaffney and Kitching (1995).

Baena arenosa Leidy 1870; hypodigm of Gaffney (1972b); as described and figured by Gaffney (1972b); personal observation of USNM 103 (holotype of *Baena arenosa*), USNM 18102, USNM 12960.

Baptemys (orig. *Emys*) *wyomingensis* (Leidy 1869); hypodigm of Hay (1908) and additional material referred by Meylan and Gaffney (1989); as described and figured by Hay (1908) and Meylan and Gaffney (1989); personal observation of USNM 13437, USNM 16711, USNM 16713, YPM 3754.

Basilemys (orig. *Compsemys*) *variolosa* (Cope 1876); as described and figured by Langston (1956); supplemented with cranial and postcranial observations made by Brinkman (1998) and Hirayama et al. (2001).

Boremys (orig. *Baena*) *pulchra* (Lambe 1906); hypodigm of Gaffney (1972b) and additional material referred by Brinkman and Nicholls (1991); as described and figured by Gaffney (1972b) and Brinkman and Nicholls (1991); personal observation of USNM 8803 (holotype of *Boremys albertensis* Gilmore 1919), USNM 12978–12979 (holotype of *Boremys grandis* Gilmore 1935).

Caribemys oxfordiensis Fuente and Iturralde-Vinent 2001; holotype only; as described and figured by Fuente and Iturralde-Vinent (2001).

Chisternon (orig. *Baena*) *undatum* (Leidy 1871); hypodigm of Gaffney (1972b); as described and figured by Gaffney (1972b); personal observation of USNM 12839, USNM 2275 (holotype *Baena hebraicum* Cope 1872a), YPM 3930.

Dinochelys whitei Gaffney 1979b; hypodigm of Gaffney (1979b) and additional material referred by Brinkman et al. (2000); as described and figured by Gaffney (1979b) and Brinkman et al. (2000); personal observation of YPM 6056–6057, YPM 6068–6075, YPM 6078–6081, YPM 6084–6085, YPM 6089–6090, YPM 6092–6093, YPM 6096, YPM 6103–6104, YPM 6106, YPM 6113, YPM 6119.

Dorsetochelys delairi Evans and Kemp 1976; as described and figured by Evans and Kemp (1976); personal observation of DCM G23 (holotype).

Dracochelys bicuspis Gaffney and Ye 1992; as described and figured by Gaffney and Ye (1992) and as scored for cladistic analysis by Parham and Hutchison (2003).

Emarginachelys cretacea Whetstone 1978; holotype only; as described and figured by Whetstone (1978).

Glyptops (orig. *Compsemys*) *plicatulus* (Cope 1877); hypodigm of hypodigm of Gaffney (1979b); as described and figured by Hay (1908) and Gaffney (1979b); personal observation of USNM 5458, USNM 5733, YPM 1357, YPM 1784, YPM 2753, YPM 4717, YPM 4741–4742, YPM 5821, YPM 6077.

Hangaiemys hoburensis Sukhanov and Narmandakh 1974; as described and figured by Sukhanov and Narmandakh (1974) and Sukhanov (2000), and as scored for cladistic analysis by Parham and Hutchison (2003), personal observation of type material (PIN).

Hoplochelys (orig. *Chelydra*) *crassa* (Cope 1888); hypodigm of Gilmore (1919); personal observation of USNM 8525; scorings supplemented using *Hoplochelys laqueata* Gilmore 1919 (personal observation of USNM 8527, holotype) and *Hoplochelys elongata* Gilmore 1919 (personal observation of USNM 8553, holotype).

Judithemys sukhanovi Parham and Hutchison 2003, hypodigm of Parham and Hutchison (2003); as described and depicted by Parham and Hutchison (2003).

Kayentachelys aprix Gaffney, Hutchison, Jenkins and Meeker 1987; personal observation of all currently available material.

Kallokibotion bajazidi Nopcsa 1923b, hypodigm of Gaffney and Meylan (1992); as described and figured by Nopcsa (1923b) and Gaffney and Meylan (1992).

Meiolania platyceps Owen 1886, hypodigm of Gaffney (1996); as described and figured by Gaffney (1983, 1985, 1996).

Mesodermochelys undulatus Hirayama and Chitoku 1996, hypodigm of Hirayama and Chitoku (1996); as described and figured by Hirayama and Chitoku (1996).

Mongolochelys efremovi Khosatzky 1997; as described and figured by Khosatzky (1997) and Sukhanov (2000); personal observation of PIN 551–459, PIN 552–276, PIN 552–325, PIN 552–390, PIN 552–459, PIN 552–923, and many uncatalogued specimens (PIN).

Neurankylus eximius Lambe 1902, hypodigm of Gaffney (1972b) and additional material referred by Brinkman and Nicholls (1993); as described and figured by Gaffney (1972b) and Brinkman and Nicholls (1993); personal observation of AMNH 6098, USNM 8344 (holotype of *Neurankylus baueri* Gilmore 1916), USNM 8531.

Notoemys laticentralis Cattoi and Freiberg 1961; hypodigm of Fernandez and Fuente (1994); as described and figured by Fernandez and Fuente (1994).

Ordosemys leios Brinkman and Peng 1993b, hypodigm of Brinkman and Wu (1999); as described and depicted by Brinkman and Peng (1993b) and Brinkman and Wu (1999).

Palaeochersis talampayensis Rougier et al. 1995; holotype only; as described and figured by Rougier et al. (1995).

Peltochelys durlstonensis Dollo 1884; holotype only; as described and figured by Meylan (1988).

Platychelys oberndorferi Wagner 1853; as described and figured by Wagner (1853); Bräm (1965); personal observation of BSPG AS I 1438, NS 8685–8688, NS 8692.

Plesiobaena (orig. *Baena*) *antiqua* (Lambe 1902); hypodigm of Gaffney (1972b) and additional material referred by Brinkman (2003); as described and figured by Gaffney (1972b) and Brinkman (2003); personal observation of USNM 8801 (holotype of *Baena antiqua*).

Plesiochelys solodurensis Rütimeyer 1873; as described and figured as *Plesiochelys solodurensis* and *Plesiochelys etalloni* by Bräm (1965) and Gaffney (1975d, 1976).

Pleurosternon (orig. *Platemys*) *bullockii* (Owen 1842); hypodigm of Milner (2004); as described and depicted by Owen (1850), Evans and Kemp (1975), and Milner (2004); personal observation of UMZC T1041 (holotype of *Mesochelys durlstonensis*), YPM PU 3363 –3364.

Portlandemys mcdowelli Gaffney 1975d; as described and figured by Parsons and Williams (1961) and Gaffney (1975d, 1976).

Proganochelys quenstedti Baur 1887; hypodigm of Gaffney (1990); as described and figured by Gaffney (1990); personal observation of SMNS 10012, SMNS 15759, SMNS 16980, and SMNS 17203–17204.

Proterochersis robusta Fraas 1913; as described and figured by Fraas (1913) and Gaffney (1986, 1990); personal observation of SMNS 17561, SMNS 17755, SMNS 18440, and SMNS 16442.

Protochelydra zangerli Erickson 1973; holotype only; as described and figured by Erickson (1973); personal observation of SMM P72.34.2 (holotype of *Protochelydra zangerli*).

Sandownia harrisi Meylan et al. 2000; as described and figured by Meylan et al. (2000).

Santanachelys gaffneyi Hirayama 1998; holotype only; as described and figured by Hirayama (1998).

Sinemys lens Wiman 1930; hypodigm of Brinkman and Peng (1993a); as described and depicted by Brinkman and Peng (1993a); scoring supplemented using *Sinemys gamera* Brinkman and Peng (1993a), as described by Brinkman and Peng (1993a).

Solnhofia parsonsi Gaffney 1975c; hypodigm of Joyce (2000); as described and depicted by Parsons and Williams (1961), Gaffney (1975c), and Joyce (2000).

"Thalassemys moseri," as described and figured by Rieppel (1980). The name is placed in quotes throughout the text because it is uncertain whether the material described by Rieppel (1980) is indeed referable to this taxon (Lapparent de Broin et al. 1996).

Toxochelys latiremis Cope 1873; hypodigm of Zangerl (1953); as described and figured by Wieland (1902), Zangerl (1953), Gaffney (1979a), and Nicholls (1988).

Trinitichelys hiatti Gaffney 1972b; holotype only; as described and figured by Gaffney (1972b); personal observation of MCZ 4070 (holotype of *Trinitichelys hiatti*).

Xinjiangchelys (orig. *Plesiochelys*) *latimarginalis* (Young and Chow 1953); hypodigm of Peng and Brinkman (1993); as described and depicted by Peng and Brinkman (1993) and as scored for cranial characters by Brinkman and Wu (1999); personal observation of numerous uncatalogued specimens (CCMGE).

Zangerlia neimongolensis Brinkman and Peng 1996; hypodigm of Brinkman and Peng 1996; as described and depicted by Brinkman and Peng 1996; scoring supplemented using *Zangerlia ukhaachelys* Joyce and Norell (2005), as described by Joyce and Norell (2005).

Recent Turtles

Apalone spinifera (LeSeur 1827); YPM R 10564, YPM R 10586, YPM R 10707, YPM R 10892–10893, YPM R 10889, YPM R 11296, YPM R 11297.

Caretta caretta (Linnaeus 1758); USNM 212329, USNM 214139–214140, YPM R 10750, YPM R 10920.

Carettochelys insculpta Ramsay 1887; CJB 582, USNM 231520.

Chelodina siebenrocki Werner 1901; YPM R 10444.

Chelonia mydas (Linnaeus 1758); YPM R 10545, YPM R 10556, YPM R 10566, YPM R 10568, YPM R 10937, YPM R 10948.

Chelydra serpentina (Linnaeus 1758); YPM R 10544, YPM R 10547–10548, YPM R 10550, YPM R 10557, YPM R 10560, YPM R 10572–10573, YPM R 10603, YPM R 10609, YPM R 10705–10706, YPM R 10749, YPM R 10797, YPM R 10808, YPM R 10821, YPM R 10824, YPM R 10835, YPM R 10856, YPM R 10900 –10901, YPM R 10932, YPM R 11426, YPM R 11429.

Dermatemys mawii Gray 1847; CM 117802, USNM 66666, USNM 66669, USNM 67732.

Dermochelys coriacea (Vandelli 1761); USNM 62754, USNM 220843, USNM 220844, USNM 243395 –243396.

Elseya dentata (Gray 1863); CJB collection.

Eretmochelys imbricata (Linnaeus 1766); YPM R 10569, YPM R 10689, YPM R 10758.

Erymnochelys madagascariensis (Linnaeus 1766); YPM R 10884.

Geoclemys hamiltonii (Gray 1831b); YPM R 10399.

Gopherus polyphemus (Daudin 1802); YPM R 10575, YPM R 10640, YPM R 10702, YPM R 10810, YPM R 10912.

Kinosternon flavescens (Agassiz 1857); YPM R 11304 –11307.

Lissemys punctata (Lacépède 1788); YPM R 10882, YPM R 11645, YPM R 13153.

Macroclemys temminckii (Troost 1835); YPM R 11304 –11306.

Pelomedusa subrufa (Lacépède 1788); YPM R 12812, YPM R 16379.

Phrynops geoffroanus (Schweigger 1812); YPM R 12611.

Platysternon megacephalum Gray 1831a; YPM R 12615 –12621.

Podocnemis expansa (Schweigger 1812); YPM R 10886, YPM R 11418.

Sternotherus odoratus (Latreille 1801); YPM R 10837–10838, YPM R 10887, YPM R 10903, YPM R 10926, YPM R 11302–11303, YPM R 12502, YPM R 12540.

Staurotypus triporcatus (Wiegmann 1828); USNM 51073.

Appendix 2: Characters from Earlier Research, Omitted in This Study

Dryden (1988)

3. Premaxillary, maxillary, and mandibular teeth: uninformative, absent in all ingroup taxa.
5. Septomaxilla: uninformative, absent in all ingroup taxa.
13. Foramen supramaxillare: uninformative, autapomorphic for *Podocnemis expansa.*
20. Processus trochlearis oticum: this character is problematic because it is considered diagnostic for a maximally inclusive PANCRYPTODIRAN clade (Gaffney et al. 1987), but cannot be scored objectively for fossil taxa. In living CRYPTODIRES, the trochlear system is associated with a synovial capsule and the ductus angularis oralis, but these anatomical systems are out of soft tissue only and thus cannot be scored for fossil taxa. The trochlear system of many living CRYPTODIRES is also characterized by a thickening of the anterior wall of the otic capsule, or even a process that protrudes from this area (the processus trochlearis oticum), but this process is commonly not developed even in many living CRYPTODIRES (e.g., *Dermochelys coriacea*). In my experience with fossil taxa, previous scorings of this character are not reproducible. For instance, the anterior wall of the otic capsule of *Kayentachelys aprix* seems to be shaped no differently than that of any living PLEURODIRE, a taxon known not to have an otic trochlear system. To avoid integrating these inconsistencies, this character complex was omitted completely.
21. Size of otic chamber: character nondiscrete.
26. Postfrontals: uninformative, absent in all ingroup taxa.
27. Postparietals: uninformative, absent in all ingroup taxa.
32. Bones contributing to the formation of the processus trochlearis oticum: see Dryden 1988, 20.
33. Double or singular articular surface of articular: character nondiscrete.
35. Bony shell and carapace: uninformative, present in all ingroup taxa.
54. Height of neural spine of posterior cervical vertebrae: character nondiscrete.

Meylan and Gaffney (1989)

4. Absence of basis tuberculi basalis: character nondiscrete.
5. Maxillary “tooth”: characters pertaining to the morphology of the labial and lingual ridges of the jaws are typically problematic, because they show considerable amount of variation and lack discrete character states.
6. Commissural ridge: see Meylan and Gaffney 1989, 5.
10. Palatines truncated anteriorly: morphology not reproducible.
14. Scute sulci of skull: morphology not reproducible.
15. Skull roofing bones sculptured: character nondiscrete, homology of different types of sculpturing problematic.
18. Retroarticular process: character nondiscrete.
25. Strong articulation of thoracic rib ends of dorsal vertebrae: character nondiscrete.
27. Number of suprapygals: morphology not reproducible. In many primitive turtles, it is difficult to differentiate objectively between suprapygals and neurals, thus making any count somewhat conjectural. Furthermore, suprapygals commonly fuse during ontogeny.
37. Thelial process: primary homology assessment problematic. The ilium of KINOSTERNIDS has a distinct anteriorly directed process halfway up the shaft, the thelial process (Zug 1971), which acts as the origination site for the musculus iliotibialis. Shaffer et al. (1997) and Hirayama et al. (2000) reported this process also to be present in *Dermatemys mawii* and in representatives of TRIONYCHIA. This observation cannot be confirmed. In *Dermatemys mawii,* the musculus iliotibialis originates roughly at the same site as it does in KINOSTERNIDS, but a process is not clearly developed. More significantly, although some representatives of TRIONYCHIDAE do have a minor process along the distinctly curved shaft of their ilium, the musculus iliotibialis does not originate at this site (Zug 1971). The processes seen in KINOSTERNIDS and TRIONYCHIDS are thus not homologous.
43. Coronoid process tall: character nondiscrete.
44. Processus trochlearis oticum: see Dryden 1988, 20.
47. Marginals overlap costals: character nondiscrete.

Gaffney et al. (1991)

6. Processus trochlearis oticum: see Dryden 1988, 20.
25. Synovial capsulate on otic chamber: see Dryden 1988, 20.
26. Ductus angularis oralis: see Dryden 1988, 20.

Rougier et al. (1995)

2. External nares elongate: uninformative, autapomorphic for *Proganochelys quenstedti.*
3. Narial platform: morphology not reproducible.
12. Processus trochlearis oticum: see Dryden 1988, 20.

14. Acute quadrate margin: uninformative, autapomorphic for *Proganochelys quenstedti.*
16. Quadrate onto the opisthotic: morphology not reproducible.
18. Sinuous cavernosus: uninformative, autapomorphic for *Proganochelys quenstedti.*
20. Vertical fenestra ovalis: uninformative, autapomorphic for *Proganochelys quenstedti.*
25. Medial process of the basisphenoid–basioccipital: uninformative, autapomorphic for *Proganochelys quenstedti.*
31. Wide transverse plane with depressions for nuchal musculature: uninformative, autapomorphic for *Palaeochersis talampayensis.*
36. Occipital condyle set on a "neck": uninformative, autapomorphic for *Proganochelys quenstedti.*
37. Foramen magnum higher than wide: uninformative, autapomorphic for *Proganochelys quenstedti.*
38. Fossa Meckelii small: uninformative, autapomorphic for *Proganochelys quenstedti.*
42. Marginals not separated by large anal notch: morphology not reproducible.
43. Plastron reaches posterior margin of ischium: morphology not reproducible.
58. Large anteromedial process of the ilium: uninformative, autapomorphic for *Palaeochersis talampayensis.*
59. Thyroid fenestra: character nondiscrete and subject to large amounts of ontogenetic variation.

Gaffney (1996)

5. Relative size of foramen palatinum posterius: character nondiscrete.
7. Processus trochlearis oticum: see Dryden 1988, 20.
28. Height of neural spine of posterior cervical vertebrae: see Dryden 1988, 54.

Shaffer et al. (1997)

Characters 1 through 39 overlap with those of Gaffney et al. (1991).

43. Diploid number of chromosomes: not reproducible, primary literature provides vastly conflicting primary data (see Joyce and Bell 2004 for discussion of this problem among TESTUDINOIDS).
44. Basioccipital contribution to occipital condyle: uninformative, autapomorphic for *Pelusios.*
52. Parietals very small: character nondiscrete and not reproducible.
53. Cervical vertebrae longer than thoracic vertebrae: uninformative, autapomorphic for *Chelodina.*
60. Origin of ilio-tibialis muscle: not reproducible.
65. Sella turcica concealed: character nondiscrete and not reproducible.
70. Thelial process: see Meylan and Gaffney (1989).
71. Caudifibularis muscle: not reproducible.
73. Maxillary tooth: see Meylan and Gaffney 1989, 5.
74. Composition of processus trochlearis oticum: see Dryden 1988, 20.
76. Palatines truncated anteriorly: see Meylan and Gaffney 1989, 10.
82. Midline scute sulcus: see Meylan and Gaffney 1989, 30.
84. Number of suprapygals: see Meylan and Gaffney 1989, 27.
105. Fore claws elongate: uninformative, autapomorphic for *Chrysemys picta.*
106. Epipterygoid contacts jugal: uninformative, autapomorphic for *Chrysemys picta.*
114. Thyroid fenestra: see Rougier et al. 1995, 59.

Brinkman and Wu (1999)

Characters 1 through 40 overlap with those of Gaffney (1996).

42. Pterygoid width anterior to basisphenoid: uninformative, autapomorphic for *Platysternon megacephalum.*
43. Length of facial region: uninformative, autapomorphic for *Platysternon megacephalum.*
45. Jugal exposure on ventral margin of cheek: morphology not reproducible.
46. Epiplastral beak: uninformative, autapomorphic for *Chelydra serpentina.*
47. Pectoral scute position relative to epiplastron: uninformative, autapomorphic for *Chelydra serpentina.*
52. Length of bridge: character nondiscrete.
58. Skull height relative to width: character nondiscrete.

Hirayama et al. (2000)

13. Number of lingual ridges: character nondiscrete and not reproducible.
21. Processus trochlearis oticum: see Dryden 1988, 20.
32. High coronoid process: see Meylan and Gaffney 1989, 43.
37. Proportions of cervical central articulation: character nondiscrete and not reproducible.
61. Shapes of suprapygals: character nondiscrete and not reproducible.
62. Marginals reach pleurals: character nondiscrete and not reproducible.
64. Midline plastral scute sulcus sinuous: see Meylan and Gaffney 1989.

Appendix 3: Primary Data Matrix Used in This Study

Abbreviations: **a,** 0/1; **b,** 0/2; **c,** 1/2; ?, unknown; –, not applicable; *, multistate character.

	Nasal A	Nasal B	Nasal C	Prefrontal A	Prefrontal B	Prefrontal C	Prefrontal D*	Prefrontal E	Lacrimal A	Frontal A	Parietal A	Parietal B	Parietal C	Jugal A	Jugal B	Quadratojugal A	Quadratojugal B
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proganochelys quenstedti	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0
Proterochersis robusta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Palaeochersis talampayensis	0	0	0	0	0	?	0	1	0	0	0	?	?	?	0	0	0
Australochelys africanus	?	?	?	?	?	?	?	1	0	?	0	?	?	?	0	0	?
Kayentachelys aprix	0	0	0	0	1	0	1	1	1	1	0	?	?	1	0	0	0
Meiolania platyceps	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	0	0
Mongolochelys efremovi	0	0	1	0	1	0	0	1	1	0	0	1	0	1	0	0	0
Kallokibotion bajazidi	0	0	1	0	?	?	0	1	1	?	0	1	?	1	0	0	0
Platychelys oberndorferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caribemys oxfordiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Notoemys laticentralis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Elseya dentata	0	1	1	0	0	1	1	1	1	1	0	1	1	1	0	1	–
Chelodina oblonga	0	1	1	0	0	1	1	1	1	1	1	1	1	1	0	1	–
Phrynops geoffroanus	0	1	1	0	0	1	1	1	1	1	0	1	1	1	0	1	–
Erymnochelys madagascariensis	1	–	–	1	0	1	0	1	1	1	1	1	1	1	0	0	0
Pelomedusa subrufa	1	–	–	1	0	1	0	1	1	1	1	1	1	1	0	0	0
Podocnemis expansa	1	–	–	1	0	1	0	1	1	1	1	1	1	1	0	0	0
Dorsetochelys delairi	0	0	1	0	1	0	0	1	1	1	0	1	?	1	0	0	0
Pleurosternon bullockii	0	1	1	0	?	?	1	1	1	1	0	1	1	1	0	0	0
Glyptops plicatulus	0	1	1	0	1	?	1	1	1	1	?	1	1	1	0	0	?
Dinochelys whitei	0	?	1	0	?	?	1	1	1	1	?	?	?	1	0	0	0
Neurankylus eximius	?	?	?	0	?	?	1	1	?	1	?	1	1	?	?	?	?
Trinitichelys hiatti	0	0	1	0	1	0	2	1	1	1	1	1	1	1	0	0	0
Plesiobaena antiqua	0	0	1	0	1	0	2	1	1	1	1	1	1	1	0	0	0
Boremys pulchra	0	0	1	0	1	0	2	1	1	1	1	1	1	1	0	0	0
Baena arenosa	1	?	?	0	1	0	2	1	1	1	0	1	1	1	0	0	0
Chisternon undatum	0	0	1	0	1	0	2	1	1	1	0	1	1	1	0	0	0
Portlandemys mcdowelli	0	0	1	1	1	0	0	1	1	1	?	1	0	?	?	?	?
Plesiochelys solodurensis	0	0	1	1	1	0	0	1	1	1	a	1	0	1	0	0	0
Solnhofia parsonsi	0	0	1	1	1	0	0	1	1	1	a	1	0	1	0	0	0
Thalassemys moseri	0	0	1	0	1	0	1	1	1	1	0	1	1	1	0	0	0
Santanachelys gaffneyi	0	0	1	0	1	0	0	1	1	1	1	1	0	1	0	0	0
Xinjiangchelys latimarginalis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hangaiemys hoburensis	0	0	1	1	1	0	0	1	1	1	0	1	1	1	0	0	0
Judithemys sukhanovi	?	?	?	1	?	?	0	1	1	1	?	1	1	1	0	0	0
Dracochelys bicuspis	?	?	?	1	1	?	0	1	1	1	1	1	1	1	0	0	0

Continued

	Nasal A	Nasal B	Nasal C	Prefrontal A	Prefrontal B	Prefrontal C	Prefrontal D*	Prefrontal E	Lacrimal A	Frontal A	Parietal A	Parietal B	Parietal C	Jugal A	Jugal B	Quadratojugal A	Quadratojugal B
Sinemys lens	0	0	1	0	?	?	1	1	1	1	1	1	1	1	0	0	0
Ordosemys leios	0	0	1	0	1	0	0	1	1	1	?	1	1	1	0	0	0
Toxochelys latiremis	0	0	1	1	1	0	0	1	1	1	1	1	?	1	0	0	0
Caretta caretta	1	–	–	1	1	0	0	1	1	a	0	1	0	1	0	0	0
Chelonia mydas	1	–	–	1	?	0	0	1	1	1	0	1	0	1	0	0	0
Mesodermochelys undulatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dermochelys coriacea	1	–	–	1	1	1	0	1	1	0	0	0	–	0	0	0	0
Protochelydra zangerli	1	–	–	1	1	?	0	1	1	0	1	1	1	1	0	0	0
Macroclemys temminckii	1	–	–	1	1	0	0	1	1	0	1	1	1	1	0	0	0
Chelydra serpentina	1	–	–	1	1	0	0	1	1	0	1	1	1	1	0	0	0
Platysternon megacephalum	1	–	–	1	1	0	0	1	1	0	1	1	1	1	0	0	1
Mongolemys elegans	1	–	–	a	1	0	0	1	1	1	1	1	1	1	0	0	0
Gopherus polyphemus	1	–	–	1	1	0	0	1	1	1	1	1	1	1	0	0	0
Chrysemys picta	1	–	–	1	1	0	0	1	1	1	1	1	1	1	0	0	0
Geoclemys hamiltonii	1	–	–	1	1	0	0	1	1	0	1	1	1	1	1	0	0
Emarginachelys cretacea	1	–	–	1	1	0	0	1	1	1	1	1	1	1	0	0	0
Baptemys wyomingensis	1	–	–	1	1	0	0	1	1	1	1	1	1	1	0	0	0
Dermatemys mawii	1	–	–	1	1	0	0	1	1	a	1	1	1	1	0	0	0
Hoplochelys crassa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Staurotypus triporcatus	1	–	–	1	1	0	0	1	1	0	1	1	1	1	1	0	1
Sternotherus odoratus	1	–	–	1	1	0	0	1	1	0	1	1	1	1	0	0	1
Kinosternon flavescens	1	–	–	1	1	0	0	1	1	0	1	1	1	1	0	0	1
Zangerlia neimongolensis	1	–	–	1	1	?	0	1	1	0	?	1	?	1	?	0	0
Basilemys variolosa	1	–	–	1	?	?	0	1	1	1	1	?	?	1	0	0	0
Adocus beatus	1	–	–	1	1	0	0	1	1	1	1	1	1	1	?	0	0
Peltochelys durlstonensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sandownia harrisi	1	–	–	1	1	0	0	1	1	1	0	1	1	1	0	0	0
Apalone spinifera	1	–	–	1	1	1	0	1	1	1	1	1	1	1	1	0	0
Lissemys punctata	1	–	–	1	1	1	0	1	1	1	1	1	1	1	1	0	0
Anosteira ornata	1	–	–	1	?	?	0	1	1	1	1	?	?	1	0	0	0
Carettochelys insculpta	1	–	–	1	1	1	0	1	1	1	1	1	1	1	0	0	1

	Squamosal A	Squamosal B	Postorbital A	Supratemporal A	Premaxilla A	Premaxilla B	Premaxilla C	Premaxilla D	Premaxilla E	Vomer A*	Vomer B	Vomer C	Palatine A	Quadrate A	Quadrate B	Quadrate C*	Quadrate D
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proganochelys quenstedti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proterochersis robusta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Palaeochersis talampayensis	0	0	0	0	0	?	?	0	0	0	0	1	?	0	?	1	0
Australochelys africanus	0	?	?	?	0	?	?	0	0	?	0	?	?	0	0	1	0
Kayentachelys aprix	0	0	0	1	1	0	0	0	0	1	0	1	0	0	1	2	0
Meiolania platyceps	0	1	0	1	a	0	0	0	0	1	0	1	0	1	1	2	0
Mongolochelys efremovi	0	1	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Kallokibotion bajazidi	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	2	0
Platychelys oberndorferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caribemys oxfordiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Notoemys laticentralis	?	?	?	?	?	?	?	?	?	?	?	?	?	2	1	2	0
Elseya dentata	2	0	1	1	1	0	0	0	0	1	0	1	0	2	1	2	0
Chelodina oblonga	2	0	1	1	1	0	0	0	0	1	0	1	0	2	1	2	0
Phrynops geoffroanus	2	0	1	1	1	0	0	0	0	1	0	1	0	2	1	2	0
Erymnochelys madagascariensis	1	0	1	1	1	0	0	0	0	2	1	1	0	2	1	2	1
Pelomedusa subrufa	3	0	1	1	1	0	0	0	0	2	1	1	0	2	1	2	1
Podocnemis expansa	1	0	1	1	1	0	0	0	0	2	1	1	0	2	1	2	1
Dorsetochelys delairi	0	0	0	1	1	0	0	0	0	1	0	1	?	1	1	2	0
Pleurosternon bullockii	0	0	?	1	1	0	0	0	0	1	?	1	0	1	1	2	0
Glyptops plicatulus	?	?	?	1	1	0	?	0	1	1	?	1	0	1	1	2	0
Dinochelys whitei	0	?	?	?	1	0	?	0	1	?	?	?	?	?	?	2	0
Neurankylus eximius	?	0	0	1	?	?	?	?	?	?	?	?	?	1	1	2	0
Trinitichelys hiatti	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Plesiobaena antiqua	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Boremys pulchra	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Baena arenosa	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Chisternon undatum	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Portlandemys mcdowelli	?	?	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Plesiochelys solodurensis	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Solnhofia parsonsi	?	0	0	1	1	0	0	0	0	1	1	1	0	1	1	2	0
Thalassemys moseri	0	0	0	1	1	0	0	0	0	1	1	1	0	1	1	2	0
Santanachelys gaffneyi	0	0	0	1	1	0	?	0	0	1	1	1	0	1	1	2	0
Xinjiangchelys latimarginalis	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?
Hangaiemys hoburensis	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	?
Judithemys sukhanovi	?	0	0	1	1	?	?	?	0	1	0	1	?	1	1	2	0
Dracochelys bicuspis	?	0	?	1	1	0	0	0	0	1	0	1	?	1	1	2	1
Sinemys lens	3	0	?	1	1	?	?	0	0	?	?	1	?	1	1	2	1
Ordosemys leios	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	1
Toxochelys latiremis	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Caretta caretta	0	0	0	1	1	0	1	0	0	1	0	1	0	1	1	2	0
Chelonia mydas	0	0	0	1	1	0	1	0	1	1	0	1	0	1	1	2	0

Continued

	Squamosal A	Squamosal B	Postorbital A	Supratemporal A	Premaxilla A	Premaxilla B	Premaxilla C	Premaxilla D	Premaxilla E	Vomer A*	Vomer B	Vomer C	Palatine A	Quadrate A	Quadrate B	Quadrate C*	Quadrate D
Mesodermochelys undulatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dermochelys coriacea	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Protochelydra zangerli	0	0	0	1	1	0	0	0	0	1	0	1	?	1	1	2	0
Macroclemys temminckii	0	0	0	1	1	0	0	0	1	1	0	1	0	1	1	2	0
Chelydra serpentina	0	0	0	1	1	0	0	0	1	1	0	1	0	1	1	2	0
Platysternon megacephalum	0	0	0	1	1	0	0	0	1	1	0	1	0	1	1	2	0
Mongolemys elegans	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Gopherus polyphemus	3	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Chrysemys picta	3	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Geoclemys hamiltonii	3	0	0	1	1	0	0	0	0	1	0	1	0	1	1	2	0
Emarginachelys cretacea	3	0	0	1	1	0	0	0	0	1	0	1	1	1	1	2	0
Baptemys wyomingensis	3	0	0	1	1	0	0	0	0	1	0	1	1	1	1	2	0
Dermatemys mawii	3	0	0	1	1	0	0	0	0	1	0	1	1	1	1	2	0
Hoplochelys crassa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Staurotypus triporcatus	3	0	0	1	1	0	0	0	1	1	0	1	1	1	1	2	0
Sternotherus odoratus	3	0	0	1	1	0	0	0	0	1	0	1	1	1	1	2	0
Kinosternon flavescens	3	0	0	1	1	0	0	0	0	1	0	1	1	1	1	2	0
Zangerlia neimongolensis	3	0	0	1	1	0	0	0	0	1	?	1	?	1	1	2	0
Basilemys variolosa	3	0	0	1	1	0	?	0	0	?	?	1	?	?	1	2	0
Adocus beatus	3	0	0	1	1	0	0	0	0	1	0	1	1	1	1	2	0
Peltochelys durlstonensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sandownia harrisi	0	0	0	1	1	a	?	0	0	1	1	1	1	1	1	2	0
Apalone spinifera	3	0	0	1	1	1	2	1	0	1	1	1	1	1	1	2	0
Lissemys punctata	3	0	0	1	1	1	2	1	0	1	1	1	1	1	1	2	0
Anosteira ornata	3	0	0	1	1	?	2	0	0	1	1	1	?	1	1	2	0
Carettochelys insculpta	3	0	0	1	1	1	2	0	0	1	1	1	1	1	1	2	0

	Quadrate E*	**Quadrate F**	**Epipterygoid A**	**Pterygoid A**	**Pterygoid B**	**Pterygoid C**	**Pterygoid D**	**Pterygoid E**	**Pterygoid F**	**Pterygoid G**	**Pterygoid H**	**Supraoccipital A**	**Supraoccipital B**	**Exoccipital A**	**Opisthotic A**	**Basisphenoid A**	**Basisphenoid B**
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proganochelys quenstedti	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proterochersis robusta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Palaeochersis talampayensis	0	1	?	0	1	0	0	0	0	0	0	0	0	?	1	?	0
Australochelys africanus	0	1	?	?	1	0	0	0	0	0	0	0	?	?	1	?	0
Kayentachelys aprix	1	1	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Meiolania platyceps	1	3	0	1	1	1	1	0	0	0	a	1	1	0	1	0	0
Mongolochelys efremovi	1	1	0	1	1	1	0	0	0	0	0	1	1	0	1	?	0
Kallokibotion bajazidi	1	3	0	1	1	1	1	?	?	0	?	?	0	0	1	0	0
Platychelys oberndorferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caribemys oxfordiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Notoemys laticentralis	?	?	?	1	1	?	0	?	?	?	?	?	?	0	1	?	0
Elseya dentata	2	3	1	1	1	1	0	1	0	0	0	1	0	0	1	0	0
Chelodina oblonga	2	3	1	1	1	1	0	1	0	0	0	0	0	1	1	0	0
Phrynops geoffroanus	2	3	1	1	1	1	0	1	0	0	0	0	0	1	1	0	0
Erymnochelys madagascariensis	2	3	1	1	1	1	0	1	0	0	0	1	0	0	1	0	0
Pelomedusa subrufa	2	3	1	1	1	1	0	1	0	0	0	1	0	0	1	0	0
Podocnemis expansa	2	3	1	1	1	1	0	1	0	0	1	1	0	0	1	0	0
Dorsetochelys delairi	1	1	0	1	1	1	1	0	0	0	0	0	0	0	1	?	0
Pleurosternon bullockii	1	1	0	1	1	1	1	0	0	1	0	0	0	0	1	0	0
Glyptops plicatulus	?	1	0	1	1	1	1	0	0	1	0	0	?	?	1	0	0
Dinochelys whitei	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
Neurankylus eximius	c	1	1	1	1	1	1	0	?	0	?	0	0	0	1	0	0
Trinitichelys hiatti	?	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0
Plesiobaena antiqua	?	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0
Boremys pulchra	1	1	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0
Baena arenosa	?	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0
Chisternon undatum	1	1	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0
Portlandemys mcdowelli	c	1	0	1	1	1	1	0	0	0	0	1	0	0	1	0	0
Plesiochelys solodurensis	1	1	0	1	1	1	1	0	1	0	–	1	0	0	1	0	0
Solnhofia parsonsi	1	1	0	1	1	1	1	0	0	0	0	1	0	0	1	0	0
Thalassemys moseri	1	1	0	1	1	1	1	0	1	0	–	0	0	0	1	0	0
Santanachelys gaffneyi	1	1	?	1	1	1	1	0	1	0	–	1	0	0	1	?	0
Xinjiangchelys latimarginalis	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	1
Hangaiemys hoburensis	c	1	?	1	1	1	1	0	0	1	0	1	0	0	1	?	1
Judithemys sukhanovi	c	1	?	1	1	1	1	0	0	0	0	1	0	0	1	0	1
Dracochelys bicuspis	c	1	?	1	1	1	1	0	0	0	0	1	0	0	1	?	?
Sinemys lens	2	2	?	1	1	1	0	0	0	0	0	1	0	0	1	?	1
Ordosemys leios	1	1	0	1	1	1	1	0	0	0	0	1	0	0	1	0	1
Toxochelys latiremis	1	1	?	1	1	1	1	0	0	0	0	1	0	0	1	0	0
Caretta caretta	1	1	0	1	1	1	1	0	2	0	–	1	0	0	1	1	0
Chelonia mydas	1	1	0	1	1	1	1	0	2	0	–	1	0	0	1	1	0

Continued

	Quadrate E*	**Quadrate F**	**Epipterygoid A**	**Pterygoid A**	**Pterygoid B**	**Pterygoid C**	**Pterygoid D**	**Pterygoid E**	**Pterygoid F**	**Pterygoid G**	**Pterygoid H**	**Supraoccipital A**	**Supraoccipital B**	**Exoccipital A**	**Opisthotic A**	**Basisphenoid A**	**Basisphenoid B**
Mesodermochelys undulatus	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?
Dermochelys coriacea	1	1	1	1	1	1	1	0	2	0	–	1	0	0	1	1	0
Protochelydra zangerli	2	2	?	1	1	1	1	0	0	0	1	1	0	0	1	?	0
Macroclemys temminckii	2	2	0	1	1	1	1	0	0	?	1	1	0	0	1	0	0
Chelydra serpentina	2	2	0	1	1	1	1	0	0	0	1	1	0	0	1	0	0
Platysternon megacephalum	1	2	0	1	1	1	1	0	0	0	1	1	0	0	1	0	0
Mongolemys elegans	2	1	0	1	1	1	1	0	0	0	0	1	0	?	1	0	0
Gopherus polyphemus	2	2	0	1	1	1	1	0	0	0	1	1	0	0	1	0	0
Chrysemys picta	2	1	0	1	1	1	0	0	0	0	1	1	0	0	1	0	0
Geoclemys hamiltonii	2	1	0	1	1	1	1	0	0	0	1	1	0	0	1	0	0
Emarginachelys cretacea	c	1	0	1	1	1	1	0	0	0	1	1	0	0	1	0	0
Baptemys wyomingensis	2	1	0	1	1	1	1	0	0	0	a	1	0	0	1	?	0
Dermatemys mawii	2	1	0	1	1	1	1	0	0	0	1	1	0	0	1	0	0
Hoplochelys crassa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Staurotypus triporcatus	2	1	0	1	1	1	1	0	0	0	1	1	0	0	1	0	0
Sternotherus odoratus	2	1	0	1	1	1	1	0	0	0	1	1	0	0	1	0	0
Kinosternon flavescens	2	1	0	1	1	1	1	0	0	0	1	1	0	0	1	0	0
Zangerlia neimongolensis	c	2	?	1	1	1	1	0	0	0	0	1	0	0	1	?	0
Basilemys variolosa	2	2	?	1	1	1	?	0	?	?	?	?	?	?	1	?	?
Adocus beatus	2	1	0	1	1	1	1	0	0	0	1	1	0	0	1	0	0
Peltochelys durlstonensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sandownia harrisi	c	2	1	1	1	1	1	0	1	0	–	0	0	0	1	0	0
Apalone spinifera	1	2	0	1	1	1	1	0	0	1	1	1	0	0	1	0	0
Lissemys punctata	1	2	0	1	1	1	1	0	0	1	1	1	0	0	1	0	0
Anosteira ornata	2	2	?	1	1	1	1	0	0	1	a	1	0	0	1	?	0
Carettochelys insculpta	2	2	0	1	1	1	1	0	0	1	1	1	0	0	1	0	0

	Hyomandibular Nerve A	**Stapedial Artery A**	**Stapedial Artery B***	**Jugular Foramina A**	**Canalis Caroticum A**	**Fenestra Perilymphatica A**	**Dentary A**	**Splenial A**	**Carapace A***	**Carapace B***	**Nuchal A**	**Nuchal B**	**Neural A**	**Peripheral A***	**Peripheral B***	**Costal A**	**Costal B***
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proganochelys quenstedti	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0
Proterochersis robusta	?	?	?	?	?	?	?	?	0	0	?	?	?	0	0	?	?
Palaeochersis talampayensis	?	1	0	0	?	?	?	?	0	0	?	?	?	?	0	?	?
Australochelys africanus	?	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?
Kayentachelys aprix	?	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Meiolania platyceps	1	1	0	1	3	0	0	0	0	0	0	0	?	1	0	0	0
Mongolochelys efremovi	?	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Kallokibotion bajazidi	?	1	0	1	0	?	0	?	0	0	0	0	0	1	0	0	0
Platychelys oberndorferi	?	?	?	?	?	?	?	?	0	0	1	0	0	1	0	0	0
Caribemys oxfordiensis	?	?	?	?	?	?	?	?	0	0	1	0	0	?	0	?	?
Notoemys laticentralis	?	1	0	1	0	?	?	?	0	0	1	0	0	1	0	0	0
Elseya dentata	1	1	0	1	2	0	0	0	0	0	1	0	0	1	0	0	2
Chelodina oblonga	1	1	0	1	2	0	1	0	0	0	1	0	0	1	0	0	2
Phrynops geoffroanus	1	1	0	1	2	0	1	0	0	0	1	0	0	1	0	0	1
Erymnochelys madagascariensis	1	1	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1
Pelomedusa subrufa	1	1	0	1	2	0	0	1	0	0	1	0	0	1	0	0	1
Podocnemis expansa	1	1	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1
Dorsetochelys delairi	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Pleurosternon bullockii	0	1	0	1	1	1	?	?	0	0	?	0	0	1	0	0	0
Glyptops plicatulus	0	1	0	1	1	?	0	0	0	0	1	0	0	1	0	0	0
Dinochelys whitei	?	1	0	1	?	?	0	?	0	0	?	?	0	1	0	0	0
Neurankylus eximius	0	1	0	1	1	1	?	0	0	0	1	0	0	1	0	0	0
Trinitichelys hiatti	0	1	0	1	1	1	0	0	0	0	1	0	0	?	0	0	?
Plesiobaena antiqua	0	1	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0
Boremys pulchra	0	1	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0
Baena arenosa	0	1	0	1	1	1	0	1	0	0	1	0	0	1	0	0	0
Chisternon undatum	0	1	0	1	1	1	0	1	0	0	1	0	0	1	0	0	0
Portlandemys mcdowelli	0	1	0	1	3	0	0	0	?	?	?	?	?	?	?	?	?
Plesiochelys solodurensis	0	1	0	1	3	0	0	0	0	0	1	0	0	1	0	0	0
Solnhofia parsonsi	0	1	0	1	3	0	0	0	0	0	?	?	0	1	?	0	0
Thalassemys moseri	0	1	0	1	3	0	?	?	0	0	1	0	0	?	0	0	?
Santanachelys gaffneyi	0	1	0	1	3	?	0	?	0	0	?	0	0	1	0	0	0
Xinjiangchelys latimarginalis	?	?	?	?	?	?	?	?	0	0	1	0	0	1	0	0	0
Hangaiemys hoburensis	0	1	0	1	3	?	?	?	0	0	1	0	0	1	0	0	0
Judithemys sukhanovi	0	1	0	1	3	?	0	?	0	0	1	0	0	1	0	0	0
Dracochelys bicuspis	0	1	0	1	3	?	?	?	?	?	?	?	?	?	?	?	?
Sinemys lens	0	1	0	1	3	0	0	?	0	0	1	0	0	1	0	0	0
Ordosemys leios	0	1	0	1	3	?	?	?	0	0	1	0	0	1	0	0	0

Continued

	Hyomandibular Nerve A	Stapedial Artery A	Stapedial Artery B*	Jugular Foramina A	Canalis Caroticum A	Fenestra Perilymphatica A	Dentary A	Splenial A	Carapace A*	Carapace B*	Nuchal A	Nuchal B	Neural A	Peripheral A*	Peripheral B*	Costal A	Costal B*
Toxochelys latiremis	0	1	0	1	3	?	0	1	0	0	2	0	0	1	0	0	0
Caretta caretta	0	1	0	1	3	0	0	1	0	0	2	0	0	0	0	0	0
Chelonia mydas	0	1	0	1	3	0	0	1	0	0	2	0	0	1	0	0	0
Mesodermochelys undulatus	?	?	?	?	?	?	0	1	1	0	2	0	0	1	0	0	0
Dermochelys coriacea	0	1	0	1	3	0	0	1	2	0	2	0	0	3	–	0	–
Protochelydra zangerli	0	1	0	1	3	0	?	?	?	?	?	?	?	?	?	?	?
Macroclemys temminckii	0	1	0	1	3	0	0	1	0	0	1	1	0	1	0	0	0
Chelydra serpentina	0	1	0	1	3	0	0	1	0	0	1	1	0	1	0	0	0
Platysternon megacephalum	0	1	0	1	3	0	0	1	0	0	1	0	0	1	0	0	0
Mongolemys elegans	0	1	0	1	3	0	0	1	0	0	1	0	0	1	0	0	0
Gopherus polyphemus	0	1	0	1	3	0	0	1	0	0	1	0	0	1	0	0	0
Chrysemys picta	0	1	0	1	3	0	0	1	0	0	1	0	0	1	0	0	0
Geoclemys hamiltonii	0	1	0	1	3	0	0	1	0	1	1	0	0	1	0	0	0
Emarginachelys cretacea	0	1	0	1	3	?	?	?	0	1	1	1	0	1	0	0	0
Baptemys wyomingensis	0	–	2	1	3	0	0	1	0	1	1	0	0	1	0	0	0
Dermatemys mawii	0	–	2	1	3	0	0	1	0	0	1	a	0	1	0	0	1
Hoplochelys crassa	?	?	?	?	?	0	?	?	0	2	1	1	0	1	0	0	0
Staurotypus triporcatus	0	1	1	1	3	0	0	1	0	2	1	1	0	2	1	0	a
Sternotherus odoratus	0	1	1	1	3	0	0	1	0	1	1	1	0	2	1	1	1
Kinosternon flavescens	0	1	1	1	3	0	0	1	0	1	1	1	0	2	1	1	1
Zangerlia neimongolensis	0	1	0	1	3	?	0	1	0	0	?	?	1	1	?	?	0
Basilemys variolosa	?	?	?	?	?	?	0	1	0	0	1	0	1	1	0	0	a
Adocus beatus	0	1	0	1	3	0	0	1	0	0	1	0	1	1	0	0	1
Peltochelys durlstonensis	?	?	?	?	?	?	?	?	0	0	1	0	0	2	0	0	1
Sandownia harrisi	0	1	0	1	3	0	0	1	?	?	?	?	?	?	?	?	?
Apalone spinifera	0	1	0	1	3	0	0	1	2	0	1	0	0	3	–	0	1
Lissemys punctata	0	1	0	1	3	0	0	1	2	0	1	0	0	3	–	0	1
Anosteira ornata	0	1	0	1	3	0	?	?	1	0	1	0	0	2	0	0	1
Carettochelys insculpta	0	1	0	1	3	0	0	1	1	0	1	0	0	2	0	0	1

	Costal C	**Cervical A**	**Supramarginal A***	**Vertebral A**	**Vertebral B**	**Vertebral C**	**Plastron A**	**Plastron B**	**Plastron C**	**Entoplastron A**	**Entoplastron B**	**Entoplastron C**	**Entoplastron D**	**Entoplastron E**	**Epiplastron A**	**Hyoplastron A**	**Mesoplastron A***
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proganochelys quenstedti	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0
Proterochersis robusta	0	?	1	1	0	?	0	0	0	0	0	1	0	0	0	0	0
Palaeochersis talampayensis	0	?	0	?	0	?	0	0	0	0	0	?	0	0	?	0	0
Australochelys africanus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kayentachelys aprix	0	0	2	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Meiolania platyceps	0	0	2	1	0	?	1	1	0	1	0	1	0	0	1	0	?
Mongolochelys efremovi	0	0	2	1	0	1	1	1	0	1	0	1	0	0	1	0	0
Kallokibotion bajazidi	0	?	2	1	0	0	0	0	0	1	?	1	0	0	0	1	1
Platychelys oberndorferi	0	0	1	1	0	0	0	1	0	1	1	1	0	0	0	1	1
Caribemys oxfordiensis	0	?	2	?	?	?	0	1	0	1	1	?	0	0	0	1	1
Notoemys laticentralis	0	0	2	1	0	0	0	1	0	1	1	?	0	0	0	1	1
Elseya dentata	0	1	2	1	1	–	0	0	0	1	1	1	0	0	0	1	2
Chelodina oblonga	0	0	2	1	1	–	0	0	0	1	1	1	0	0	0	1	2
Phrynops geoffroanus	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	1	2
Erymnochelys madagascariensis	0	1	2	1	1	1	0	0	0	1	1	1	0	0	0	1	1
Pelomedusa subrufa	0	1	2	1	1	1	0	0	0	1	1	1	0	0	0	1	1
Podocnemis expansa	0	1	2	1	1	1	0	0	0	1	1	1	0	0	0	1	1
Dorsetochelys delairi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pleurosternon bullockii	0	0	2	1	0	1	0	0	0	1	?	?	0	0	0	?	0
Glyptops plicatulus	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	1	0
Dinochelys whitei	0	0	2	1	0	1	0	0	0	1	1	1	0	0	0	?	0
Neurankylus eximius	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	1	0
Trinitichelys hiatti	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	1	0
Plesiobaena antiqua	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	1	0
Boremys pulchra	0	2	2	1	1	1	0	0	0	1	1	1	0	0	0	1	0
Baena arenosa	0	2	2	1	1	1	0	0	0	1	1	1	0	0	0	1	1
Chisternon undatum	0	2	2	1	1	–	0	0	0	1	1	1	0	0	0	1	0
Portlandemys mcdowelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Plesiochelys solodurensis	0	2	2	1	0	1	0	a	0	1	1	1	0	0	0	1	2
Solnhofia parsonsi	0	0	2	1	0	1	1	1	0	?	?	?	0	0	0	0	2
Thalassemys moseri	0	?	2	?	0	?	?	1	0	?	?	?	?	?	?	1	2
Santanachelys gaffneyi	1	0	2	1	0	0	1	1	0	1	1	1	0	0	0	0	2
Xinjiangchelys latimarginalis	0	0	2	1	1	1	1	0	0	1	1	1	0	0	0	0	2
Hangaiemys hoburensis	0	0	2	1	1	1	1	0	0	1	1	1	0	0	1	0	2
Judithemys sukhanovi	0	0	2	1	1	1	1	0	0	1	1	1	0	0	1	0	2
Dracochelys bicuspis	?	?	?	?	?	?	1	?	?	?	?	?	?	?	1	?	?
Sinemys lens	0	1	2	1	1	1	1	a	?	1	1	1	0	0	–	0	2
Ordosemys leios	0	0	2	1	1	1	1	1	?	?	?	?	0	0	?	0	2
Toxochelys latiremis	1	0	2	1	1	1	1	1	0	1	1	1	0	0	1	0	2
Caretta caretta	1	0	2	1	1	1	1	1	0	1	1	1	0	0	1	0	2

Continued

	Costal C	**Cervical A**	**Supramarginal A***	**Vertebral A**	**Vertebral B**	**Vertebral C**	**Plastron A**	**Plastron B**	**Plastron C**	**Entoplastron A**	**Entoplastron B**	**Entoplastron C**	**Entoplastron D**	**Entoplastron E**	**Epiplastron A**	**Hyoplastron A**	**Mesoplastron A***
Chelonia mydas	1	0	2	1	1	1	1	1	0	1	1	1	0	0	1	0	2
Mesodermochelys undulatus	1	?	2	?	?	?	1	1	0	1	1	1	0	0	1	0	2
Dermochelys coriacea	1	–	2	–	–	–	1	1	–	1	1	1	0	0	1	0	2
Protochelydra zangerli	0	?	?	?	?	?	1	0	0	1	1	1	0	0	1	0	2
Macroclemys temminckii	0	0	1	1	1	1	1	1	0	1	1	1	0	0	1	0	2
Chelydra serpentina	0	0	2	1	1	1	1	1	0	1	1	1	0	0	1	0	2
Platysternon megacephalum	0	0	2	1	1	1	1	0	0	1	1	1	0	0	0	0	2
Mongolemys elegans	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	1	2
Gopherus polyphemus	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	1	2
Chrysemys picta	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	1	2
Geoclemys hamiltonii	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	1	2
Emarginachelys cretacea	0	?	2	1	1	1	1	0	0	1	1	1	0	0	0	0	2
Baptemys wyomingensis	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	1	2
Dermatemys mawii	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	1	2
Hoplochelys crassa	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	0	2
Staurotypus triporcatus	0	0	2	1	1	1	0	0	1	1	1	1	0	0	0	0	2
Sternotherus odoratus	0	0	2	1	1	1	0	0	1	1	1	1	?	1	0	0	2
Kinosternon flavescens	0	0	2	1	1	1	0	0	1	1	1	1	?	1	0	0	2
Zangerlia neimongolensis	0	?	2	1	1	?	0	0	0	1	1	1	0	0	0	0	2
Basilemys variolosa	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	0	2
Adocus beatus	0	0	2	1	1	1	0	0	0	1	1	1	0	0	0	0	2
Peltochelys durlstonensis	0	?	2	1	1	0	0	0	0	1	1	1	0	0	0	0	2
Sandownia harrisi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apalone spinifera	–	–	2	–	–	–	1	1	–	1	1	1	1	0	–	0	2
Lissemys punctata	–	–	2	–	–	–	1	1	–	1	1	1	1	0	–	0	2
Anosteira ornata	0	0	2	1	1	?	1	0	–	1	1	1	0	0	0	0	2
Carettochelys insculpta	0	–	2	–	–	–	1	0	–	1	1	1	0	0	0	0	2

	Hypoplastron A	**Xiphiplastron A**	**Xiphiplastron B**	**Plastral Scutes A**	**Plastral Scutes B**	**Gular A**	**Extragular A**	**Extragular B**	**Extragular C**	**Intergular A**	**Humeral A**	**Pectoral A**	**Abdominal A***	**Anal A**	**Inframarginal A**	**Cervical Rib A**	**Cervical Vertebra A**
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proganochelys quenstedti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0
Proterochersis robusta	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?
Palaeochersis talampayensis	0	0	0	0	0	?	?	?	0	?	?	?	?	0	?	0	?
Australochelys africanus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kayentachelys aprix	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	0
Meiolania platyceps	0	0	0	0	0	0	0	0	1	0	0	?	?	?	?	0	0
Mongolochelys efremovi	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Kallokibotion bajazidi	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	0
Platychelys oberndorferi	1	1	0	0	0	1	0	0	1	0	0	0	0	0	2	?	0
Caribemys oxfordiensis	1	?	0	0	0	1	0	0	1	0	0	0	0	?	2	?	0
Notoemys laticentralis	?	1	0	0	0	?	?	?	1	?	0	0	0	0	2	?	0
Elseya dentata	1	1	0	0	0	1	0	0	1	0	0	0	0	0	2	1	0
Chelodina oblonga	0	1	0	0	0	1	0	1	1	0	0	0	0	0	2	1	0
Phrynops geoffroanus	1	1	0	0	0	1	0	0	1	0	0	0	0	0	2	1	0
Erymnochelys madagascariensis	1	1	0	0	0	1	0	0	1	0	0	0	0	0	2	1	0
Pelomedusa subrufa	1	1	0	0	0	1	0	0	1	0	0	0	0	0	2	1	0
Podocnemis expansa	1	1	0	0	0	1	0	0	1	0	0	0	0	0	2	1	0
Dorsetochelys delairi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pleurosternon bullockii	?	0	0	0	0	1	0	0	1	0	0	0	0	0	0	?	0
Glyptops plicatulus	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	0
Dinochelys whitei	?	0	0	0	0	0	0	0	1	0	0	0	0	a	0	1	0
Neurankylus eximius	1	?	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?
Trinitichelys hiatti	1	?	0	0	0	0	0	0	1	0	0	0	0	?	0	?	0
Plesiobaena antiqua	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	0
Boremys pulchra	1	?	0	0	0	0	0	2	1	0	0	0	0	?	0	1	0
Baena arenosa	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	?	?
Chisternon undatum	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	?	0
Portlandemys mcdowelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Plesiochelys solodurensis	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?
Solnhofia parsonsi	0	0	0	0	0	?	?	?	?	?	0	0	0	0	0	1	1
Thalassemys moseri	?	?	?	0	0	?	?	?	?	?	0	0	0	?	0	1	1
Santanachelys gaffneyi	0	0	0	?	0	?	?	?	?	?	?	?	?	?	?	1	1
Xinjiangchelys latimarginalis	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	?	1
Hangaiemys hoburensis	0	0	0	0	0	0	1	–	1	0	0	0	0	a	0	1	1
Judithemys sukhanovi	0	0	0	0	0	0	1	–	1	0	0	0	0	a	0	1	1
Dracochelys bicuspis	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Sinemys lens	0	0	0	0	0	?	?	?	1	?	0	0	0	?	0	?	?
Ordosemys leios	0	0	0	0	0	?	?	?	1	?	0	0	0	1	0	1	1
Toxochelys latiremis	0	0	1	0	0	?	?	?	1	?	0	?	0	1	0	1	1
Caretta caretta	0	0	1	0	0	0	1	–	1	1	0	0	0	0	0	1	1

Continued

	Hypoplastron A	**Xiphiplastron A**	**Xiphiplastron B**	**Plastral Scutes A**	**Plastral Scutes B**	**Gular A**	**Extragular A**	**Extragular B**	**Extragular C**	**Intergular A**	**Humeral A**	**Pectoral A**	**Abdominal A***	**Anal A**	**Inframarginal A**	**Cervical Rib A**	**Cervical Vertebra A**
Chelonia mydas	0	0	1	0	0	0	1	–	1	1	0	0	0	0	0	1	1
Mesodermochelys undulatus	0	0	1	?	0	?	?	?	?	?	?	?	?	?	?	1	1
Dermochelys coriacea	0	0	1	1	0	–	–	–	1	–	–	–	–	–	–	1	1
Protochelydra zangerli	0	0	0	0	0	?	1	–	1	0	0	0	1	1	0	?	?
Macroclemys temminckii	0	0	0	0	0	0	1	–	1	0	0	0	1	1	0	1	1
Chelydra serpentina	0	0	0	0	0	0	1	–	1	0	0	0	1	1	0	1	1
Platysternon megacephalum	0	1	0	0	0	0	1	–	1	0	0	0	0	0	0	1	1
Mongolemys elegans	1	1	0	0	0	0	1	–	1	0	0	0	0	0	0	?	?
Gopherus polyphemus	1	1	0	0	0	0	1	–	1	0	0	0	0	0	1	1	1
Chrysemys picta	1	1	0	0	0	0	1	–	1	0	0	0	0	0	1	1	1
Geoclemys hamiltonii	1	1	0	0	0	0	1	–	1	0	0	0	0	0	1	1	1
Emarginachelys cretacea	0	0	0	0	0	0	1	–	1	0	0	?	?	0	0	1	1
Baptemys wyomingensis	1	0	0	0	0	0	1	–	1	0	0	1	0	0	0	1	1
Dermatemys mawii	0	1	0	0	0	0	1	–	1	1	0	1	0	0	0	1	1
Hoplochelys crassa	0	0	0	0	0	0	1	–	1	0	0	1	1	0	0	?	?
Staurotypus triporcatus	0	0	0	0	0	0	1	–	1	0	0	1	2	0	0	1	1
Sternotherus odoratus	0	0	0	0	0	0	1	–	1	1	1	1	2	0	0	1	1
Kinosternon flavescens	0	0	0	0	0	0	1	–	1	1	1	1	2	0	0	1	1
Zangerlia neimongolensis	0	0	0	0	1	0	0	2	1	0	0	0	0	0	0	1	1
Basilemys variolosa	0	0	0	0	1	0	0	b	1	0	0	0	0	0	0	1	1
Adocus beatus	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1
Peltochelys durlstonensis	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	?	?
Sandownia harrisi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apalone spinifera	0	0	–	1	–	–	–	–	1	–	–	–	–	–	–	1	1
Lissemys punctata	0	0	–	1	–	–	–	–	1	–	–	–	–	–	–	1	1
Anosteira ornata	0	0	0	1	–	–	–	–	1	–	–	–	–	–	–	?	?
Carettochelys insculpta	0	0	0	1	–	–	–	–	1	–	–	–	–	–	–	1	1

	Cervical Vertebra B	**Cervical Vertebra C**	**Cervical Articulation A**	**Cervical Articulation B**	**Cervical Articulation C**	**Cervical Articulation D**	**Cervical Articulation E**	**Cervical Articulation F**	**Cervical Articulation G**	**Cervical Articulation H**	**Dorsal Rib A**	**Dorsal Rib B**	**Dorsal Rib C**	**Dorsal Vertebra A**	**Chevron A**	**Caudal Vertebra A**	**Caudal Vertebra B**
Hypothetical ancestor	0	0	0	–	–	–	–	–	–	–	0	0	0	0	0	0	0
Proganochelys quenstedti	0	0	0	–	–	–	–	–	–	–	0	0	0	0	0	0	0
Proterochersis robusta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Palaeochersis talampayensis	?	?	0	–	–	–	–	–	–	–	0	?	?	?	?	1	?
Australochelys africanus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kayentachelys aprix	0	?	0	–	–	–	–	–	–	–	0	0	0	0	0	1	0
Meiolania platyceps	0	0	1	0	0	1	1	1	1	1	0	0	?	0	0	0	c
Mongolochelys efremovi	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	1	3
Kallokibotion bajazidi	?	?	0	–	–	–	–	–	–	–	0	?	?	?	0	?	0
Platychelys oberndorferi	?	?	1	?	?	?	?	?	?	?	1	0	1	0	1	?	?
Caribemys oxfordiensis	?	?	1	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Notoemys laticentralis	?	?	1	0	0	?	?	?	?	?	2	0	1	?	?	?	?
Elseya dentata	0	0	1	0	0	0	1	1	0	1	2	0	1	0	1	1	1
Chelodina oblonga	0	0	1	0	0	0	1	1	0	1	2	0	1	0	1	1	1
Phrynops geoffroanus	0	0	1	0	0	0	1	1	0	1	2	0	1	0	1	1	1
Erymnochelys madagascariensis	0	0	1	1	1	1	1	1	1	1	2	0	1	0	1	1	1
Pelomedusa subrufa	0	0	1	1	1	1	1	1	1	1	2	0	1	0	1	1	1
Podocnemis expansa	0	0	1	1	1	1	1	1	1	1	2	0	1	0	1	1	1
Dorsetochelys delairi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pleurosternon bullockii	?	?	0	–	–	–	–	–	–	–	0	?	?	?	?	?	?
Glyptops plicatulus	0	0	0	–	–	–	–	–	–	–	0	0	1	0	?	?	?
Dinochelys whitei	?	?	0	–	–	–	–	–	–	–	0	?	1	?	?	1	?
Neurankylus eximius	?	?	?	?	?	?	?	?	?	?	1	0	1	?	?	?	?
Trinitichelys hiatti	0	0	0	–	–	–	–	–	–	–	?	?	1	0	?	?	?
Plesiobaena antiqua	0	0	1	?	?	?	1	1	1	1	1	0	1	0	0	1	0
Boremys pulchra	0	0	0	–	–	–	–	–	–	–	1	0	1	0	0	1	2
Baena arenosa	?	?	?	?	?	?	?	?	?	?	1	0	1	0	?	?	?
Chisternon undatum	0	0	1	0	0	1	1	1	1	1	1	0	1	0	0	1	2
Portlandemys mcdowelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Plesiochelys solodurensis	?	?	?	?	?	?	?	?	?	?	0	0	1	0	?	?	?
Solnhofia parsonsi	0	?	0	–	–	–	–	–	–	–	?	?	1	?	?	1	0
Thalassemys moseri	?	?	0	–	–	–	–	–	–	–	1	?	?	?	?	?	?
Santanachelys gaffneyi	?	?	?	?	?	?	?	?	?	?	0	?	1	?	?	?	?
Xinjiangchelys latimarginalis	0	0	0	–	–	–	–	–	–	–	2	0	1	0	0	1	3
Hangaiemys hoburensis	1	?	1	0	0	1	1	1	1	1	2	?	1	0	?	?	?
Judithemys sukhanovi	1	?	1	0	0	1	1	1	1	1	2	?	1	0	1	1	3
Dracochelys bicuspis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sinemys lens	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?	1	?
Ordosemys leios	?	0	1	?	0	1	?	?	0	1	0	?	1	0	1	1	3
Toxochelys latiremis	?	1	1	0	0	1	1	1	1	1	?	0	1	0	0	1	1

Continued

	Cervical Vertebra B	Cervical Vertebra C	Cervical Articulation A	Cervical Articulation B	Cervical Articulation C	Cervical Articulation D	Cervical Articulation E	Cervical Articulation F	Cervical Articulation G	Cervical Articulation H	Dorsal Rib A	Dorsal Rib B	Dorsal Rib C	Dorsal Vertebra A	Chevron A	Caudal Vertebra A	Caudal Vertebra B
Caretta caretta	1	1	1	0	0	1	1	1	1	1	2	0	1	1	1	1	1
Chelonia mydas	1	1	1	0	0	1	1	1	1	1	2	0	1	1	1	1	1
Mesodermochelys undulatus	1	0	1	?	?	?	?	?	?	?	2	0	1	0	1	1	1
Dermochelys coriacea	1	1	1	0	0	1	1	1	1	1	2	0	–	0	1	1	1
Protochelydra zangerli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macroclemys temminckii	1	1	1	0	0	1	1	1	1	1	2	0	1	1	0	1	3
Chelydra serpentina	1	1	1	0	0	1	1	1	1	1	2	0	1	1	0	1	3
Platysternon megacephalum	1	1	1	0	0	1	1	1	0	1	2	0	1	1	0	1	3
Mongolemys elegans	?	?	1	0	0	1	1	1	0	1	2	?	1	1	0	1	?
Gopherus polyphemus	1	1	1	0	0	1	1	1	0	1	2	0	1	1	1	1	1
Chrysemys picta	1	1	1	0	0	1	1	1	0	1	2	0	1	1	1	1	1
Geoclemys hamiltonii	1	1	1	0	0	1	1	1	0	1	2	0	1	1	1	1	1
Emarginachelys cretacea	?	?	1	0	0	1	1	1	1	1	?	?	1	?	?	?	?
Baptemys wyomingensis	1	1	1	0	1	1	1	1	1	1	2	?	1	1	1	1	3
Dermatemys mawii	1	1	1	1	1	1	1	1	1	1	2	0	1	1	1	1	1
Hoplochelys crassa	?	?	?	?	?	?	?	?	?	?	2	0	1	?	?	?	?
Staurotypus triporcatus	1	1	1	0	1	1	1	1	1	1	2	1	1	1	1	1	1
Sternotherus odoratus	1	1	1	0	1	1	1	1	1	1	2	1	1	1	1	1	1
Kinosternon flavescens	1	1	1	0	1	1	1	1	1	1	2	1	1	1	1	1	1
Zangerlia neimongolensis	1	1	1	0	0	0	0	0	0	1	2	?	?	1	?	?	?
Basilemys variolosa	1	1	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?
Adocus beatus	1	1	1	0	0	0	0	0	0	0	2	?	1	1	?	?	?
Peltochelys durlstonensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sandownia harrisi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apalone spinifera	0	1	1	0	0	0	0	0	0	2	2	0	1	–	1	1	1
Lissemys punctata	0	1	1	0	0	0	0	0	0	2	2	0	1	–	1	1	1
Anosteira ornata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Carettochelys insculpta	0	1	1	0	0	0	0	0	0	1	2	0	1	1	1	1	1

	Cleithrum A*	Scapula A	Scapula B	Scapula C	Coracoid A	Pelvis A	Ilium A	Ilium B	Ilium C	Ilium D	Ischium A	Hypoischium A	Manus A	Manus B*	Manus C*	Pes A	Pes B
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proganochelys quenstedti	0	0	0	0	0	0	0	–	–	0	0	0	0	0	0	0	0
Proterochersis robusta	0	?	?	?	?	?	1	?	?	0	0	?	?	?	?	?	?
Palaeochersis talampayensis	0	0	0	?	0	?	0	?	?	0	1	0	0	0	0	0	0
Australochelys africanus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kayentachelys aprix	1	1	0	0	1	0	1	–	–	0	1	1	?	?	?	?	?
Meiolania platyceps	1	1	0	0	1	0	1	–	–	0	1	?	0	0	0	?	0
Mongolochelys efremovi	1	1	0	0	1	0	1	–	–	0	?	?	1	0	0	1	1
Kallokibotion bajazidi	1	?	?	0	?	0	?	–	–	?	?	?	?	?	?	?	?
Platychelys oberndorferi	?	?	?	?	?	1	1	0	0	0	1	?	?	?	?	?	?
Caribemys oxfordiensis	?	?	?	?	?	1	?	1	0	?	?	?	?	?	?	?	?
Notoemys laticentralis	?	?	?	?	?	1	?	1	1	?	?	?	1	0	0	1	1
Elseya dentata	2	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1
Chelodina oblonga	2	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1
Phrynops geoffroanus	2	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1
Erymnochelys madagascariensis	2	1	1	0	1	1	1	1	1	0	1	1	1	0	0	1	1
Pelomedusa subrufa	2	1	1	0	1	1	1	1	1	0	1	1	1	0	0	1	1
Podocnemis expansa	2	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1
Dorsetochelys delairi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pleurosternon bullockii	?	?	?	?	?	?	1	?	?	0	?	?	?	?	?	?	?
Glyptops plicatulus	1	1	1	1	1	0	1	–	–	0	1	1	?	?	?	?	?
Dinochelys whitei	1	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	1
Neurankylus eximius	?	?	?	?	?	0	?	–	–	?	?	?	?	?	?	?	?
Trinitichelys hiatti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Plesiobaena antiqua	?	1	1	1	1	0	1	–	–	0	1	1	1	0	0	1	1
Boremys pulchra	2	?	?	?	?	0	?	–	–	?	?	?	?	?	?	?	?
Baena arenosa	2	?	?	?	?	0	?	–	–	0	1	1	?	?	?	?	?
Chisternon undatum	?	1	1	1	1	0	1	–	–	?	1	1	?	?	?	?	?
Portlandemys mcdowelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Plesiochelys solodurensis	?	1	1	1	1	0	1	–	–	0	1	1	1	0	0	1	1
Solnhofia parsonsi	?	1	1	1	1	0	?	–	–	?	1	1	1	0	0	1	1
Thalassemys moseri	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Santanachelys gaffneyi	?	1	1	?	1	0	?	–	–	0	1	1	1	1	0	1	1
Xinjiangchelys latimarginalis	1	1	1	1	1	0	1	–	–	0	1	1	?	?	?	?	?
Hangaiemys hoburensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Judithemys sukhanovi	?	1	1	?	1	0	1	–	–	0	1	1	1	0	0	1	1
Dracochelys bicuspis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sinemys lens	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	1
Ordosemys leios	?	1	1	1	1	0	1	–	–	0	1	1	?	?	?	?	?
Toxochelys latiremis	?	1	1	1	1	0	?	–	–	0	1	1	1	1	0	1	1
Caretta caretta	2	1	1	1	1	0	1	–	–	0	1	1	1	2	0	1	1
Chelonia mydas	2	1	1	1	1	0	?	–	–	0	1	1	1	2	0	1	1

Continued

	Cleithrum A*	**Scapula A**	**Scapula B**	**Scapula C**	**Coracoid A**	**Pelvis A**	**Ilium A**	**Ilium B**	**Ilium C**	**Ilium D**	**Ischium A**	**Hypoischium A**	**Manus A**	**Manus B***	**Manus C***	**Pes A**	**Pes B**
Mesodermochelys undulatus	2	1	1	1	1	0	1	–	–	0	1	1	?	?	?	?	?
Dermochelys coriacea	2	1	1	1	1	0	1	–	–	0	1	1	1	2	0	1	1
Protochelydra zangerli	2	1	1	0	1	0	1	–	–	0	?	?	?	?	?	?	?
Macroclemys temminckii	2	1	1	0	1	0	1	–	–	0	1	1	1	0	0	1	1
Chelydra serpentina	2	1	1	0	1	0	1	–	–	0	1	1	1	0	0	1	1
Platysternon megacephalum	2	1	1	0	1	0	1	–	–	0	1	1	1	0	0	1	1
Mongolemys elegans	2	1	1	0	1	0	1	–	–	0	1	1	1	0	0	?	?
Gopherus polyphemus	2	1	1	0	1	0	1	–	–	0	1	1	0	0	0	1	1
Chrysemys picta	2	1	1	0	1	0	1	–	–	0	1	1	1	0	0	1	1
Geoclemys hamiltonii	2	1	1	0	1	0	1	–	–	0	1	1	1	0	0	1	1
Emarginachelys cretacea	?	1	1	0	1	0	1	–	–	0	1	1	1	0	0	1	1
Baptemys wyomingensis	2	1	1	0	1	0	1	–	–	1	1	1	1	0	0	1	1
Dermatemys mawii	2	1	1	0	1	0	1	–	–	0	1	1	1	0	0	1	1
Hoplochelys crassa	2	?	?	0	1	0	?	–	–	?	?	?	?	?	?	?	?
Staurotypus triporcatus	2	1	1	0	1	0	?	–	–	1	1	1	1	0	0	1	1
Sternotherus odoratus	2	1	1	0	1	0	1	–	–	1	1	1	1	0	0	1	1
Kinosternon flavescens	2	1	1	0	1	0	?	–	–	1	1	1	1	0	0	1	1
Zangerlia neimongolensis	?	1	1	0	1	0	1	–	–	0	1	1	0	0	0	?	1
Basilemys variolosa	2	1	1	?	1	0	1	–	–	0	1	1	0	0	0	?	?
Adocus beatus	2	1	1	0	1	0	1	–	–	0	1	1	1	0	0	1	1
Peltochelys durlstonensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sandownia harrisi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apalone spinifera	2	1	1	0	1	0	1	–	–	0	1	1	1	0	1	1	1
Lissemys punctata	2	1	1	0	1	0	1	–	–	0	1	1	1	0	1	1	1
Anosteira ornata	?	1	1	?	?	0	?	–	–	?	1	1	1	0	2	1	1
Carettochelys insculpta	2	1	1	0	1	0	1	–	–	0	1	1	1	0	2	1	1

Literature Cited

Agassiz, L. 1857. Contributions to the Natural History of the United States of America. Vol. 1, Parts 1 and 2. Boston: Little, Brown. 452 pp.

Albrecht, P. W. 1967. The cranial arteries and cranial arterial foramina of the turtle genera *Chrysemys, Sternotherus,* and *Trionyx*: a comparative study with analysis of possible evolutionary implications. Tulane Studies in Zoology 14:81–99.

Baur, G. 1887. Ueber den Ursprung der Extremitaeten der Ichthyopterygia. Bericht des Oberrheinischen Geologischen Vereins 20: 17–20.

Boddaert, P. 1770. Over de kraakbeenige schildpad. Amsterdam: Kornelis van Tongerlo. 39 pp.

Bonnaterre, P. J. 1789. Tableau encyclopédique et méthodique des trois règnes de la nature. Erpétologie. Paris: Panckoucke. 72 pp.

Boulenger, G. A. 1889. Catalogue of Chelonians, Rhynchocephalians and Crocodiles in the British Museum (Natural History). London: Taylor and Francis. 311 pp.

Bräm, H. 1965. Die Schildkröten aus dem oberen Jura (Malm) der Gegend von Solothurn. Schweizerische Paläontologische Abhandlungen 83:1–190.

Brinkman, D. B. 1998. The skull and neck of the Cretaceous turtle *Basilemys* (Trionychoidea, Nanhsiungchelyidae), and the interrelationships of the genus. Paludicola 1:150–157.

——2003. Anatomy and systematics of *Plesiobaena antiqua* (Testudines; Baenidae) from the mid-Campanian Judith River Group of Alberta, Canada. Journal of Vertebrate Paleontology 23:146–155.

Brinkman, D. B. and E. L. Nicholls. 1991. Anatomy and relationships of the turtle *Boremys pulchra* (Testudines: Baenidae). Journal of Vertebrate Paleontology 11:302–315.

——1993. The skull of *Neurankylus eximius* (Testudines: Baenidae) and a reinterpretation of the relationships of this taxon. Journal of Vertebrate Paleontology 13:273–281.

Brinkman, D. B. and J.-H. Peng. 1993a. New material of Sinemys (Testudines, Sinemydidae) from the Early Cretaceous of China. Canadian Journal of Earth Sciences 30:2139 –2152.

——1993b. *Ordosemys leios* n. gen., n. sp., a new turtle from the Early Cretaceous of the Ordos Basin, Inner Mongolia. Canadian Journal of Earth Sciences 30:2128–2138.

——1996. A new species of *Zangerlia* (Testudines: Nanhsiungchelyidae) from the Upper Cretaceous redbeds and Bayan Mandahu, Inner Mongolia, and the relationships of the genus. Canadian Journal of Earth Sciences 33:526 –540.

Brinkman, D. B., K. Stadtman, and D. Smith. 2000. New material of *Dinochelys whitei* Gaffney, 1979, from the Dry Mesa Quarry (Morrison Formation, Jurassic) of Colorado. Journal of Vertebrate Paleontology 20:269 –274.

Brinkman, D. B. and X.-C. Wu. 1999. The skull of *Ordosemys,* an Early Cretaceous turtle from Inner Mongolia, People's Republic of China, and the interrelationships of Eucryptodira (Chelonia, Cryptodira). Paludicola 2:134–147.

Carroll, R. L. 1988. Vertebrate Paleontology and Evolution. New York: Freeman. 698 pp.

Cattoi, N. and M. A. Freiberg. 1961. Nuevo hallazgo de chelonia extinguidos en la República Argentina. Physis 22:202.

Clark, J. 1932. A new anosteirid from the Uinta Eocene. Annals of the Carnegie Museum 21: 161–170.

Cope, E. D. 1872a. Description of some new vertebrata from the Bridger group of the Eocene. Proceedings of the American Philosophical Society 12:460–465.

——1872b. [Description of specimens found near Sheridan, Kansas]. Proceedings of the Academy of Natural Sciences of Philadelphia 1872: 127–129.

——1873. [Description of *Toxochelys latiremis*]. Proceedings of the Academy of Natural Sciences of Philadelphia 1873:10.

——1876. Description of some vertebrate remains from the Fort Union Beds of Montana. Proceedings of the Academy of Natural Sciences of Philadelphia 1876:248–261.

——1877. On reptilian remains from the Dakota Beds of Colorado. Proceedings of the American Philosophical Society 17:193–196.

——1888. Synopsis of the vertebrate fuana of the Puerco series. Transactions of the American Philosophical Society 16:298–361.

Cornalia, E. 1849. Vertebratorum synopsis in musaeo mediolanense extantium quae per novum orbem cajetanas osculati collegit annis 1846–47–48. [Milan]: Mediolani. 16 pp.

Crumly, C. R. 1982. A cladistic analysis of *Geochelone* using cranial osteology. Journal of Herpetology 16:215–234.

Danilov, I. G. and V. B. Sukhanov. 2001. New data on lindholmemydid turtle *Lindholmemys* from the Late Cretaceous of Mongolia. Acta Palaeontologica Polonica 46:125–131.

Daudin, F. M. 1802. Histoire naturelle, générale et particulière, des reptiles; ouvrage faisant suite aux oeuvres de Leclerc de Buffon, et partie du cours complet d'histoire naturelle rédigée par C. S. Sonnini. Paris: F. Dufart. 256 pp.

Dollo, M. L. 1884. Première note sur les chéloniens de Bernissart. Bulletin du Musée Royal d'Histoire Naturelle de Belgique 3:63–79.

Dryden, L. S. 1988. Paraphyly of the Cryptodira and phylogenetic systematics of turtles [master's thesis]. Lawrence, KS: University of Kansas.

Duméril, A. M. C. and G. Bibron. 1851. In: A. M. C. Duméril and A. H. A. Duméril, eds. Catalogue méthodique de la collection des reptiles du Muséum d'Histoire de Paris. Paris: Gide et Baudry.

Erickson, B. R. 1973. A new chelydrid turtle *Protochelydra zangerli* from the late Paleocene of North Dakota. Scientific Publications of the Science Museum of Minnesota 2:1–16.

Evans, J. and T. S. Kemp. 1975. The cranial morphology of a new Lower Cretaceous turtle from southern England. Palaeontology 18:25–40.

——1976. A new turtle skull from the Purbeckian of England and a note on the early dichotomies of cryptodire turtles. Palaeontology 19:317–324.

Fernandez, M. S. and M. S. de la Fuente. 1994. Redescription and phylogenetic position of *Notoemys*: the oldest Gondwanian pleurodiran turtle. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 193: 81–105.

Fraas, E. 1913. *Proterochersis,* eine pleurodire Schildkroete aus dem Keuper. Jahreshefte der Gesellschaft für Naturkunde in Württemberg 69:13–90.

Fuente, M. S. de la and M. Iturralde-Vinent. 2001. A new pleurodiran turtle from the Jagua Formation (Oxfordian) of Western Cuba. Journal of Paleontology 75:860–869.

Fuente, M. S. de la, F. de Lapparent de Broin, and T. Manera de Bianco. 2001. The oldest and first nearly complete skeleton of a chelid, of the *Hydromedusa* sub-group (Chelidae, Pleurodira), from the Upper Cretaceous of Patagonia. Bulletin de la Société géologique de France 172:237–244.

Fujita, M. K., T. N. Engstrom, D. E. Starkey, and H. B. Shaffer. 2004. Turtle phylogeny: Insights from a novel nuclear intron. Molecular Phylogenetics and Evolution 31:1031–1040.

Gaffney, E. S. 1972a. An illustrated glossary of turtle skull nomenclature. American Museum Novitates 2486:1–33.

——1972b. The systematics of the North American family Baenidae (Reptilia, Cryptodira). Bulletin of the American Museum of Natural History 147:243–319.

——1975a. A phylogeny and classification of the higher categories of turtles. Bulletin of the American Museum of Natural History 155: 389–436.

——1975b. Phylogeny of the chelydrid turtles: a study of shared derived characters in the skull. Fieldiana Geology 33:157–178.

——1975c. *Solnhofia parsonsi* a new cryptodiran turtle from the Late Jurassic of Europe. American Museum Novitates 2576:1–25.

——1975d. A taxonomic revision of the Jurassic turtles *Portlandemys* and *Plesiochelys.* American Museum Novitates 2574:1–19.

——1976. Cranial morphology of the European Jurassic turtles *Portlandemys* and *Plesiochelys.* Bulletin of the American Museum of Natural History 157:488–543.

——1977. The side-necked turtle Family Chelidae: a theory of relationships using shared derived characters. American Museum Novitates 2620:1–28.

——1979a. Comparative cranial morphology of Recent and fossil turtles. Bulletin of the American Museum of Natural History 164: 65–376.

——1979b. The Jurassic turtles of North America. Bulletin of the American Museum of Natural History 162:91–135.

——1983. The cranial morphology of the extinct horned turtle, *Meiolania platyceps,* from the Pleistocene of Lord Howe Island. Bulletin of the American Museum of Natural History 175:361–479.

——1984. Historical analysis of theories of chelonian relationship. Systematic Zoology 33: 283–301.

——1985. The cervical and caudal vertebrae of the cryptodiran turtle, *Meiolania platyceps,* from the Pleistocene of Lord Howe Island, Australia. American Museum Novitates 2805:1–29.

——1986. Triassic and Early Jurassic turtles. In: K. Padian, ed. The Beginning of the Age of Dinosaurs. New York: Cambridge University Press. pp. 183–187.

——1990. The comparative osteology of the Triassic turtle *Proganochelys.* Bulletin of the American Museum of Natural History 194:1–263.

——1996. The postcranial morphology of *Meiolania platyceps* and a review of the Meiolaniidae. Bulletin of the American Museum of Natural History 229:1–166.

Gaffney, E. S., J. H. Hutchison, F. A. Jenkins, and L. J. Meeker. 1987. Modern turtle origins: the oldest known cryptodire. Science 237:289–291.

Gaffney, E. S. and J. W. Kitching. 1994. The most ancient African turtle. Nature 369:55 –58.

——1995. The morphology and relationships of *Australochelys,* an early Jurassic turtle from South Africa. American Museum Novitates 3130:1–29.

Gaffney, E. S. and P. A. Meylan. 1988. A phylogeny of turtles. In: M. J. Benton, ed. The Phylogeny and Classification of the Tetrapods. Volume 1, Amphibians, Reptiles, Birds. Oxford: Clarendon Press. pp. 157–219.

——1992. The Transylvanian turtle, *Kallokibotion,* a primitive cryptodire of Cretaceous age. American Museum Novitates 3040:1–37.

Gaffney, E. S., P. A. Meylan, and A. R. Wyss. 1991. A computer assisted analysis of the relationships of the higher categories of turtles. Cladistics 7:313–335.

Gaffney, E. S. and X. Ye. 1992. *Dracochelys,* a new cryptodiran turtle from the Early Cretaceous of China. American Museum Novitates 3048:1–13.

Gauthier, J., A. G. Kluge, and T. Rowe. 1988. Amniote phylogeny and the importance of fossils. Cladistics 4:105–209.

Gervais, P. 1872. Osteologie du *Sphargis* Luth. Nouvelles archives du Muséum d'histoire naturelle 8:199–228.

Gilmore, C. W. 1916. Vertebrate faunas of the Ojo Alamo, Kirtland, and Fruitland Formations. United States Geological Survey Professional Paper 98:279–302.

——1919. Reptilian faunas of the Torrejon, Puerco, and underlying Upper Cretaceous Formations of San Juan County, New Mexico. United States Geological Survey Professional Papers 119:1–68.

——1935. On the Reptilia of the Kirtland Formation of New Mexico with descriptions of new species of fossil turtles. Proceedings of the United States National Museum 83:159–188.

Grandidier, A. 1867. Liste des reptiles nouveaux découverts, en 1866, sur la côte sud-ouest de Madagascar. Revue et Magasin de Zoologie Pure et Appliquée 19:232–233.

Gray, J. E. 1831a. Characters of a new genus of freshwater tortoise from China. Proceedings of the Zoological Society of London 1831: 106–107.

——1831b. Synopsis reptilium, Part I. Cataphracta. Tortoises, Crocodiles, Enaliosauria. London: Treuttel, Wurtz and Co. 85 pp.

——1841. A catalogue of the species of reptiles and amphibia hitherto described as inhabiting Australia, with a description of some new species from western Australia. Appendix E. In: G. Grey, ed. Journals of two expeditions of discovery in north-western and western Australia, during the years 1837, 38, and 39, under the authority of her majesty's government, Volume 2. London: Boone. pp. 422–449.

——1847. Description of a new genus of Emydae. Proceedings of the Zoological Society of London 15:55–56.

——1863. On the species of Chelymys from Australia, with the description of a new species. Annals and Magazine of Natural History 3:98–99.

——1867. Description of a new Australian tortoise (*Elseya latisternum*). Annals and Magazine of Natural History 3:43–45.

Hay, O. P. 1908. The fossil turtles of North America. Carnegie Institute of Washington, Publication 75:1–568.

——1911. Descriptions of eight new species of fossil turtles from west of the one hundredth meridian. Proceedings of the United States National Museum 38:307–326.

Hirayama, R. 1985. Cladistic analysis of batagurine turtle (Batagurinae: Emydidae: Testudinidea); a preliminary result. Studia Palaeocheloniologica 1:141–157.

——1998. Oldest known sea turtle. Nature 392: 705–708.

Hirayama, R., D. B. Brinkman, and I. G. Danilov. 2000. Distribution and biogeography of non-marine Cretaceous turtles. Russian Journal of Herpetology 7:181–198.

Hirayama, R. and T. Chitoku. 1996. Family Dermochelyidae (Superfamily Chelonioidea) from the Upper Cretaceous of North Japan. Transactions and Proceedings of the Palaeontological Society of Japan 184: 597–622.

Hirayama, R. and Y. Hikida. 1998. *Mesodermochelys* (Testudines; Chelonioidea; Dermochelyidae) from the Late Cretaceous of Nakagawa-cho, Hokkaido, North Japan. Bulletin of the Nakagawa Museum of Natural History 1:69–76.

Hirayama, R., S. Kazuhiko, C. Tsutomu, K. Gentaro, and K. Norio. 2001. *Anomalochelys angulata,* an unusual land turtle of family Nanhsiungchelyidae (superfamily Trionychoidea; order Testudines) from the Upper Cretaceous of Hokkaido, North Japan. Russian Journal of Herpetology 8:127–138.

Hutchison, J. H. and D. M. Bramble. 1981. Homology of the plastral scales of the Kinosternidae and related turtles. Herpetologica 37:73–85.

Jamniczky, H. A. 2003. The potential utility of cranial arterial canals and foramina in the resolution of problems in turtle systematics. Palaeontology Association Newsletter 53:69 –71.

Joyce, W. G. 2000. The first complete skeleton of *Solnhofia parsonsi* (Cryptodira, Eurysternidae) from the Upper Jurassic of Germany and its taxonomic implications. Journal of Paleontology 74:684–700.

——2003. A new Late Jurassic turtle specimen and the taxonomy of *Palaeomedusa testa* and *Eurysternum wagleri.* PaleoBios 23:1–8.

Joyce, W. G. and C. J. Bell. 2004. A review of the comparative morphology of extant testudinoid turtles (Reptilia: Testudines). Asiatic Herpetological Research 10:53–109.

Joyce, W. G. and J. A. Gauthier. 2004. Paleoecology of Triassic stem turtles sheds new light on turtle origins. Proceedings of the Royal Society of London, B 271:1–5.

Joyce, W. G., F. A. Jenkins, Jr., and T. Rowe. 2006. The presence of cleithra in the basal turtle *Kayentachelys aprix.* Fossil Turtle Research 1:93–103 (Russian Journal of Herpetology 13, Suppl).

Joyce, W. G., and H.-V. Karl. 2006. The world's oldest fossil turtle: fact versus fiction. Fossil Turtle Research 1:104–111 (Russian Journal of Herpetology 13, Suppl).

Joyce, W. G. and M. A. Norell. 2005. *Zangerlia ukhaachelys,* n. sp., a nanhsiungchelyid turtle from the Late Cretaceous of Ukhaa Tolgod, Mongolia. American Museum Novitates 3481:1–19.

Joyce, W. G., J. F. Parham, and J. A. Gauthier. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. Journal of Paleontology 78:989 –1013.

Khosatzky, L. I. 1997. Big turtle of the late Cretaceous of Mongolia. Russian Journal of Herpetology 4:148–154.

Kunkel, B. W. 1912. The development of the skull of *Emys lutaria.* Journal of Morphology 23:693–780.

Lacépède, B. G. E. 1788. Histoire naturelle des quadrupèdes ovipares et serpens. Paris: Imprimerie du Roi. 41 pp.

Lambe, L. M. 1902. New genera and species from the Belly River Series (Mid-Cretaceous). Contributions to Canadian Palaeontology 3: 23–81.

——1906. Description of new species of *Testudo* and *Baena* with remarks on some Cretaceous forms. Ottawa Naturalist 19:187–196.

Langston, W. 1956. The shell of *Basilemys varialosa* (Cope). Bulletin of the National Museum of Canada 142:155–165.

Lapparent de Broin, F. de, B. Lange-Badré, and M. Dutrieux. 1996. Nouvelles découvertes de tortues dans le Jurassique supérieur du Lot (France) et examen du taxon Plesiochelyidae. Revue de Paléobiologie 15:533–570.

Lapparent de Broin, F. de and X. Murelaga. 1999. Turtles from the Upper Cretaceous of Lano (Iberian Peninsula). Estudios del Museo de Ciencias Naturales de Alava 14:135–211.

Latreille, P. A. 1801. In: C. N. S. Sonnini de Manoncourt and P. A. Latreille. Histoire naturelle des reptiles, avec figures déssinnées d'après nature, Volume 1. Paris: Détérville. 280 pp.

LeConte, J. 1830. Description of the species of North American tortoises. Annals of the Lyceum of Natural History of New York 3: 91–131.

Leidy, J. 1865. Memoir on the extinct reptiles of the Cretaceous formations of the United States. Smithsonian Contributions to Knowledge 14(6):1–135.

——1869. Notice of some extinct vertebrates from Wyoming and Dakota. Proceedings of the Academy of Natural Sciences of Philadelphia 1869:63–67.

——1870. [Description of *Emys jeanesi* n. sp., *Emys haydeni* n. sp., *Baena arenosa* n. g. n. sp., and *Saniwa ensidens* n. g. n. sp.]. Proceedings of the Academy of Natural Sciences of Philadelphia 1870:123–124.

——1871. Remarks on fossil vertebrates from Wyoming. American Journal of Science 2: 372–373.

LeSueur, C. A. 1827. Note sur duex espêces de tortues du genre Trionyx Grf. St. H. Mémoires du Muséum d'Histoire Naturelle 15: 257–268.

Linnaeus, C. 1758. Systema naturæ. Volume 1. 10th ed. Holmia: Laurentius Salvius. 824 pp.

——1766. Systema naturae. Volume 1. 12th ed. Holmia: Laurentius Salvius. 532 pp.

Maddison, W. P. and D. R. Maddison. 1999. MacClade. Version 3.08. Sunderland, MA: Sinauer Associates.

Marsh, O. C. 1890. Notice of some extinct Testudinata. American Journal of Science 40:177 –179.

McDowell, S. B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proceedings of the Zoological Society of London 143:239 –279.

Meylan, P. A. 1987. The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). Bulletin of the American Museum of Natural History 186:1–101.

——1988. *Peltochelys* Dollo and the relationships among the genera of the Carettochelyidae (Testudines, Reptilia). Herpetologica 44:440 –450.

Meylan, P. A. and E. S. Gaffney. 1989. The skeletal morphology of the Cretaceous cryptodiran turtle, Adocus, and the relationships of the Trionychoidea. American Museum Novitates 2941:1–60.

Meylan, P. A., R. T. J. Moody, C. A. Walker, and S. D. Chapman. 2000. *Sandownia harrisi,* a highly derived trionychoid turtle (Testudines: Cryptodira) from the Early Cretaceous of the Isle of Wight, England. Journal of Vertebrate Paleontology 20:522 –532.

Milner, A. R. 2004. The turtles of the Purbeck Limestone Group of Dorset, southern England. Palaeontology 47:1441–1467.

Mlynarski, M. 1976. Handbuch der Paläoherpetologie. Part 7, Testudines. Stuttgart: Gustav Fischer Verlag. 130 pp.

Nicholls, E. L. 1988. New material of *Toxochelys latiremis* Cope, and a revision of the genus *Toxochelys* (Testudines, Chelonioidea). Journal of Vertebrate Paleontology 8:181–187.

Nopcsa, F. B. 1923a. Die Familien der Reptilien. Fortschritte der Geologie und Palaeontologie 2:1–210.

——1923b. *Kallokibotion,* a primitive amphichelydean tortoise from the uppermost Cretaceous of Hungary. Palaeontologia Hungarica 1:1–34.

Ogushi, K. 1911. Anatomische Studien an der japanischen dreikralligen Lippenschildkroete (*Trionyx japanicus*). Morphologisches Jahrbuch 43:1–106.

Owen, R. 1842. Report on British fossil reptiles. Part II. Report of the British Association for the Advancement of Science 11:60–204.

——1850. Monograph on the fossil reptilia of the Oxford Clay. 1. Chelonia, Supplement 1. Palaeontographical Society Monographs 5: 1–4.

——1886. Description of fossil remains of two species of a *Megalania* genus (*Meiolania,* Ow.), from Lord Howe's Island. Proceedings of the Royal Society of London 40:315–316.

Parham, J. F. and J. H. Hutchison. 2003. A new eucryptodiran turtle from the Late Cretaceous of North America (Dinosaur Provincial Park, Alberta, Canada). Journal of Vertebrate Paleontology 23:783–798.

Parsons, T. S. and E. E. Williams. 1961. Two Jurassic turtle skulls: a morphological study. Bulletin of the Museum of Comparative Zoology at Harvard College 125:43–107.

Patterson, C. 1982. Cladistics and classification. New Scientist 94:303–306.

——1988. Homology in classical and molecular biology. Molecular Biology and Evolution 5:603–625.

Peng, J.-H. and D. B. Brinkman. 1993. New material of *Xinjiangchelys* (Reptilia: Testudines) from the Late Jurassic Qigu Formation (Shishugou Group) of the Pingfengshan locality, Junggar Basin, Xinjiang. Canadian Journal of Earth Sciences 30:2013–2026.

Ramsay, E. P. 1887. On a new genus and species of fresh-water tortoise from the Fly River, New Guinea. Proceedings of the Linnean Society of New South Wales 11:158–162.

Rieppel, O. 1980. The skull of the Upper Jurassic cryptodire turtle *Thalassemys,* with a reconsideration of the chelonian braincase. Palaeontographica, Abt. A 171:105–140.

——1993. Studies on skeleton formation in reptiles: Patterns of ossification in the skeleton of *Chelydra serpentina* (Reptilia, Testudines). Journal of Zoology 231:487–509.

Riggs, E. S. 1906. The carapace and plastron of *Basilemys sinuosus,* a new fossil tortoise from the Laramie Beds of Montana. Field Columbian Museum, Geological Series 2:249–256.

Romer, A. 1956. Osteology of Reptiles. Chicago: University of Chicago Press. 772 pp.

Rougier, G. W., M. S. de la Fuente, and A. B. Arcucci. 1995. Late Triassic turtles from South America. Science 268:855–858.

Rütimeyer, L. 1873. Die fossilen Schildkröten von Solothurn. Neue Denkschrift der allgemeinen schweizerischen naturforschenden Gesellschaft 25:1–185.

Schneider, J. G. 1783. Allgemeine Naturgeschichte der Schildkröten, nebst einem systematischen Verzeichnisse der einzelnen Arten und zwey Kupfern. Leipzig: Johan Gotfried Müllerschen Buchhandlung. 365 pp.

Schoepff, J. D. 1793. Historia testudinum. Erlanga: Ioannes Iacobus Palm. 136 pp.

Schumacher, G. H. 1954. Beitrage zur Kiefermuskulatur der Schildkröten. Wissenschaftliche Zeitschrift der Universität Greifswald 3:149–210.

Schweigger, A. F. 1812. Prodromus monographiae cheloniorum. Königsberger Archiv für Naturwissenschaft und Mathematik 1: 271–368.

Shaffer, H. B., P. Meylan, and M. L. McKnight. 1997. Tests of turtle phylogeny: molecular, morphological, and paleontological approaches. Systematic Biology 46: 235–268.

Shah, R. V. 1963. The neck musculature of a cryptodire (*Deirochelys*) and a pleurodire (*Chelodina*) compared. Bulletin of the Museum of Comparative Zoology 129:345–368.

Sheil, C. A. 2003. Osteology and skeletal development of *Apalone spinifera* (Reptilia: Testudines: Trionychidae). Journal of Morphology 256:42–78.

Sorenson, M.D. 1999. TreeRot. Version 2. Boston, MA: Boston University.

Sukhanov, V. B. 2000. Mesozoic turtles of middle and central Asia. In: M. J. Benton, M. A. Shishkin, D. M. Unwin, and E. N. Kurochkin, eds. The age of dinosaurs in Russia and Mongolia. Cambridge: Cambridge University Press. pp. 309–367.

——2006. An archaic turtle, *Heckerochelys romani* gen. et sp. nov., from the Middle Jurassic of Moscow Region, Russia. Fossil Turtle Research 1:112–118 (Russian Journal of Herpetology 13, Suppl).

Sukhanov, V. B. and P. Narmandakh. 1974. New Early Cretaceous turtle from continental deposits of the Northern Gobi. Transactions of the Joint Soviet-Mongolian Paleontological Expedition 1:192–220.

Swofford, D. L. 2002. PAUP. Version 4.0b10. Sunderland, MA: Sinauer Associates.

Troost, G. 1835. In: R. Harlan. Medical and Physical Researches or Original Memoires in Medicine, Surgery, Physiology, Geology, Zoology, and Comparative Anatomy. Philadelphia: Lydia R. Bailey. p. 653.

Vandellii, D. 1761. Epistola de holothurio, et testudine coriacea ad celeberrinum Carolum Linneaum equitem. Padua: Conzetti. 12 pp.

Wagner, A. 1853. Beschreibung einer fossilen Schildkroete und etlicher anderer Reptilienueberreste aus den lithographischen Schiefern und dem Gruensandstein von Regensburg. Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-physikalische Klasse 7:239–264.

Walther, W. G. 1922. Die Neu-Guinea-Schildkröte *Carettochelys insculpta* Ramsay. Nova Guinea (Zoology) 13:607–704.

Werner, F. 1901. Über Reptilien und Batrachier aus Ecuador und Neu-Guinea. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien. 51:593–603.

Whetstone, K. N. 1978. A new genus of cryptodiran turtles (Testudinoidea, Chelydridae) from the Upper Cretaceous Hell Creek Formation on Montana. University of Kansas Science Bulletin 51:539–563.

White, R. S. 1972. A recently collected specimen of *Adocus* (Testudines; Dermatemydidae) from New Jersey. Notulae Naturae 447:1–10.

Wiegmann, A. F. A. 1828. Beyträge zur Amphibienkunde. Isis von Oken. Jena 21:364–383.

Wieland, G. R. 1902. Notes on the Cretaceous turtles, *Toxochelys* and *Archelon,* with a classification of the marine Testudinata. American Journal of Science 14:95–108.

Wiens, J. J. and R. E. Etheridge. 2003. Phylogenetic relationships of hoplocercid lizards: Coding and combining meristic, morphometric and polymorphic data using step matrices. Herpetologica 59:375–398.

Williams, E. E. 1950. Variation and selection in the cervical articulation of living turtles. Bulletin of the American Museum of Natural History 94:509–561.

Wiman, C. 1930. Fossile Schildkroeten aus China. Palaeontologia Sinica, Ser. C 3:5–53.

Young, C.-C. and M.-C. Chow. 1953. New fossil reptiles from Szechuan China. Acta Scientia Sinica 2:216–243.

Zangerl, R. 1953. The vertebrate fauna of the Selma Formation of Alabama. Part IV. The turtles of the family Toxochelyidae. Fieldiana Geology Memoirs 3:137–277.

——1969. The turtle shell. In: C. Gans, A. d'A. Bellairs, and T. S. Parsons, eds. Biology of the Reptilia. Volume 1, Morphology A. New York: Academic Press. pp. 311–339

Zug, G. R. 1971. Buoyancy, locomotion, morphology of the pelvic girdle and hindlimb, and systematics of cryptodiran turtles. Miscellaneous Publications Museum of Zoology, University of Michigan 142:1–98.