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The Phylogeny of Cheloniid Sea Turtles Revisited

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ABSTRACT. – **Thirteen chelonioid taxa are examined cladistically using 24 cranial and post-cranial osteological characters. Shell characters are found to be useful in elucidating phylogenetic relationships within the Cheloniidae. The results of this study support a monophyletic Osteopyginae. The mutual affinities of the Eocene stem cheloniines are not resolved. *Syllomus* is the sister taxon to all the Cheloniinae (not just to *Natator*) and *Eretmochelys* is the sister taxon to the Carettini.**

KEY WORDS. – **Reptilia; Testudines; Cheloniidae; *Toxochelys*; *Ctenochelys*; *Osteopygis*; *Erquelinnesia*; *Argillochelys*; *Eochelone*; *Puppigerus*; *Syllomus*; *Natator*; *Chelonia*; *Eretmochelys*; *Caretta*; *Lepidochelys*; systematics; paleontology; phylogeny**

Cryptodiran turtles have invaded the marine realm twice: once in the Jurassic and once in the early Cretaceous (Gaffney and Meylan, 1988; Hirayama, 1994). By Campanian time, the Cretaceous radiation (Chelonioidea) had already diversified into three major clades: Cheloniidae, Dermochelyidae, and Protostegidae. The latter two families form the monophyletic Dermochelyoidea (Gaffney and Meylan, 1988), the sister-taxon to Cheloniidae. Pelagic adaptations such as the loss of moveable articulations in the manus to form a paddle, straightening of the humerus, and reduction of the plastral bones were all apparently independently acquired in dermochelyids, protostegids, and cheloniids (Hirayama, 1994). Of the three clades, Cheloniidae seems to have retained the primitive condition the longest; even Recent cheloniids (*Caretta*, *Chelonia*, *Eretmochelys*, *Lepidochelys*, *Natator*) have not developed the level of pelagic specialization (e.g., broad flat humeri, extremely reduced shells, greatly elongated forelimbs) exhibited by dermochelyoids (epitomized in Recent *Dermochelys*).

Classification within the Cheloniidae has traditionally been based on the abundant shell material (Zangerl, 1953, 1958). While the appendicular skeleton was given some consideration, cranial material was essentially ignored. More recently, descriptions of new and neglected cranial material (Moody, 1974; Gaffney, 1979; Foster, 1980; Fastovsky, 1985) combined with cladistic methodology have resulted in hypotheses based almost entirely on cranial characters, particularly from the basicranium (Fastovsky, 1985; Gaffney and Meylan, 1988). Hirayama (1994) was the first to attempt to treat cranial and post-cranial characters equally.

This study pools the data of previous workers who have studied the evolutionary relationships of cheloniids and expands them with additional shell characters. Combination of all the available data should produce the most defendable hypothesis of cheloniid phylogeny to date.

SYSTEMATICS

Cheloniidae. — This is a well-known family of marine turtles comprised of five living genera (*Natator*, *Chelonia*, *Eretmochelys*, *Caretta*, *Lepidochelys*) and numerous extinct taxa (see Pritchard and Trebbau, 1984). Excluding the problematical extinct genera *Toxochelys* and *Ctenochelys* (whose affinities are discussed below), the Cheloniidae can be subdivided into three, not necessarily monophyletic, groups: 1) Osteopyginae (Zangerl, 1953); 2) Eocene stem cheloniines ("Eochelyinae" of Moody, 1968); and 3) Cheloniinae (defined here as the crown-group of the Cheloniidae, i.e., those taxa that share the most recent common ancestor of the extant cheloniids; see de Queiroz and Gauthier, 1990).

Toxochelys and *Ctenochelys* (Late Cretaceous) are among the earliest chelonioids represented by ample cranial and post-cranial material. They were considered to be members of the Toxochelyidae (Zangerl, 1953) until Fastovsky (1985) demonstrated that *Ctenochelys* (referred to as FMNH PR444; Gaffney and Meylan [1988] have since referred this specimen to *Ctenochelys*) is more closely related to Recent cheloniids than to *Toxochelys*. As a result, the family Toxochelyidae (*sensu* Zangerl, 1953) was rendered paraphyletic.

These findings have been incorporated into two hypotheses. Gaffney and Meylan (1988) suggested that *Ctenochelys* should be considered a sister taxon to all chelonioids except *Toxochelys* (Fig. 1a). Hirayama (1994), however, argued that *Toxochelys* and *Ctenochelys* should be considered as members of an expanded Cheloniidae (Fig. 1b). The latter hypothesis is based on an analysis comprised of more taxa and more characters and is adopted here. However, we have included neither Dermochelyidae nor Protostegidae in our data set and therefore cannot comment further on this problem.

We use a stem-based definition (de Queiroz and Gauthier, 1990) of Cheloniidae as those turtles that share a more recent common ancestor with extant marine turtles (exclusive of *Dermochelys*) than with *Dermochelys* or *Protostega*. This definition agrees with Hirayama (1994) and differs only slightly from Gaffney and Meylan (1988) who recognized an Osteopygidae (Osteopyginae here and in Zangerl, 1953, 1971, Fastovsky, 1985). The three major groupings of Cheloniidae (Osteopyginae, stem cheloniines, Cheloniinae) are discussed below in detail.

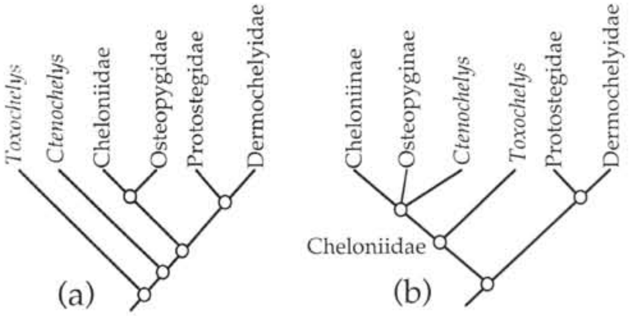

Figure 1. Hypotheses of the phylogenetic relationships of sea turtles (Chelonioidea) showing alternative relationships of *Toxochelys* and *Ctenochelys* to Cheloniidae: **(a)** Gaffney and Meylan, 1988; **(b)** Hirayama, 1994.

Osteopyginae. — This subfamily is composed of two taxa, *Osteopygis* (Late Cretaceous) and *Erquelinnesia* (Early Eocene), both known from cranial and post-cranial material. The skulls of osteopygines are easily identifiable due to their extremely long secondary palates and broad, flat, dentaries. Like *Toxochelys* and *Ctenochelys*, osteopygines were once considered to be members of the Toxochelyidae (Zangerl, 1953, 1971). This assignment was based on the presence of wide plastra and curved humeri, characters that are now considered to be primitive for cheloniids (Gaffney and Meylan, 1988). Hirayama (1994) inferred that, like *Toxochelys* and *Ctenochelys*, osteopygines retain movable articulations in the first and second digits (suggesting that they lack the pelagic adaptation of a well-developed paddle); however, osteopygine specimens which retain these elements are not known to us.

Fastovsky (1985) used cranial characters, such as a basioccipital depression and the presence of a secondary palate, to ally the osteopygines with Recent cheloniids (Cheloniinae). Because the taxa included both have long palates and the coinciding extensive symphyses, the monophyly of osteopygines has never been challenged. However, the dentaries of turtles are notoriously plastic (Gaffney and Meylan, 1988) and the shells of the two taxa are quite different; *Osteopygis* possesses an extremely ankylosed shell with no post-nuchal or costo-peripheral fontanelles whereas *Erquelinnesia* has both (Fig. 2). For these reasons the monophyly of the Osteopyginae requires testing.

Eocene Stem Cheloniines. — The subfamily "Eochelyinae" was established by Moody (1968) to include three taxa from the Eocene of Europe (*Argillochelys*, *Eochelone*, *Puppigerus*), each with character distributions intermediate between the osteopygines and cheloniines. Eocene stem cheloniines possess some of the presumed pelagic adaptations of the Cheloniinae (the loss of movable articulations in the manus, straight humeri, elongate and/or reduced plastra), but an unambiguous character has never been proffered which unites even two of these taxa into a monophyletic group (Gaffney and Meylan, 1988; Hirayama, 1994). Even Moody's (1974) emended diagnosis of the subfamily did not include a single character that could be considered uniquely "eochelyine."

Perhaps the most interesting attribute of these stem cheloniines is the disparate palatal and dentary morphologies that they exhibit. Prior to the appearance of these taxa in the fossil record, all well-known cheloniids (*Toxochelys*, *Ctenochelys*, and the osteopygines) exhibit flat palates and dentaries of varying lengths. Each of the Eocene stem cheloniines possess a different morphology. The symphysis of *Puppigerus* does not extend beyond the foramina dentofaciale majus, as it does in osteopygines (Zangerl, 1971), but *Puppigerus* does have a secondary palate equal to the extent of that in osteopygines. *Eochelone*, however, lacks a secondary palate (Casier, 1968), and this has been interpreted as a reversal (Gaffney, 1979; Hirayama, 1994). Finally, *Argillochelys* retains the secondary palate, but with a groove to receive a markedly ridged dentary (the ridge occurring along the symphysis). A ridged dentary is not restricted to *Argillochelys*; some lower jaws from the Late Cretaceous of New Jersey (AMNH 14205), not referable to any known taxon, also have an elevated symphysis. Furthermore, some cheloniine taxa have a symphyseal ridge on the dentary.

Cheloniinae. — This subfamily is defined here as those turtles that share the most recent common ancestor of the living cheloniids. *Syllomus*, a Miocene cheloniid with pseudodont dentition, has recently been assigned to this group by Hirayama (1994). He hypothesized that *Syllomus* and *Natator* form a monophyletic sister group to the rest of the cheloniines.

Some morphological analyses have divided the Cheloniinae into two groups, Chelonini (*Chelonia* and *Eretmochelys*; Zangerl, 1958) and Carettini (*Caretta* and *Lepidochelys*; Gray, 1825; as Carettidae). A monophyletic Chelonini has been based primarily on characters which are now considered to be primitive for cheloniines (e.g., an elevated symphysis, a wide angle formed by the scapular processes, and the number of peripherals and pleural scutes; Zangerl, 1958; Gaffney and Meylan, 1988). However, a

Figure 2. Carapaces of two osteopygine turtles: **(a)** *Osteopygis* (after Zangerl, 1953); **(b)** *Erquelinnesia* (after Zangerl, 1971).

phenetic analysis by Carr (1942) suggested that the Chelonini is paraphyletic, with *Eretmochelys* being more similar to the Carettini than to *Chelonia*. This is supported by serological (Frair, 1977) and molecular evidence (Bowen et al., 1993; Dutton et al., 1996).

The monophyly of the carettines, on the other hand, has long been well established. *Caretta* and *Lepidochelys* share a unique shell morphology characterized by the presence of additional carapace elements. The presence of a dentary without ridges is also a presumed synapomorphy for carettines.

CHARACTER ANALYSIS

Our data set consists of 24 osteological characters (10 cranial, 9 non-shell post-cranial, 5 shell) for 13 taxa. Character polarity is established by reference to *Toxochelys* and *Ctenochelys* as a paraphyletic outgroup for the rest of Cheloniidae. The utility of these taxa for the problem investigated here is corroborated by Fastovsky (1985) and Gaffney and Meylan (1988). Through his inclusion of the problematical *Allopleuron* within the Cheloniidae, Hirayama (1994) rejected *Toxochelys* and *Ctenochelys* as a paraphyletic outgroup of the remaining cheloniids. *Allopleuron* is excluded here. It exhibits presumably cheloniid features such as a secondary palate (which protostegids and dermochelyids lack), but as noted by Hirayama (1994), "it shows a complex combination of presumed primitive and apomorphic characters often shared by the protostegids and dermochelyids." It would be an aberrant form in any of the present clades, and only an outgroup comparison, for all chelonioids, can improve our understanding of its affinities.

Analysis of the data was performed using the branch and ound algorithm of PAUP 3.1.1 (Swofford, 1990). Character descriptions and distributions are listed below, and shown in Table 1.

Cranial

1. Secondary palate involving vomer: (0) absent; (1) present; (2) extensive (ordered). A secondary palate occurs twice within the chelonioids. Once in the Cheloniidae (Fastovsky, 1985) and once in the basal dermochelyoid *Allopleuron* (Hirayama, 1994). *Toxochelys* lacks a secondary palate, while *Ctenochelys* possesses a less extensive shelving than any of the members of the ingroup except for *Eochelone*, which lacks a secondary palate (Casier, 1968). *Osteopygis*, *Erquelinnesia*, and *Puppigerus* have extensive secondary palates.

2. Foramen palatinum posterius: (0) wide; (1) greatly reduced; (2) lost (ordered). The presence of a foramen palatinum posterius is primitive for chelonioids. Foramina are present in *Allopleuron*, an undescribed basal protostegid (Hirayama, 1994), and the basal cheloniids *Toxochelys* and *Ctenochelys*, but are lost in all advanced cheloniids and dermochelyoids.

3. Contact of vomer with premaxillae: (0) broad; (1) reduced. A broad contact of the vomer with the premaxillae is primitive for chelonioids. Fastovsky (1985) noticed that a reduced contact is present in most of the Recent taxa (all except *Natator*). *Caretta* has lost the contact entirely and the maxillae contact each other in palatal view.

4. Foramen caroticum laterale much larger than foramen anterius canalis caroticus interni: (0) absent; (1) present. This character is absent in basal dermochelyoids (*Desmatochelys*, *Allopleuron*, and *Notochelone*; Gaffney, 1975; Hirayama, 1994) and protostegids, but seems to have been derived independently in Cheloniidae and Dermochelyidae. Within the Cheloniidae, the genera *Toxochelys*, *Ctenochelys*, and *Eochelone* lack this character (Gaffney, 1975).

5. Orientation and position of the foramina orbito-nasale: (0) with a vertical component; (1) horizontally trending and in extensive contact with the prefrontals. In most cheloniids the foramina orbito-nasale are vertically trending and bounded by the prefrontals, maxillae, and palatines. *Osteopygis* and *Erquelinnesia* possess a unique morphology; in these taxa the foramina are horizontally trending, are bounded on either side by the prefrontals (Fastovsky, 1985), and contact with the maxillae is lost. This character is probably related to the extension of the palatal region seen in these turtles.

6. Dentary: (0) flat triturating surface; (1) lingual ridges present; (2) ridge along length of symphysis (ordered). The primitive condition for cheloniids is to have a relatively

Table 1. Matrix of character states and taxa. The primitive (plesiomorphic) state (0) for each character state is based on the assumption that *Toxochelys* and *Ctenochelys* are a paraphyletic outgroup to the rest of the Cheloniidae.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Toxochelys	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenochelys	1	1	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Osteopygis	2	2	0	1	1	0	1	0	0	0	0	0	0	1	0	0	?	0	?	0	0	1	0	1
Erquelinnesia	2	2	0	1	1	0	1	0	1	0	0	0	0	1	0	0	?	0	0	0	1	0	0	?
Argillochelys	1	2	0	1	?	2	0	0	1	0	0	0	?	0	1	0	?	1	1	1	?	1	0	1
Eochelone	0	2	0	0	?	0	0	0	1	0	0	?	0	0	1	0	1	1	1	1	1	1	0	1
Puppigerus	2	2	0	1	0	0	0	0	1	0	0	0	0	0	1	1	?	1	1	1	1	1	0	0
Syllomus	1	2	?	1	?	2	0	0	?	?	1	1	1	0	1	1	?	1	1	1	?	1	0	0
Natator	1	2	1	1	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	2	1	0	0
Chelonia	1	2	1	1	0	2	0	1	1	0	1	1	2	0	0	1	1	1	1	1	1	1	0	0
Eretmochelys	1	2	1	1	0	1	0	1	1	1	1	1	2	0	0	1	1	1	1	1	2	1	0	0
Caretta	1	2	1	1	0	0	0	1	1	1	0	1	2	0	0	1	1	1	1	1	2	1	1	0
Lepidochelys	1	2	1	1	0	0	0	1	1	1	0	1	2	0	0	1	1	1	1	1	2	1	1	0

short, flat symphysis. The ingroup has a longer symphysis and many taxa possess an elevated symphysis (symphyseal ridge). When it occurs, the symphyseal ridge occludes with a corresponding groove in the palate. Hirayama (1994) recorded *Natator* and *Eretmochelys* as having a symphyseal ridge that is visible from lateral view, but this is just an extension of the lingual ridge which extends partially onto the dentary. This is different from the symphyses of *Syllomus* and *Chelonia* which are elevated along their entire length. Juvenile specimens of *Lepidochelys* exhibit elevated symphyses, but this condition is lost in adults.

The symphyses of cheloniids vary in lengths from very short in *Toxochelys* to extremely long in *Erquelinnesia*. *Puppigerus* has an extensive symphysis, but the triturating surface does not extend beyond a line connecting the foramina dentofaciale majus as it does in *Osteopygis* and *Erquelinnesia* (Zangerl, 1971). In all cases the extent of the symphysis closely matches the extent of the secondary palate (above) and it would be redundant to code for both.

7. Tomial ridge: (0) pronounced; (1) low. The cutting surface of all cheloniids is pronounced with the exception of *Osteopygis* and *Erquelinnesia* (Fastovsky, 1985). This is consistent with the large, flat jaws of these two genera which are presumably indicative of durophagy.

8. Surangular extending anteriorly onto dentary: (0) absent; (1) present. Hirayama (1994) coded this character as absent for *Natator*, but Zangerl et al. (1988) stated that the surangular actually extends as far forward as the foramen dentofaciale majus.

9. Shape of vomer: (0) constant width; (1) variable width. *Toxochelys* and *Ctenochelys* both possess a vomer which, in palatal view, is of constant width. Therefore, the presence of a vomer of variable width is probably a derived feature within the Cheloniidae.

10. Prefrontal scutes: (0) one pair; (1) two pairs. The preservation of sulci on skulls allow for the coding of this character for some fossil taxa.

Non-Shell Post-Cranial

11. Dorsal process of scapula forming relatively wide angle with acromion: (0) absent; (1) present. The primitive condition is to have a roughly perpendicular angle between the scapular prong and the acromion. Wider angles, upwards of 110°, occur in *Syllomus* and the non-carettine Recent taxa.

12. Metischial processes: (0) pronounced; (1) reduced. In Recent taxa the metischial processes are significantly reduced. This is exemplified by *Chelonia* in which they are almost absent. Of all the Recent taxa, *Natator* has the largest metischial processes, but they are much reduced from the condition seen in *Toxochelys* and *Ctenochelys* (Zangerl, 1953).

13. Femoral trochanters: (0) separated by a fossa; (1) separated by a notch; (2) connected by a ridge (ordered). Primitively the femoral trochanters are separated by a discernible intertrochanteric fossa which extends onto the ventral surface of the bone (Zangerl, 1953). In most Recent taxa the trochanters are connected by a ridge, obliterating the ventral extent of the intertrochanteric fossa. *Natator* and *Syllomus* possess the ridge, but a distinct notch remains between the trochanters. Zangerl et al. (1988) hypothesized that the notch is intermediate between the condition seen in primitive cheloniids and the ridged condition seen in the Recent taxa (and *Syllomus*). This notch is also seen in juvenile specimens of the remaining cheloniines.

Hirayama (1994) stated that in *Syllomus* and *Natator* the trochanter major is much higher than the trochanter minor. This is definitely the case in *Syllomus* (see Weems, 1974), but *Natator* has subequal trochanters and does not appear to be significantly different from the other Recent taxa (see Zangerl et al., 1988).

14. Ventral knob on nuchal for articulation with the eighth cervical vertebra: (0) present; (1) absent. A ventral knob on the nuchal is present in both members of the outgroup. Hirayama (1994) coded it as absent for *Ctenochelys*, but Zangerl (1953) indicated that the character is present in this taxon. Within the Cheloniidae, the only taxa which lack the knob are the osteopygines.

15. Tibial pit for pubotibialis and flexor tibialis internus muscles (Zangerl, 1988; Hirayama, 1994): (0) absent; (1) present. This character is only found in the Eocene stem cheloniines and *Natator*. It occurs as a deep pit on the ventromedial side of the tibia.

16. Centra of the seventh cervical vertebra: (0) procoelous; (1) platycoelous. Williams (1950) recognized the platycoelous condition for modern taxa and Moody (1974) described its occurrence in *Puppigerus*.

17. Articulations of first and second digits: (0) movable; (1) immovable.

18. Straight humerus with V-shaped or triangular lateral process: (0) absent; (1) present. Hirayama (1994) recognized five humeral morphologies among chelonioids, two of which occur in cheloniids. The "toxochelyid" humerus is characterized by a narrow, curved shaft. The "cheloniid" humerus is straighter and the V-shaped or triangular lateral process is more distal. The "cheloniid" morphology is shared by stem cheloniines, Cheloniinae, and the dermochelyoid *Allopleuron*.

19. Coracoid length in relation to humerus: (0) shorter; (1) longer.

Shell

20. Elongated plastron with a broad bridge: (0) absent; (1) present. The outgroup condition is a cruciform plastron that is wider than long. This primitive condition was once used to unite the Toxochelyidae (Zangerl, 1953), now considered paraphyletic.

21. Rib-free peripherals: (0) anterior and posterior to ribs; (1) between seventh and eighth ribs; (2) between sixth and

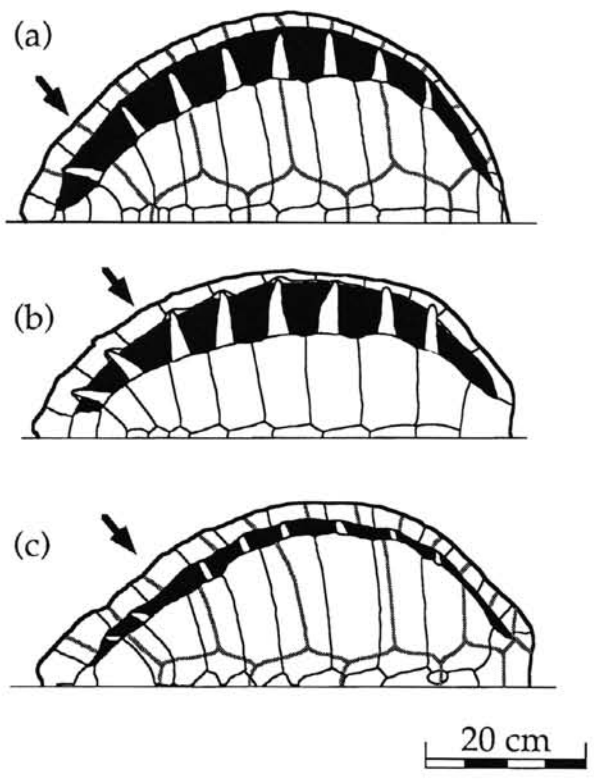

Figure 3. Carapaces of three cheloniine taxa exhibiting points of rib insertion; **(a)** *Chelonia*; **(b)** *Eretmochelys*; **(c)** *Caretta* (after Zangerl, 1958). Arrows indicate the rib-free peripheral bone.

seventh ribs (unordered). With the exception of *Chelonia*, cheloniines possess a unique shell morphology. In *Chelonia* the rib-free peripheral lies between the seventh and eighth costal ribs (Fig. 3a). In *Natator*, *Eretmochelys*, *Caretta*, and *Lepidochelys* there is a rib-free peripheral between the insertion points of the sixth and seventh costal ribs (Figs. 3b, 3c).

22. Post-nuchal fontanelles: (0) present; (1) absent. Post-nuchal fontanelles are present in the outgroup and *Erquelinnesia* (Zangerl, 1971). Adult specimens of the remaining taxa lack these fontanelles, but they are present in juveniles of the Recent taxa.

23. Additional carapace elements: (0) absent; (1) present. The primitive condition for cheloniids is to have eleven peripheral bones and four pleural scutes on each side of the carapace. *Caretta* and *Lepidochelys* have at least twelve peripheral bones and five pleural scutes on each side. *Lepidochelys* also exhibits extensive fragmentation of the neural bones (Zangerl and Turnbull, 1955).

24. Shape of pygal: (0) notched posteriorly; (1) not notched.

RESULTS

Using the 24 characters, no fewer than 12 equally parsimonious cladograms can be produced. The multiple cladograms result from an inability to resolve the phylogenetic relationships of the Eocene stem cheloniines and the positions of *Natator* and *Chelonia*. In Fig. 4, cheloniid phylogenetic relationships are outlined with these problematical affinities left unresolved.

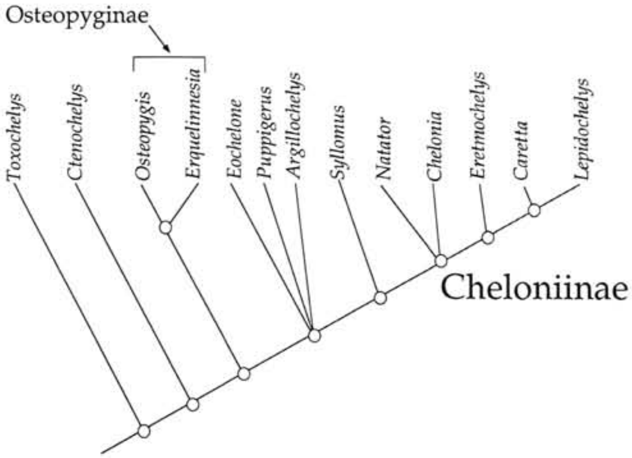

Figure 4. Phylogenetic relationships of 13 cheloniid sea turtle genera based on 24 characters (see Table 1). This cladogram represents a consensus of 12 equally parsimonious hypotheses (49 steps, CI = 0.75).

A monophyletic Osteopyginae is based chiefly on characters of the palate and dentary. Acceptance of this hypothesis requires that, at least within the osteopygine clade, there is the potential for variation in the shell. Despite their putative plasticity, shell characters apparently do not hinder the elucidation of phylogenetic relationships suggested by cranial and non-shell post-cranial characters in cheloniids. Ultimately, our hypotheses on the relationships of Osteopyginae and Cheloniinae to each other and to the Eocene stem cheloniines are in agreement with Hirayama (1994) and Gaffney and Meylan (1988), phylogenies in which skull characters weigh heavily. Some shell characters presented here support cranial and appendicular-based hypotheses of cheloniid phylogeny. For example, the elongation of the plastron unites stem cheloniines and Cheloniinae and the additional carapace elements are a synapomorphy for a monophyletic Carettini.

Hirayama (1994) hypothesized that *Argillochelys* should be considered a sister taxon to the cheloniines based upon the presence of a ridged dentary, but *Puppigerus* and the cheloniines both possess a platycoelous seventh cervical vertebra. Thus, we cannot support an *Argillochelys* – Cheloniinae clade over a *Puppigerus* – Cheloniinae clade. As a result, the Eocene stem cheloniines remain completely unresolved.

There is no evidence to suggest that *Natator* and *Syllomus* form a monophyletic group. Hirayama (1994) allied these taxa on the relative positions of the femoral trochanters, but the condition in *Natator* is not different from the rest of the Cheloniinae. Additionally, our analysis suggests that *Syllomus* can not be considered a cheloniine. Instead, *Syllomus* is the sister taxon to Cheloniinae (Fig. 4).

The hypothesis presented here also differs from those of previous workers using morphology in terms of the phylogenetic interrelationships of the cheloniine taxa. In the past decade, many different views of cheloniine phylogeny have

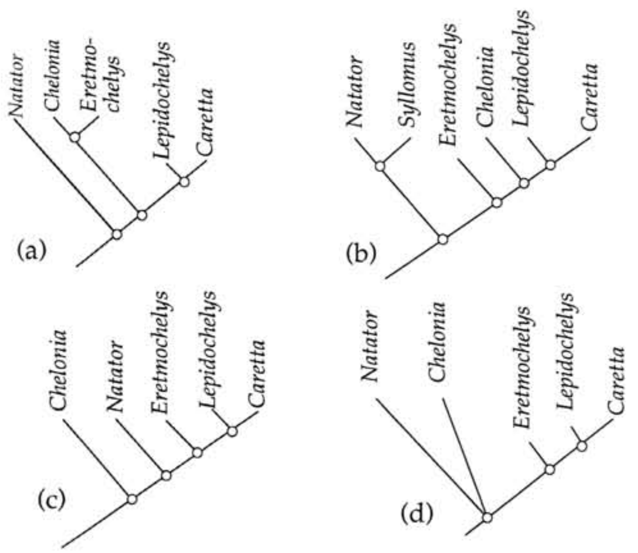

Figure 5. Recent hypotheses of the phylogenetic relationships of Cheloniinae: **(a)** based on morphology (Zangerl et al., 1988); **(b)** based on morphology (Hirayama, 1994); **(c)** based on cytochrome b and ND4-leucine sequences of mtDNA (Dutton et al., 1996); **(d)** based on morphology (present study).

been presented (Figs. 5a–d). As noted above, the monophyly of the Chelonini is based on morphological characters (ridged dentary, wide scapular angle) which are now considered to be primitive for Cheloniinae, but the polarity of these characters cannot be recognized unless *Syllomus* and *Natator* are included in the analysis. Hirayama (1994) was the first to include these taxa and in doing so, questioned the monophyly of Chelonini. He suggested that *Eretmochelys* is the sister-taxon to a *Chelonia* – Carettini clade (Fig. 5b).

Our hypothesis (Fig. 5d) suggests that *Eretmochelys* is the sister taxon to the Carettini, based on but one character, the presence of two prefrontal scutes. It should be noted, however, that an *Eretmochelys* – Carettini clade is supported by non-osteological evidence. Serological (Frair, 1979) and molecular (Bowen et al., 1993; Dutton et al., 1996) studies of living taxa corroborate a paraphyletic Chelonini by indicating that, genetically, *Eretmochelys* is more similar to carettines than to *Chelonia* (Fig. 5c).

Bowen et al. (1993) proposed that *Eretmochelys* be considered a carettine, corroborating the earlier conclusions of Carr (1942) and Pritchard and Trebbau (1984). If we define the Carettini as those taxa that are more closely related to *Caretta* than to *Chelonia* or *Natator*, then *Eretmochelys* should be considered a carettine. Given the unique features shared by *Lepidochelys* and *Caretta* and absent in *Eretmochelys* (low scapular angle, additional carapacial elements, and broad, flat, dentaries), it might be best to define Carettini as those taxa which are more closely related to *Caretta* and *Lepidochelys* than to any of the other Recent genera (a node-based definition; de Queiroz and Gauthier, 1990).

Previous morphological analyses (Zangerl et al., 1988; Hirayama, 1994) have suggested that *Natator* is the sister taxon to the rest of the Cheloniinae (Fig. 5a). Dutton et al. (1996) examined the ND4-leucine tRNA region of mtDNA and combined their data with the cytochrome b data from Bowen et al. (1993). This "total molecular evidence" (Fig. 5c) approach suggested that *Chelonia* is the sister taxon to a clade comprised of *Natator*, *Eretmochelys*, and the Carettini.

In this case, the rib-free peripheral pattern of *Natator*, *Eretmochelys*, and the Carettini would have only evolved once. Because *Natator* retains characters considered primitive for Cheloniinae (an intertrochanteric notch and a tibial pit) the osteological data presented here are unable to resolve which taxon, *Natator* or *Chelonia*, is the sister taxon to the rest of the Cheloniinae. Because our results are equivocal, we did not combine the osteological data with the molecular data. Our results agree with Bowen et al. (1993) and Dutton et al. (1996) in suggesting that neither *Natator* nor *Chelonia* forms a monophyletic group with each other or any other Recent genus unless all cheloniines are included.

CONCLUSIONS

Our data support a monophyletic Osteopyginae, but like Gaffney and Meylan (1988) and Hirayama (1994), challenge the monophyly of the "Eochelyinae." Until further analysis of these taxa can be performed, it is best to continue to refer to the "Eochelyinae" as Eocene stem cheloniines. In our study, the inclusion of shell characters did not hinder, but facilitated, the elucidation of phylogenies established using cranial and non-shell post-cranial characters.

Cheloniines share a most recent common ancestor as early as the Middle Miocene. However, whether as a result of their long generation times (Ehrhart and Witham, 1992; Zug et al., 1997; Parham and Zug, in press) or relative lack of isolation in their marine environment, cheloniines have evolved into an assemblage of turtles characterized by few morphological differences. Consequently, many of the osteological characters used to establish relationships among fossil taxa are too stable to be useful in the estimation of a cheloniine phylogeny. Osteological characters useful in phylogeny reconstruction (e.g., in the establishment of Carettini) generally are derived from the dentary and carapace, due to the plasticity of these regions. A detailed cladistic analysis of non-osteological characters (e.g., scutes, behavior, additional genes) for living taxa may be necessary in order to establish well-defined clades within the Cheloniinae.

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