

A REASSESSMENT OF THE REFERRAL OF SEA TURTLE SKULLS TO THE GENUS *OSTEOPYGIS* (LATE CRETACEOUS, NEW JERSEY, USA)

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ABSTRACT—Specimens referred to *Osteopygis* (Late Cretaceous–Paleocene, North America) represent a chimera, a polyphyletic mixture of taxa. The holotype of *Osteopygis* (AMNH 1485) and more complete referred postcranial specimens resemble non-marine stem cryptodires (“macrobaenids”). Because the skull material historically referred to *Osteopygis* shares synapomorphies with cheloniid sea turtles, all current workers accept *Osteopygis* as a stem-cheloniid sea turtle. Multiple lines of evidence combine to support the hypothesis that sea turtle cranial material is not attributable to *Osteopygis*. These lines of evidence include: phylogenetic hypotheses of character evolution, the tenuous historical attribution of specimens, and the taphonomy of the Hornerstown Formation. The name-bearing *Osteopygis* material and referred postcrania are best considered Eucryptodira incertae sedis (cf. “Macrobaenidae”). The cranial specimens formerly assigned to the Osteopyginae now are restricted to the clade *Euclastes* and those referred to *Osteopygis emarginatus* are here referred to *Euclastes wielandi* (comb. nov.). The ‘decapitation’ of *Osteopygis* reconciles morphological trends within stem cheloniids.

INTRODUCTION

“Regarding the skull of *Osteopygis* we are as yet uncertain. It may prove to be like that of the prior genus *Euclastes*, as was thought possible by Cope or has since been assumed on grounds not known to me. This remains to be carefully proven or disproven” Wieland, 1904a:126.

Osteopygis emarginatus Cope, 1869b (Fig. 1), from the Cretaceous/Paleocene sediments of the Atlantic Coastal Plain of North America, is currently considered a close relative of Cheloniidae Bonaparte, 1832, the living hard-shelled sea turtles (Fig. 2; Fastovsky, 1985; Hirayama, 1994; Parham and Fastovsky, 1997). Postcranial elements referred to *O. emarginatus* previously were used to suggest an affinity with non-marine, stem-cryptodiran turtles (Nopcsa, 1930; Bohlin, 1953).

Here I argue that specimens referred to *Osteopygis emarginatus* are actually a mixture of more than one turtle taxon. I propose that the skulls referred to *Osteopygis* (e.g., Fig. 3A) belong to stem-cheloniid sea turtles (*Euclastes* Cope, 1867; Fig. 3C), but the holotype and other postcrania (Figs. 1, 4A) belong to a stem cryptodire similar to those referred to the provisional grade “Macrobaenidae” Sukhanov, 1964 (recently reviewed in Sukhanov, 2000; Parham and Hutchison, 2003).

Suprageneric taxonomy

Cheloniidae—Parham and Fastovsky (1997) were the first to propose a phylogenetic definition of Cheloniidae. In order to include all fossil taxa considered cheloniids by Hirayama (1994) they chose a stem-based definition: “those turtles that share a more recent common ancestor with extant sea turtles (exclusive of *Dermochelys*) than with *Dermochelys* or *Protostega*” (Parham and Fastovsky, 1997:548). Here, I follow Joyce et al. (2004) and restrict Cheloniidae to the crown. Turtles outside of Cheloniidae that share a more recent common ancestor with Cheloniidae than with dermochelyoids are considered stem Cheloniidae; together these are pancheloniids.

Cryptodira—In this study, I refer to the crown group of cryptodires as Cryptodira Cope, 1868b, based on the arguments presented by Lee (1995, 1997) and Joyce et al. (2004). Turtles outside of Cryptodira that share a more recent common ancestor

with Cryptodira than with pleurodires are considered stem Cryptodira; together these are pancryptodires.

“Macrobaenidae”—The turtles referred to Macrobaenidae represent a grade of freshwater and estuarine stem cryptodires that originated in the Early Cretaceous, but went extinct in the late Paleocene (Parham and Hutchison, 2003). “Macrobaenidae” may not be a monophyletic group. Although they are all very similar, there are no synapomorphies that distinguish them from the hypothesized ancestral condition for Cryptodira. I will refer to the taxa considered cf. “Macrobaenidae” by Parham and Hutchison (2003) as “macrobaenids” (in quotes). I do not wish to promote a gradistic taxonomy, but it is much simpler to continue to refer to *Macrobaena* Tatarinov, 1959, et al. as “macrobaenids” than as ‘the plesiomorphic, potentially polyphyletic grouping of stem cryptodires more closely related to Cryptodira than to *Sinemys* Wiman, 1930.’

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, USA; ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA; ChM, Charleston Museum, Charleston, South Carolina, USA; IGPH, Institut für Geologie und Paläontologie, Salzburg, Austria; I.R.Sc.N.B., Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; MDE t, Musée des Dinosaures d’Espéraza, Aude, France; NJSM, New Jersey State Museum, Trenton, New Jersey, USA; UCMP, University of California Museum of Paleontology, Berkeley, California; USNM, United States National Museum, Washington D.C.; YPM, Yale Peabody Museum, New Haven, Connecticut.

BACKGROUND

The Referral of Sea Turtle Skulls to *Osteopygis*

The report of the first North American dinosaur (*Hadrosaurus*; Leidy, 1858) generated increased scientific interest in fossils from the Late Cretaceous and Tertiary formations of the New Jersey coastal plain. The richest source of fossils is near the K/T boundary in the Hornerstown Formation (Gallagher, 1993). The Hornerstown Formation boasts a vertebrate assemblage that includes turtles (freshwater and marine), mosasaurs, and crocodylians (Gallagher, 1993). In 1868a, Cope briefly announced the

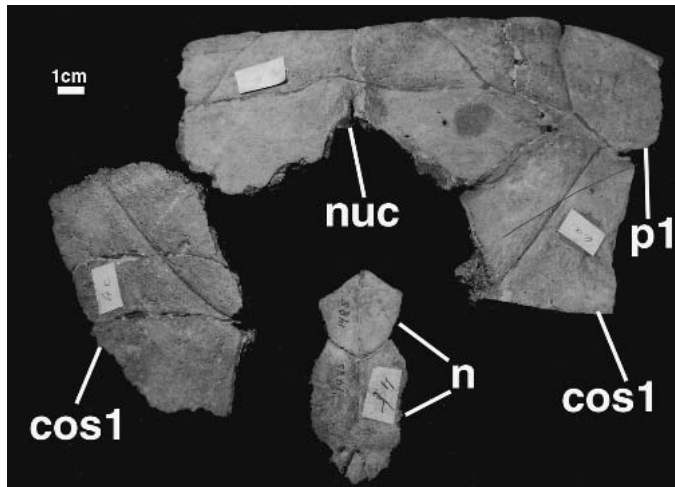


FIGURE 1. The type specimen *Osteopygis emarginatus* (AMNH 1485). **Abbreviations:** *cos*, costal; *n*, neural; *nuc*, nuchal; *p*, peripheral.

discovery of new turtle remains from the Hornerstown Formation and proposed the name *Osteopygis* to accommodate them as well as *Chelone sopita* Leidy, 1865 (nomen vanum, Zangerl, 1953). *Osteopygis* was a nomen nudum until Cope reviewed it in 1869b (Hay, 1908; Zangerl, 1953; Kuhn, 1964). The early taxonomic history of *Osteopygis* includes many now defunct species and is intertwined with that of *Propleura* Cope, 1869a, *Cataleura* Cope, 1870, and *Lytoloma* Cope, 1870. Rather than restating the work of others, especially Hay (1908) and Zangerl (1953), I refer interested readers to those works and focus on the referral of sea turtle skulls to *Osteopygis*.

When Hay (1908) reviewed all known turtle specimens from the New Jersey greensands, he discovered a specimen in the Cope collection that included a broad, crushing dentary (AMNH 2216) associated with a partial shell. The locality and collection information for AMNH 2216 were lost and Hay (1908) doubted that the dentary and shell were part of the same individual. The shell parts of AMNH 2216 are referable to *Osteopygis* (Hay, 1908; Zangerl, 1953).

Zangerl (1953) accepted that the broad dentary and shell material assigned to AMNH 2216 belonged to a single individual. Based on this, Zangerl (1953) referred additional durophagous

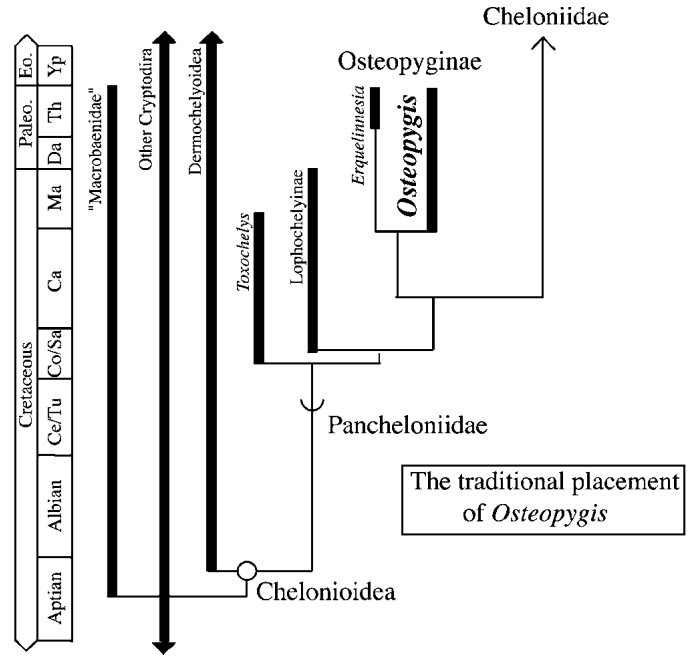


FIGURE 2. A phylogeny of turtles showing the traditional placement of *Osteopygis*. The phylogeny is based on Parham and Fastovsky (1997) and Parham and Hutchison (2003). Taxa are stem based (open semi-circle) or node based (circle). Black bars indicate known temporal range.

skull specimens (several dentaries and a snout, YPM 913a) to *Osteopygis*. Zangerl (1953) considered the snout and jaws of *Osteopygis* to be so morphologically specialized that he erected a new higher taxon, Osteopyginae Zangerl, 1953, for *Osteopygis* and *Euclastes* (= *Rhetechelys*) *platyops* Cope, 1867. Later, Zangerl (1971) referred two Eocene stem cheloniids known only from skulls to Osteopyginae.

Fastovsky (1985) subsequently described a nearly complete skull (NJSM 11872; Fig. 3A) of a durophagous sea turtle from the Hornerstown Formation. He referred it to *Osteopygis* because of its similarity to YPM 913a. Based on the morphology of NJSM 11872, especially the basicranium, Fastovsky (1985) hypothesized that osteopygines shared a more recent common ancestry with the living Cheloniidae than with any Cretaceous stem

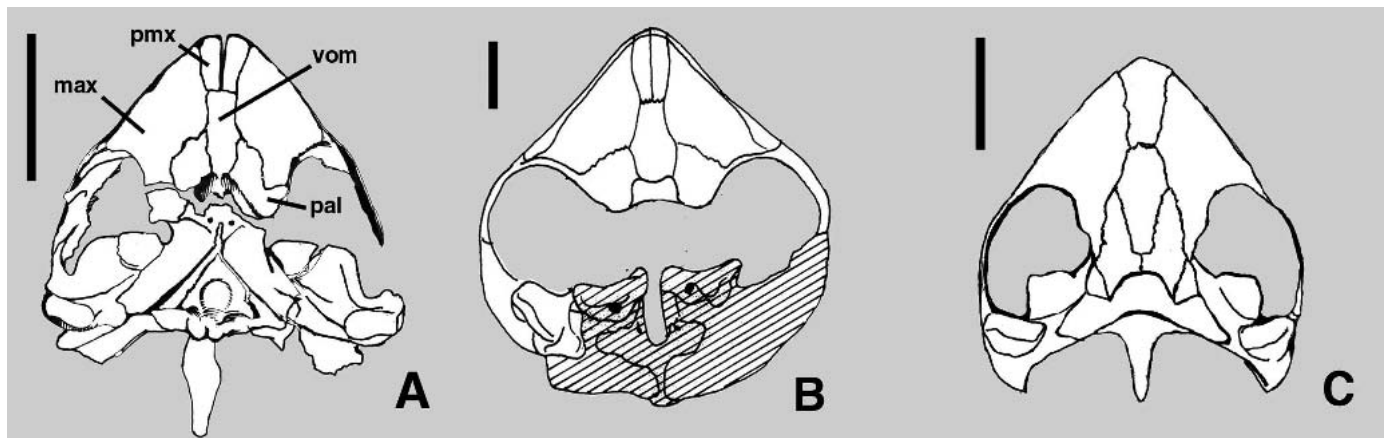


FIGURE 3. Ventral views of skulls of durophagous stem cheloniids. Skull roofing bones are not shown. **A**, NJSM 11872, referred to *Osteopygis emarginatus* (after Fastovsky, 1985). **B**, ANSP 10187, the holotype of *Euclastes platyops* (after de la Fuente and Casadío, 2000). **C**, I.R.Sc.N.B. No. 1563, the type specimen of *Erquelinnestia gosseleti* (after Zangerl, 1971, and de la Fuente and Casadío, 2000). **Abbreviations:** *max*, maxilla; *pal*, palatine; *pmx*, premaxilla; *vom*, vomer. Scale bar equals 5 cm.

cheloniids. In cladistic analyses since that time, the Osteopyginae (or Osteopygidae sensu Gaffney and Meylan, 1988; Moody, 1993; Karl et al., 1998; de Lapparent de Broin, 2001) has occupied a phylogenetic position just crownward of Lophochelyinae Zangerl, 1953 (Hirayama, 1994; Parham and Fastovsky, 1997; Fig. 2).

Most recently, skulls and jaws of early Paleocene stem cheloniids from the Ouled Abdoun Basin of Morocco were referred to *Osteopygis emarginatus* (Hirayama and Tong, 2003). These specimens included the type series of *Osteopygoides priscus* Karl, Tichy, and Ruschak, 1998.

Historic Comparisons of *Osteopygis* Postcrania with Stem Cryptodires

Because the morphology of postcranial elements assigned to *Osteopygis* is plesiomorphic, these elements often were compared with those of stem cryptodires from Europe and Asia. Hay (1908) was impressed that the plastron of *Osteopygis* had a non-sutured, but intimate (gomphotic) contact with the peripherals (Fig. 4A). At that time, the only other turtles known to have this shell morphology were the Thalassemydidae Zittel, 1889, from the Jurassic deposits of Europe. Therefore, Hay considered *Osteopygis* a thalassemydid.

In more than one instance, paleontologists linked *Osteopygis* with non-marine stem cryptodires from Asia. For example, Nopsca (1930) affiliated the Early Cretaceous stem cryptodire *Sinemys* Wiman, 1930, with sea turtles based upon its similarity to *Osteopygis*. Bohlin (1953) tentatively assigned specimens of

small stem cryptodires from the Early Cretaceous of China to *Osteopygis* based on their shell morphology. Nessov and Khozatsky (1978) have since rejected the placement of the Chinese species within *Osteopygis*. Unaware of that study, Foster (1980) independently dismissed Bohlin's assignment to *Osteopygis* by citing the non-diagnostic fragmentary material, the vast difference in size, the non-marine deposits in which they were discovered, and even Bohlin's own uncertainty.

A REASSESSMENT OF *OSTEOPYGIS*

Phylogenetic Considerations

Figure 5 compares the characters of postcranial specimens referred to *Osteopygis* to the synapomorphies of chelonioid sea turtles in a phylogenetic context. A complete reappraisal of the phylogeny of these groups is outside the scope of this work, so this comparison is limited to characters relevant to *Osteopygis* postcrania. My placement of referred *Osteopygis* specimens ultimately relies upon a phylogenetic hypothesis based on other taxa that have more reliably associated crania and postcrania (e.g., Parham and Hutchison, 2003; Lynch and Parham, 2003). Most of the postcranial synapomorphies of stem Cheloniidae would be obscured by the inclusion of *Osteopygis* as a stem cheloniid. Therefore, the synapomorphies of chelonioids are determined minus *Osteopygis*.

Character 1 (Hyoplastral Insertions)—In many stem cryptodires and *Osteopygis*, the anterior prong of the hyoplastron inserts into the second peripheral (Fig. 4a). This character is lost in all known Cryptodira (Parham and Hutchison, 2003).

Character 2 (Plastral Connection to Peripherals Lost)—In all chelonioids the lateral extensions of the plastron do not reach the peripherals. In *Osteopygis* the attachment is intimate (Fig. 4A).

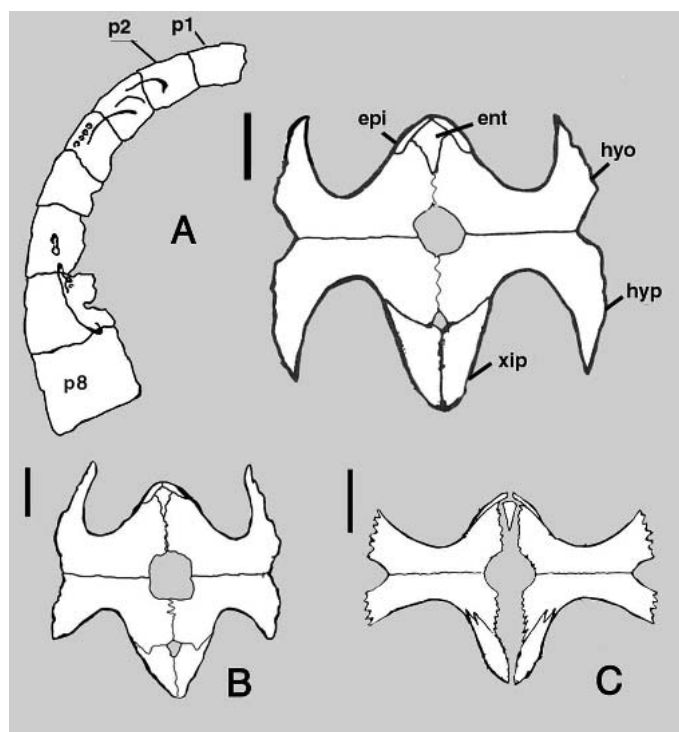


FIGURE 4. **A**, YPM 783, *Osteopygis emarginatus*; left: dorsal view of peripherals (after Hay, 1908). Peripherals two through four and six through eight have pits and notches to receive the lateral edges of the hyoplastron and hypoplastron; right: ventral view of plastron (after Zangerl, 1953). **B**, YPM 16235, cf. '*Clemmys*' *backmani*, ventral view of plastron. **C**, reconstruction of the ventral view of the plastron of *E. gosseleti* based largely on I.R.Sc.N.B. No. 1563, the type specimen of *Erquelinnesia gosseleti* (after Zangerl, 1971). **Abbreviations:** ent, entoplastron; epi, epiplastron; hyo, hyoplastron; hyp, hypoplastron; p, peripheral; xip, xiphoplastron. Scale bar equals 5 cm.

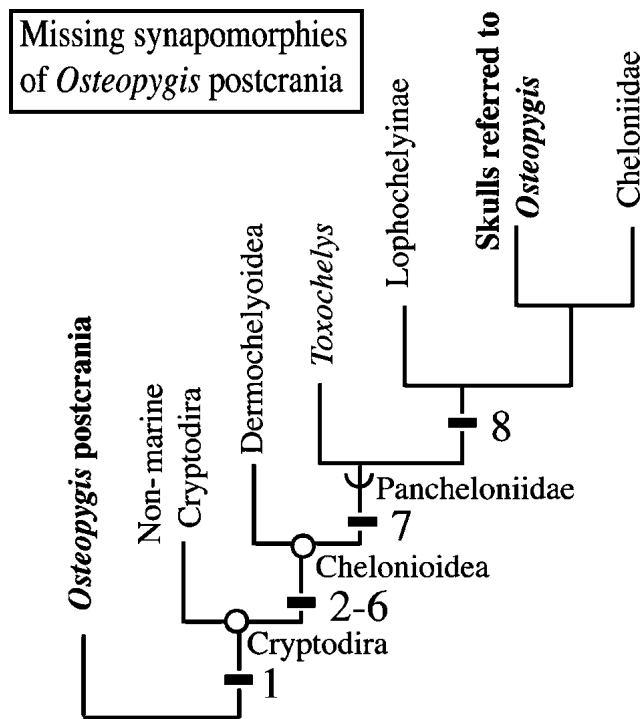


FIGURE 5. Phylogenetic tree showing the postcranial synapomorphies missing in postcrania referred to *Osteopygis*. The phylogeny is based on Lynch and Parham (2003) and Parham and Hutchison (2003). Taxa are stem based (open semi-circle) or node based (circle). See text for character descriptions.

Character 3 (Scale Sulci)—In all chelonioids the plastral scale sulci are greatly reduced or lost. In *Osteopygis* the scale sulci are strong.

Character 4 (Knob on Nuchal)—Chelonioids have a knob on the nuchal that attaches to the 8th cervical vertebra. *Osteopygis* lacks this feature (Parham and Fastovsky, 1997).

Character 5 (Humerus Length)—In all described chelonioids the humerus is longer than the femur. In *Osteopygis* the femur is longer than the humerus (Wieland, 1904a; Zangerl, 1953; Hirayama, 1992).

Character 6 (Lateral Process of Humerus)—In chelonioids the lateral process of the humerus is shifted distally, but not in *Osteopygis* (Hirayama, 1992).

Character 7 (Midline Plastral Suture Lost)—In all panchelonioids the midline suture between the hyoplastra and hypoplastra on each side is lost, and the left and right halves of the plastron are separated (Fig. 4C). *Osteopygis* has a sutured contact in this region (Fig. 4A).

Character 8 (8th Rib Insertion)—In the clade that includes Lophochelyiinae and Cheloniidae, the 8th costal rib inserts into the peripheral next to the pygal (Parham and Fastovsky, 1997). *Osteopygis* has a rib-free peripheral next to the pygal, the plesiomorphic condition.

Summary of Characters—The postcranial skeleton of *Osteopygis* lacks all of the synapomorphies of stem-cheloniid sea turtles (characters 2–7). The morphology of the hyoplastron (character 1) implies a phylogenetic position outside of Cryptodira. *Osteopygis* would be considered a stem cryptodire if only the postcrania were known. Therefore, it is necessary to reexamine the details of the referral of sea turtle skulls to *Osteopygis*.

A History of Mixed Specimens in the Hornerstown Formation

The root of the referral of the sea turtle skull material to *Osteopygis* is Hay's (1908) discovery of a broad crushing dentary associated with an *Osteopygis*-like shell from Cope's collection (AMNH 2216). But there are several documented examples of misattributed specimens from Cope's extensive collections. Hay (1908:138) himself discounted the attribution of another dentary to *Osteopygis*: "Accompanying the bones... is the lower jaw of a turtle... It is hardly conceivable that he would not have mentioned this jaw had it been present when he described the other bones. It is difficult to understand why he should have referred it to this genus and species without some good reason... The matter is very obscure." In describing Cope's work on fossil turtles from New Jersey, Hay (1908) cites other examples of mislabeled elements (p. 137), mislabeled specimens (p. 141), lost locality data (p. 156), and even the referral of specimens from different formations to a single taxon without apparent justification (p. 163).

Apart from the vagaries of Cope's collections, there is additional cause to question the association of cranial and postcranial remains in the Hornerstown Formation: it is notorious for its mixed specimens. AMNH 2216, would not be the first chimeric specimen involving *Osteopygis* postcrania or stem-cheloniid crania. Gaffney (1975) reported that the type of *Amblypeza* Hay, 1908, is a chimera including a mixture of pleurodire, trionychoid, and *Osteopygis* postcranial elements. Also, the nearly complete skull that Fastovsky (1985) referred to *Osteopygis emarginatus* (NJSM 11872) was found associated with remains of the pleurodiran turtle *Taphrosphys* Cope, 1869a (NJSM 12183). The skull was found 'in place' near the front of the shell and was logically assumed to belong to *Taphrosphys* until further preparation revealed that it actually belonged to a stem-cheloniid sea turtle.

The reason for all these mixed specimens is "the closely associated manner in which the numerous forms from the New Jersey Greensands occur" (Wieland 1904b:183). Baird (1964) and

Gaffney (1975) also described how Hornerstown Formation turtle specimens are usually found with the plates 'shingled' over one another and consolidated into a compact mass that can only be separated by careful preparation. This concentration of elements has been attributed to slow wave action and scavengers (Gallagher, 1993). The concentrating effects cannot be taken lightly because the low rate of sedimentary deposition in the greensands would leave carcasses unburied for some time. Gallagher (1993) proposed that turtle carcasses were a significant boon to the benthic communities and even acted as 'trophic islands' on the ocean floor.

Osteopygis is a thick-shelled turtle and the dentaries of durophagous sea turtles are similarly stout and readily preserved. The fact that these elements are relatively common and found near each other could result from taphonomic bias. Considering the uncomfortable signal resulting from this association, the hypothesis of taphonomic bias seems plausible. As a final note, private collectors working in the early Paleogene sediments of the Ouled Abdoun Basin of Morocco encounter a similar fauna and taphonomy. Unencumbered by knowledge of subordinal divisions with turtles, fossil traders have assumed that the skulls of stem-cheloniid sea turtles (*Osteopygis*) and the shells of the pleurodire *Taphrosphys* represent a single species and have con-

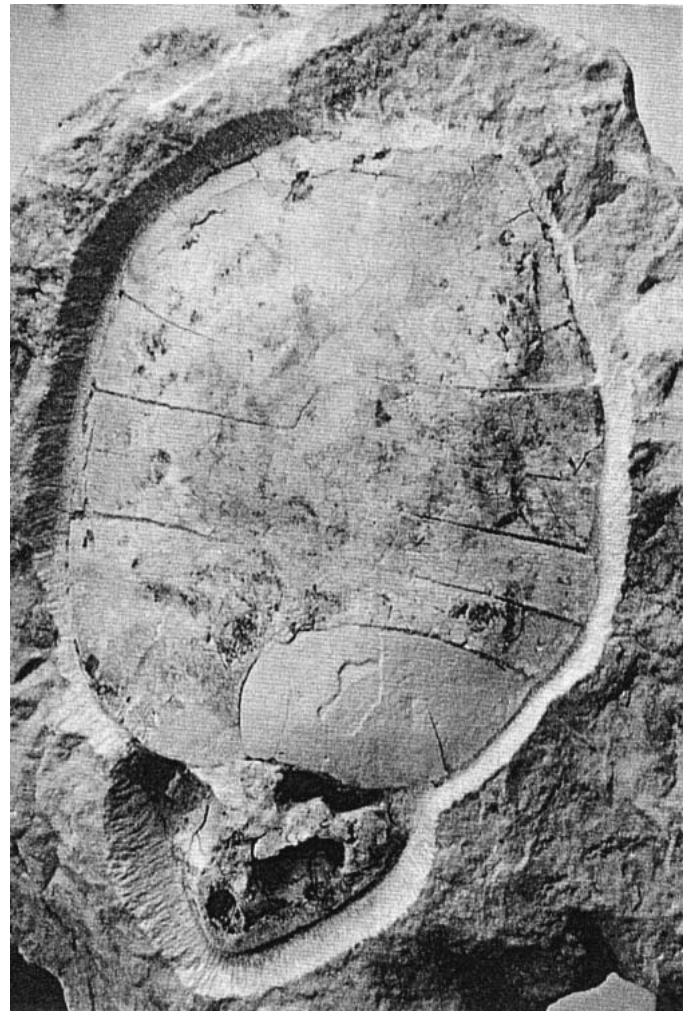


FIGURE 6. An artificial chimera created by private collectors working in early Paleogene sediments of the Ouled Abdoun Basin of Morocco. The skull is from a stem-cheloniid turtle, the shell is from the marine pleurodire *Taphrosphys* (see discussion in de Lapparent de Broin, 2000: 62).

structed elaborate chimeras accordingly (Fig. 6; de Lapparent de Broin, 2000:62).

The ‘Decapitation’ of *Osteopygis*

Considering the conflicting phylogenetic signals from the crania and postcrania, the history of mixed specimens, and the taphonomy of turtles from the Hornerstown Formation, stem-cheloniid cranial materials cannot be referred to *Osteopygis* with confidence. Additional material may provide an independent test of cranial and postcranial linkages. Durophagous ‘*Osteopygis*’-like sea turtles are known from many localities including South America (Gasparini and Biro-Bagoczky, 1986; de la Fuente and Casadío, 2000) and Africa (Karl et al., 1998; de Lapparent de Broin, 2000). Yet, at the time of this writing, no stem-cryptodire shell material is known from these deposits. There are only two instances where turtles with skulls similar to those previously referred to *Osteopygis* have well-associated postcrania: *Euclastes gosseleti* and UCMP V79088/123616 (referred to *Osteopygis* sp. by Foster, 1980). In these specimens the associated postcrania are typically stem cheloniid and not like *Osteopygis*.

Osteopygis as a Stem Cryptodire

A better understanding of the affinities of true *Osteopygis* (the postcrania) requires a more detailed analysis of eucryptodiran phylogeny than is currently available. Based on its thickened peripherals and hyoplastral insertions, it is most likely a stem cryptodire (*Eucryptodira incertae sedis*) of the “macrobaenid” grade. The recognition of *Osteopygis* as such extends the geographical distribution of “macrobaenids” from Asia and Western North America to the Atlantic coast (Fig. 7). Weems (1988) and Hutchison and Weems (1999) referred several specimens from Atlantic formations to *Osteopygis*, but those based on the cranial material of stem cheloniids must be reassigned. Some of the *Osteopygis* fossils from the Paleocene of South Carolina (ChM PV4762; Hutchison and Weems, 1999) and Maryland (USNM 357710; Weems, 1988) are still referable to *Osteopygis* sensu stricto or at least cf. “Macrobaenidae” (Fig. 7). *Osteopygis* sensu stricto can be diagnosed as a stem cryptodire of the “macrobaenid” grade or else as *Eucryptodira incertae sedis*.

Although *Osteopyginae* Zangerl, 1953, predates *Macrobaenidae* Sukhanov, 1964, it is undesirable that a higher taxon that represented specialized sea turtles for almost 50 years (throughout the entirety of the name’s existence), should be applied to stem cryptodires. I recommend that the name *Osteopyginae* be discarded.

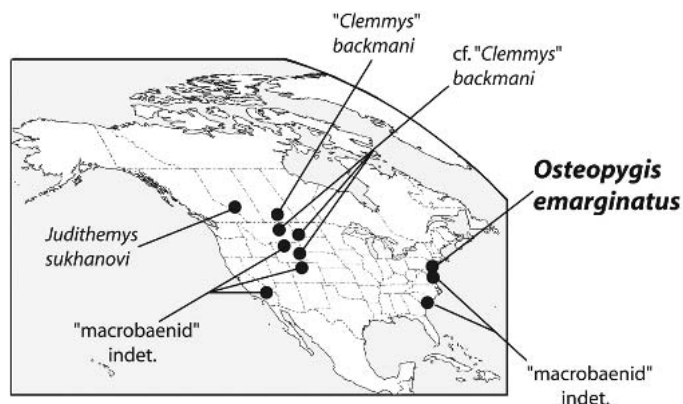


FIGURE 7. Map showing the known localities of “macrobaenid” turtles in North America.

Euclastes (= Former *Osteopyginae*)

The non-*Osteopygis* taxa of the former *Osteopyginae* are monotypic genera separated by relatively plastic characters of the palate and based on few specimens. Hence, Lynch and Parham (2003) recommended that all species be restricted to the oldest generic name, *Euclastes* Cope, 1867. This convention would effectively solve two taxonomic problems within the group: 1) the proliferation of generic names based on fragmentary material; 2) the need to replace the *Osteopyginae*. Lynch and Parham (2003: 22) proposed the following phylogenetic definition for *Euclastes*: “those taxa that share a more recent common ancestor with *Euclastes platyops* Cope, 1867, than with *Chelonia* Brongniart, 1800, *Argillochelys* Lydekker, 1889, or *Puppigerus* Cope, 1870.” This definition restricts *Euclastes* to the former *Osteopyginae* while maintaining the integrity of other well-known genera of stem cheloniids. For a review of species within *Euclastes* see Lynch and Parham (2003).

Euclastes wielandi (= *Crania* Previously Referred to *Osteopygis emarginatus*)

The formal decapitation of *Osteopygis* necessitates an inquiry into the taxonomic status of cranial specimens referred to *Osteopygis emarginatus*. The referral of all osteopygine species to *Euclastes* (see above) solves the issue of the generic name, but what is the appropriate specific epithet for the New Jersey form? Hay (1908) designated two dentary specimens of stem cheloniids from the Hornerstown Formation as species holotypes (YPM 913 for *Lytoloma wielandi* and ANSP 9220 for *Erquelinnesia molaria*). Both specimens were referred to *Osteopygis emarginatus* by Zangerl (1953). I tentatively accept the assertion of Zangerl (1953) that YPM 913 and the holotype of *E. molaria* represent the same morpho-species as the snouts (YPM 913a and NJSM 12273) and skull (NJSM 11872). Consequently, I recommend that all of the cranial material referred to *Osteopygis emarginatus* should be referred to *Euclastes wielandi* (comb. nov.). It is appropriate that this taxonomic decision should honor George Wieland of Yale because his caveats about greensand turtle associations and detailed morphological descriptions were invaluable in this study.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788

EUCRYPTODIRA Gaffney, 1984

CRYPTODIRA Cope, 1868b

CHELONIOIDEA Baur, 1893

PANCHELONIIDAE Joyce, Parham, and Gauthier, 2004

EUCLASTES Cope, 1867

EUCLASTES WIELANDI (Hay, 1908)

Synonymy—*Lytoloma wielandi* Hay, 1908; *Erquelinnesia molaria* Hay, 1908; *Osteopygoides priscus* Karl, Tichy, and Ruschak, 1998 (based on a skull later synonymized with “*Osteopygis emarginatus*” by Hirayama and Tong, 2003); *Euclastes priscus* Lynch and Parham, 2003.

Holotype—YPM 913, a partial dentary.

Type Locality—Hornerstown Formation, New Jersey.

Referred Specimens—The following dentaries from the New Jersey greensands: AMNH 2216 (dentary only), YPM 490, YPM 1001, and ANSP 9220 (*Erquelinnesia molaria* holotype). YPM 913a, the anterior portion of a skull, a snout, including the premaxillae, and parts of the maxillae, frontals, and vomer from the Hornerstown Formation figured by Wieland (1904b), Hay (1908), and Karl et al. (1998). NJSM 11872, a nearly complete skull from the Hornerstown Formation described by Fastovsky (1985) and also figured by Hirayama (1994), de la Fuente and Casadío (2000), and this study (Fig. 3A). NJSM 12273, an unde-

scribed section of palate comprised of partial maxillae and premaxillae and an associated dentary and humerus fragment. USNM 412113, a section of the palate comprised of the premaxillae, maxillae, and vomer from the Brightseat Formation of Maryland first reported and referred to *O. emarginatus* by Weems (1988). IGPS No. 590/1 and IGPS 590/2, the type and paratype skulls of *Osteopygoides priscus* from Ouled Abdoun phosphates in Morocco (Karl et al., 1998). Hiarayama and Tong (2003) reported on the following specimens from the Ouled Abdoun basin: three skulls without lower jaws (AMNH 3022, 3031, and MDE t 27), one complete but crushed skull (AMNH 30030), and two isolated lower jaws (MDE t 28, 29).

Diagnosis—Based on its referred skulls, *Euclastes wielandi* can be assigned to the Pancheloniidae on the basis of the following combination of characters: (1) V-shaped basisphenoid; (2) secondary palate; (3) closely positioned foramina for the exits of the anterior carotids; and (4) rod-shaped rostrum basisphenoidale. *Euclastes gosseleti* (Dollo, 1886) and *Euclastes meridionalis* (de la Fuente and Casadío, 2000) have more extensive secondary palates that exceed the length seen in *Euclastes wielandi*. *Euclastes planimenta* (Owen, 1842) has a wider, more robust head than *E. wielandi*. *Euclastes wielandi* can be distinguished from *Euclastes platyops* by its shallow tomial ridge, dorsally directed orbits, and non-concave triturating surface, and from *Euclastes roundsi* (Weems, 1988) by having a less developed secondary palate.

Description—See Fastovsky (1985), Karl et al. (1998) and Hiarayama and Tong (2003) for descriptions of complete skulls of *Euclastes wielandi*.

TESTUDINES Batsch, 1788

EUCRYPTODIRA Gaffney, 1984

cf. "MACROBAENIDAE" Sukhanov, 1964

OSTEOPYGIS Cope, 1869b

OSTEOPYGIS EMARGINATUS Cope, 1869b

Synonymy—The following list does not include *Chelone sopita* Leidy, 1865, or its derivatives because they are nomina vana (Zangerl, 1953). *Osteopygis emarginatus* Cope, 1868a (nomen nudum); *Osteopygis chelydrinus* Cope, 1868a (nomen nudum); *Osteopygis emarginatus* Cope, 1869b; *Osteopygis chelydrinus* Cope, 1869b; *Osteopygis platylomus* Cope, 1869b; *Osteopygis erosus* Cope, 1875; *Catapleura chelydrina* Cope, 1875; *Osteopygis gibbi* Wieland, 1904a; *Propleura borealis* Wieland, 1904b; *Amblypeza entellus* Hay, 1908; *Osteopygis borealis* Hay, 1908; *Osteopygis robustus* Hay, 1908.

Holotype—AMNH 1485, a partial carapace (Fig. 1).

Locality—Hornerstown Formation (Cretaceous/Tertiary, Maastrichtian/Danian), Gloucester County, New Jersey.

Referred Specimens—See Zangerl (1953) minus those listed under *Euclastes wielandi* above, but including NJSM 11342 and 11343 (parts of the *Amblypeza entellus* holotype, probably from the Hornerstown Formation) and NJSM 16130, a well-preserved, but undescribed partial shell from the Hornerstown Formation.

Diagnosis—*Osteopygis emarginatus* is a eucryptodire because it lacks mesoplastra and a fused pelvis. It resembles "macrobaenid" stem cryptodires in the presence of thickened peripherals, a hyoplastral buttress that inserts into the second peripheral, and an intimate gomphotic contact between the plastron and carapace. *Osteopygis emarginatus* can be distinguished from '*Clemmys*' *backmani* by its thicker shell as well as the shape and position of plastral fontanelles. Additional differential characters may exist, but await a formal redescription of '*C.*' *backmani*. *Osteopygis emarginatus* can be distinguished from *Judithemys* and most Asian "macrobaenids" by its larger size, thicker shell, and the presence of plastral fontanelles.

Description—See Wieland (1904a), Hay (1908), and Zangerl (1953).

CONCLUSIONS

The postcranial skeleton of *Osteopygis* is like that of contemporaneous and geographically proximal "macrobaenids." Because of phylogenetic considerations, the tenuous historical (Cope-Zangerl) attribution of specimens, and the taphonomy of the Hornerstown Formation, I submit that the most conservative solution is to separate the stem-cheloniid cranial material from *Osteopygis*. All of the durophagous sea turtles formerly assigned to Osteopyginae are here referred to *Euclastes* and the skull material referred to *Osteopygis emarginatus* is referred to *Euclastes wielandi*. In the past, a chimeric *Osteopygis* was the sole exception to the trend of increasing pelagic specialization through time for stem cheloniids. The 'decapitation' of *Osteopygis* simplifies this trend while adding to a growing knowledge of North American "macrobaenid"-grade stem cryptodires (Fig. 7C).

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