NEW SEA TURTLE FROM THE MIOCENE OF PERU AND THE ITERATIVE EVOLUTION OF FEEDING ECOMORPHOLOGIES SINCE THE CRETACEOUS

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ABSTRACT—The seven species of extant sea turtles show a diversity of diets and feeding specializations. Some of these species represent distinctive ecomorphs that can be recognized by osteological characters and therefore can be identified in fossil taxa. Specifically, modifications to the feeding apparatus for shearing or crushing (durophagy) are easily recognizable in the cranium and jaw. New sea turtle fossils from the Miocene of Peru, described as a new genus and species (Pacifichelys urbina n. gen. and n. sp.), correspond to the durophagous ecomorph. This new taxon is closely related to a recently described sea turtle from the middle Miocene of California, USA (Pacifichelys hutchisoni n. comb.), providing additional information on the osteological characters of this lineage. A phylogenetic analysis of Pacifichelys and other pan-chelonoid sea turtle lineages shows that at least seven lineages independently evolved feeding specialized for shearing or crushing. The iterative evolution of these morphologies is plausibly linked to ecological factors such as the development of seagrass communities and the opening of niches through extinction that occurred from the Cretaceous to the Miocene.

INTRODUCTION

CROWN GROUP sea turtles (Chelonioida Baur, 1893; Fig. 1) are divided into two clades, the Dermochelyidae Gray, 1825 and the Cheloniiidae Bonaparte, 1832. Dermochelyids are represented by a single extant species, Dermochelys coriacea (Vandellius, 1761), a highly specialized, deep-diving, gigantothermic cendivore with a carapace comprised of several hundred tiny ossicles. The shell morphology of D. coriacea is so unlike that of other turtles that some workers considered it the sister to all other species (e.g., Hay, 1908). In contrast, the cheloniids (six extant species of “hardshell” sea turtles) possess a carapace much more like other turtles. Cheloniids possess morphological and physiological adaptations to a pelagic lifestyle, like D. coriacea, but some species also show feeding specializations that correspond to different diets (Bjørndal, 1997; Wyneken, 2001). For example, the loggerhead sea turtle, Caretta caretta (Linnaeus, 1758), processes hard-shelled prey (e.g., mollusks, crustaceans) with flat crushing jaws and a wide muscular head. In contrast, the green sea turtle, Chelonia mydas (Linnaeus, 1758), lacks the hypertrophied jaw musculature of Ca. caretta and feeds primarily on seagrass using sharply-ridged jaws for shearing. Some species of extinct sea turtles also show evidence of feeding specializations, but the evolution of these features has never been studied in a phylogenetic context. Understanding the evolution of feeding extremes in sea turtles can shed light on the specialization and differentiation seen in extinct cheloniids, as well as on macroevolutionary trends for the entire lineage (Pan-Chelonioida).

In this study, we describe a new genus and species of a durophagous stem-chelonoid fossil sea turtle from the Miocene of Peru (Fig. 2). A phylogenetic analysis of this species and other fossil taxa (Fig. 3) reveals an evolutionary history of feeding specializations among pan-chelonoids that includes the independent and iterative evolution of similar ecomorphologies. The timing of these evolutionary events is consistent with ecological replacement following extinction because the appearance of independently derived ecomorphs generally follows the disappearance of similarly adapted forms. Taxonomy used.—All higher names follow Joyce et al. (2004; Fig. 1) with one addition: the term Caretta Zangerl, 1958 was created to accommodate the extant Ca. caretta and two extant species of Lepidochelys Fitzinger, 1843. These taxa share a number of osteological features of the crania (correlated to durophagy) and postcrania (relating to supernumerary bones and scales) as well a long-established molecular signal of monophyly (Dutton et al., 1996). For these reasons, Parham and Fastovsky (1997) proposed a phylogenetic definition for Caretta that preserved the original usage while naming a clade that is generally useful for turtle biologists. Without justification or relevant discussion, Naro-Maciel et al. (2008) applied the name Caretta more broadly, expanding it to include the related Eretmochelys imbricata (Linnaeus, 1766). This convention changes the traditional use of the name Caretta and simultaneously creates the need for a new clade name for the Ca. caretta and Lepidochelys node. Here, we wish to reemphasize the traditional usage of Caretta as a clade that includes Ca. caretta and Lepidochelys and none of the other extant chelonids with the following definition: Caretta refers to the crown clade originating with the most recent common ancestor of Caretta (orig. Testudo) caretta (Linnaeus, 1758) and Lepidochelys (orig. Testudo) olivacea (von Eschscholtz, 1829). This definition maintains the traditional and original usage of this name.

Based on the phylogenetic analysis and discussion of Joyce (2007, p. 66) we provisionally do not consider the extinct marine turtle clade Protostegidae Cope, 1872 as part of the Pan-Chelonioida but rather an earlier, independent radiation of marine turtles. Consequently, the content of Chelonioida in this paper differs from that of most previous authors (e.g., Hirayama, 1994, 1998). Understanding whether some
Cretaceous taxa are protostegids or pan-chelonioids, or where the dermochelyids fit within Pan-Chelonioida, will require a much larger and more comprehensive matrix than the one employed in this study. Here, we consider only those taxa that can be confidently considered pan-chelonioids, and our discussions and analysis emphasize the pan-cheloniid lineage.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BMNH, British Museum of Natural History, London, UK; CNHM, “Chicago Natural History Museum” now Field Museum, Chicago, USA; IRSNB, L’Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; LACM, Natural History Museum of Los Angeles County, Los Angeles, USA; ROM, Royal Ontario Museum, Toronto, Canada; SMC, Sedgwick Museum, Cambridge, UK; UNMSM, Universidad Nacional Mayor de San Marcos, Lima, Peru; USNM, United States National Museum, Washington DC, USA; YPM, Yale Peabody Museum, New Haven, USA.

**SYSTEMATIC PALEONTOLOGY**

**REPTILIA**

Laurenti, 1768

**TESTUDINES**

Batsch, 1788

**CRYPTODIRA**

Cope, 1868

**PAN-CHELONIOIDEA** Joyce, Parham, and Gauthier, 2004

**MEXICHELYS** n. gen.

Type species.—**Mexichelys coahuilaensis**. (Brinkman, Aquillón-Martinez, de Leon Dávila, Jamnizky, Eberth, and Colbert, 2009) n. comb., by monotypy.

Diagnosis.—Numbers in parentheses refer to characters used in the phylogenetic analysis (Appendix 1). Diagnosed as Testudines by its shell. Diagnosed from protostegids and dermochelyids by a basioccipital depression with a v-shaped crest of the basioccipital (14). Distinguished from early pan-chelonioids such as *Toxochelys* Cope, 1873 and the Lophochelyinae as either stem cheloniids or stem chelonioids are shown.

Diagnosed from all pan-cheloniids by its lack of a rod-like crest of the basioccipital (14). Distinguished from early pan-dermochelyids by a basioccipital depression with a v-shaped crest of the basioccipital (14). Differentiation from other species of this genus. The cladistic analysis of Brinkman et al. (2009) placed “Eu.” *coahuilaensis* among Cretaceous pan-chelonioids (that are potentially not even pan-cheloniids). This placement of a species referred to *Euclastes* Cope, 1867 is in contrast to that of Lynch and Parham (2003), who hypothesized that Cenozoic “Euclastes” (“Eu.” *gosseleti* Dollo, 1886) and “Eu.” *hutchisoni* Lynch and Parham, 2003) were on the stem of Cheloniidae. In the present study, we include “Eu.” *coahuilaensis* and Cenozoic durophagous stem cheloniids in a cladistic analysis for the first time. Our results confirm the basal placement of “Eu.” *coahuilaensis* by Brinkman et al. (2009) but also the crownward placement of durophagous stem cheloniids suggested by Lynch and Parham (2003). In other words, the results of both analyses are supported, but, when combined, it becomes clear that “Eu.” *coahuilaensis* is not closely related to Cenozoic forms. Primitive states for cranial characters (5, 14–17) separate Eu. *coahuilaensis* from Cenozoic taxa, and most also distinguish it from *Eu. wielandi* and, by extension, the type species of the genus *Euclastes*, *Eu. platyops* Cope, 1867. Because a new genus name is warranted for “Eu.” *coahuilaensis*, we coined the name *Mexichelys*.


**EUCLASTES** *coahuilaensis* Brinkman, Carolina, Aquillon-Martinez, Dávila, Jamnizky, Eberth, and Colbert, 2009 (original description).

**MEXICHELYS coahuilaensis** This study (n. comb.).

**CHELONIOIDEA** Baur, 1893

**PAN-CHELONIIDAE** Joyce, Parham, and Gauthier, 2004

“DUROPHAGOUS STEM CHELONIIDS”


**EUCLASTES** LYNCH AND PARHAM, 2003, p. 22.

“Euclastes group” Jalil, de Lapparent de Brion, Bardet, Vacant, Bouya, Mamgez, and Meslouhi, 2009, p. 3.

**Discussion.**—Among fossil species referred to the stem of Cheloniidae, all of the recent changes to binomial names have involved the classification of durophagous forms. To be clear, we recognize that other species (e.g., the extinct *Puppigerus*...
**Figure 3**—Phylogenetic hypothesis generated by this study. Numbers below nodes refer to support values (decay indices/bootstrap proportions). Values of "-" indicate decay indices of 1 or bootstraps of <50. Grey fields correspond to highly specialized feeders as indicated by thin dentaries with significant symphyseal ridges (shearing) or flat, wide dentaries (crushing). Roman numerals indicate hypothesized independent origins of feeding specializations. Dashed lines indicate the extinction of protostegids, timing of seagrass origin in the Late Cretaceous, and a lack of integrated fossil taxa in the late Paleogene. Numbers next to vertical dashed lines correspond to the known ranges of non-integrated specialized pan-chelonioids: 1, *T. moorevillensis*; 2, *Mes. undulatus*; 3, *Al. hofmanni*; 4, *Ar. antiqua*; 5, known range of *Ch. mydas* (earliest record from Dodd and Morgan, 1992); 6, known range of durophagous stem cheloniiids from *Eu. wielandi* to *G. planimentum*; 7, known range of pan-Caretini as evinced by *Procolpochelys grandaeva* Leidy, 1851 (date based on Sugarman et al., 1993), not a confirmed durophage; 8, known range of *Lepidochelys* (earliest record from Dodd and Morgan, 1992); 9, known range of *Caretta* Rafinesque, 1814 (earliest record from Dodd and Morgan, 1992); 10, *Ca. patriciae*.

*camperi* (Gray, 1831) could be classified as durophages based on their long secondary palate or known diet. For the purpose of this study, we consistently use the term “durophagous” to refer to flat-jawed, broad-headed forms, i.e., hyper-durophages, all of which were previously placed in Osteopyginae Zangerl, 1953, Carettini, or Euclastes.

For 50 years, durophagous stem cheloniiids were traditionally considered members of the Osteopyginae Zangerl, 1953 (e.g., Zangerl, 1971; Foster, 1980; Fastovsky, 1986; Parham and Fastovsky, 1997; Hirayama and Tong, 2003). Parham (2005) showed that the type species of *Osteopygis* Cope 1869 was not a stem chelonid nor even a cheloniod, but rather a
non-marine cryptodire of the “macrobaenid” grade sensu Parham and Hutchison (2003). This discovery rendered the name Osteopyginae unavailable for durophagous stem cheloniids. Lynch and Parham (2003) considered durophagous cheloniids to be overly split, with many poorly known taxa given monotypic/redundant genus names (e.g., Erquelinnesia Dollo, 1887; Glossochelys Seeley, 1871; Osteopygoides Karl, Tichy, and Ruschak, 1998; Pampaemys de la Fuente and Casadío, 2000). To resolve the status of “Osteopygus” skulls and perceived over-splitting, Lynch and Parham (2003) referred all assigned species of osteopygonines to the oldest available genus name, Euclastes. Jalil et al. (2009) accepted the inappropriateness of using Osteopygus and Osteopyginae for durophagous stem cheloniids, but pointed out that a full taxonomic revision of this group should be based on a detailed phylogenetic analysis that, in turn, will require much more detailed description of new material. We wholeheartedly agree with that position, especially because the monophyly of durophagous stem cheloniids rests entirely on homoplastic feeding apparatus characters. We submit that an overall poor understanding of stem-cheloniid morphology has reinforced the significance of these feeding-related characters. After all, the eight species of hyper-durophagous stem cheloniids (AKA, the “former Osteopygidae sensu Lynch and Parham, 2003”) are recognized here, five are known only by skull material, and only two species (Euclastes wielandi [Hay, 1908]; Pa. urbinai) have described and figured braincases (Fastovsky, 1986; this study).

In the absence of a robust phylogenetic hypothesis for most durophagous stem cheloniids, a provisionally over-split taxonomic arrangement (i.e., the traditional scheme) is arguably more conservative than an overly lumped one (i.e., Euclastes sensu Lynch and Parham, 2003). For the sake of explicitness, we present a full nomenclatural accounting of durophagous stem cheloniids (AKA, the “former Osteopyginae,” AKA the “Euclastes group” sensu Jalil et al., 2009). Our taxonomic arrangement recognizes eight species in four genera (only one of which is monotypic/redundant). This scheme is the first attempt to consider all durophagous stem chelonioids and group them according to shared diagnostic characters.

**Erquelinnesia** Dollo, 1887

Pachyrhynchus Dollo, 1886, p. 129 (preoccupied by Pachyrhynchus Germar, 1824).

Pampaemys de la Fuente and Casadío, 2000, p. 238.

Type species—Erquelineasia gosseleti. Incluced species—Erq. meridionalis n. comb.

Discussion.—We refer Pampaemys meridionalis de la Fuente and Casadío, 2000 to the genus Erquelineasia based on the shared presence of an extremely long secondary palate.

**Erquelineasia gosseleti** (Dollo, 1886)

Pachyrhynchus gosseleti Dollo, 1886, p. 138 (original description, preoccupied genus).

Erquelineasia gosseleti Dollo 1887, p. 393 (n. comb.).

Euclastes gosseleti Dollo, 1888, p. 115 (n. comb.).

**Erquelineasia meridionalis** (de la Fuente and Casadío, 2000) n. comb.

Pampaemys meridionalis de la Fuente and Casadío, 2000, p. 238 (original description).

Euclastes meridionalis Lynch and Parham, 2003, p. 23 (n. comb.).

Erquelineasia meridionalis This study (n. comb.).

**Euclastes** Cope, 1867

Rhetechelys Hay, 1908, p. 162.


Included species.—Euclastes includes three species. The type species is Eu. platyops. There are two referred species, Eu. acutirostris Jalil, de Lapparent de Broin, Bardet, Vacant, Bouya, Amaghzaz, and Meslouh, 2009 and Eu. wielandi.

Discussion.—Resolving the taxonomy of Euclastes requires a review of the assumptions associated with the referral of species to the genus Euclastes. Lynch and Parham (2003:22) phylogenetically defined Euclastes as those taxa that share a more recent common ancestor with Euclastes platyops Cope 1867 than to extant sea turtles or two relatively well-known Paleogene taxa. Unfortunately, the only known specimen of Eu. platyops (see Hay, 1908) is too incomplete to include in a phylogenetic analysis, and so its precise affinities to other pano-cheloniids remain cladistically untested. This situation could arguably discount the utility of this genus name; however, Eu. platyops is clearly a durophagous pano-cheloniid, and so it can be plausibly linked to phenetically similar, geographically proximal, and nearly contemporaneous durophagous pano-cheloniids (such as Eu. wielandi). Jalil et al. (2009) tentatively referred Eu. acutirostris to the genus Euclastes. We provisionally follow that referral here for the sake of stability as well as the fact that all three species show dorsally facing orbits (a feature lacking in other durophagous stem cheloniids).

**Euclastes acutirostris** Jalil, de Lapparent de Broin, Bardet, Vacant, Bouya, Amaghzaz, and Meslouh, 2009

**Euclastes platyops** Cope, 1867

Euclastes platyops Cope, 1867, p. 41.

Rhetechelys platyops Hay, 1908, p. 162 (n. comb.).

**Euclastes wielandi** (Hay, 1908)


Lytoloma wielandi Hay, 1908, p. 157 (original description).

Osteopygus borealis Hay, 1908, p. 145 (in part).

Erquelineasia molaria Hay, 1908, p. 160 (junior synonym).

Osteopygus emarginatus Zangerl, 1953, p. 205 (in part)

Osteopygus roundsi Weems, 1988, p. 120 (junior synonym).


Euclastes pris cus Lynch and Parham, 2003, p. 23 (n. comb., junior synonym).

Euclastes wielandi Parham, 2005, p. 75 (n. comb.).

**Glossochelys** Seeley, 1871:227

Glossochelys planimentum (Owen, 1842) n. comb.

Chelone planimentum Owen, 1842, p. 178 (original description).

Chelone crassicostata Owen and Bell, 1849, p. 25 (in part)

Thalassochelys planimentum Cope, 1870, p. 146 (n. comb.).

Pappigerus crassicostatus Cope, 1870, p. 60 (in part).

Glossochelys harvincensis Seeley, 1871, p. 227 (junior synonym).

Pachyrhynchus planimentum Dollo, 1886, p. 138 (n. comb.).

Lytoloma planimentum Lydekker, 1889c, p. 64 (n. comb.).

Glossochelys planimentera Zangerl, 1971, p. 27 (n. comb.).

Euclastes planimenta Lynch and Parham, 2003, p. 23 (n. comb.).
**Glossochelys planimentum** This study (n. comb.).

**Discussion.**—Zangerl (1971) inexplicably changed the specific epithet of this taxon to the feminine form *planimenta* and all later authors followed this convention. We revert the name to the *planimentum* because *Glossochelys* is not a feminine genus name. This taxon is known from poorly preserved postcrania and one well-preserved skull. Whereas *G. planimentum* is clearly a durophagous pan-cheloniod, it lacks the dorsally directed orbits of *Euclastes* and the elongated secondary palate of *Erquelinessia*. The absence of these characters, along with its highly vaulted (tall) skull, precludes a comfortable assignment into any other genus.

**Pacifichelys** n. gen.

**Type species.**—*Pacifichelys urbina* (Lynch and Parham, 2003) n. comb.

**Included species.**—*Pacifichelys hutchisoni* (Lynch and Parham, 2003) n. comb.

**Diagnosis.**—Numbers in parentheses refer to characters used in the phylogenetic analysis (Appendix 1). Testudines because of its shell. Pan-chelonoid by having a humerus with a distally shifted lateral process. Diagnosed from protostegids and dermochelyids by a basioccipital depression with a v-shaped crest of the basisphenoid. Distinguished from early pan-chelonoids such as *Toxochelys* and the Lophochelyinae by extensive secondary palate (1) and laterally facing orbits (12). Diagnosed from *Mex. coahuilensis* by its laterally facing orbits (12), a low skull (7), a pterygoid with a ventral ridge (14), a high dorsum sellae (16), weak temporal emargination (17), and a notched pygal (35). Diagnosed from most other pan-chelonoids by its wide skull and flat triturating surfaces (6, 7). Diagnosed from *Euclastes, Erquelinessia*, and carettenes by a vomerine pillar that is visible in ventral view (2). Further diagnosed from carettenes by having a broad vomer-premaxillae contact on the palate (4), a low temporal ridge (7), a surangular that does not extend onto the dentary (8), and a humerus that lacks the v-shaped lateral process (25). Further diagnosed from *Euclastes* by its laterally facing orbits (12). Further diagnosed from *Erquelinessia* spp. by its much less extensive secondary palate and from *Erq. gosseleti* in particular also by its scapulae that form a wide angle (18) and lack of post-nuchal fontanelles (30). Further diagnosed from *G. planimentum* by more laterally facing orbits and a skull with a much lower profile.

**Etymology.**—Pacific- for the Pacific Ocean, reflecting its distribution from coastal localities of the eastern Pacific Ocean (California, USA and Ica, Peru); -chelys for turtle (Gr.).

**Discussion.**—“*Euclastes*” *hutchisoni* was described from the middle Miocene of California, USA. In the present paper we describe a new but closely related species of this lineage from the middle Miocene of Peru. Both species are readily identifiable by their plesiomorphic postcranial characters, unknown in any other Neogene sea turtle. Additionally, *Pacifichelys* is the only durophagous stem chelonid with a vomerine pillar that is visible in ventral view. We coin a new name for this lineage, *Pacifichelys* n. gen. The presence of *Pacifichelys* in two coastal localities of the eastern Pacific during the middle Miocene (Fig. 2) helps to constrain the temporal and geographic range of this phylogenetically relictual taxon. As shown by Lynch and Parham (2003) and this study (Fig. 3), *Pacifichelys* represents the last vestige of a Paleogene radiation of stem-chelonids that otherwise had been replaced by the crown group.

**Pacifichelys urbina** (Lynch and Parham, 2003) n. sp.

**Figures 5–8**

**Diagnosis.**—As for genus, but can be diagnosed from *Pa. hutchisoni* by palatal characters including the possession of a ventrally unfused premaxillae, the lack of a ventrally straight-sided vomer, and by having a vomer, premaxillae, and maxillae that are not incised to receive a horny raphotheca. **Description.**—Broad skull in adults, secondary palate (1) with vomerine visible in ventral view (2), foramina palatinum posterius lost (3), broad contact of vomer with premaxillae (4), un-fused premaxillae (13), anterior width of vomer variable (9), low tomial ridge (7), processus pterygoideus externus reduced (11), mid-ventral ridge on pterygoids (14), rod-like rostrum basisphenoidale (15), high dorsum sellae (16), laterally facing orbits (12), weak temporal emargination (17), dentary with flat triturating surface (6), surangular not extending onto dentary (8), platycoelous centrum of seventh cervical (24), dorsal process of scapula forming wide angle with acromion (18), humerus lacking v-shaped lateral process (25), coracoid longer than humerus (26), post-nuchal fontanelles absent (30), un-textured carapace elements (34). For detailed description see section entitled “Description of *Pacifichelys urbina*” below.

**Etymology.**—Named for the prolific fossil collector and expert on the Pisco Basin, Mario Urbina of the Museo de Historia Natural de Universidad Nacional Mayor de San Marcos, who collected all of the known material of this taxon.

**Types.**—UNMSM 1447 (holotype), a large skull (Figs. 5.1, 5.4, 6.1). UNMSM 1448, a specimen with associated limb, neck, skull, and shell material (Figs. 5.2, 5.5, 6.3, 6.4, 8); UNMSM 1449, a skull (Figs. 5.3, 5.6, 6.2); UNMSM 1450–3, four partial lower jaws (Fig. 7). The type series of *Pa. urbinae* (UNMSM 1448–1453) was collected from the Pisco Formation, at the Cerro Colorado locality (14.333 S, 75.900 W; Fig. 2), in northern part of the Pisco Basin, Department of Ica, Peru. At the Cerro Colorado locality, two different marine formations are exposed, both of which contain siliciclastic and diatomaceous units: the widespread Pisco Formation, which ranges from middle Miocene to late Pliocene in age (de Muizon and DeVries, 1985); and the underlying Chilcatay Formation, which is ranges from late Oligocene to middle Miocene in age (DeVries, 1998). All specimens are reported from the Pisco Formation (Urbina, personal commun.) although detailed locality data are lacking for most specimens. UNMSM 1453 was collected from basal Pisco Formation rocks at Cerro Colorado, along with an associated assemblage that includes lamnid sharks (*Isurus Rafinesque, 1810*), seabirds (*Sulidae Reichenbach, 1849*), turritellid gastropods and a pontoporiid odontocete. The turritellids belong to the species *Inacella hupei* (DeVries, 2007), which occurs in both the underlying Chilcatay and basal Pisco formations. A partial pontoporiid skull (UNMSM 566) belongs to the genus *Brachydelphis* de Muizon, 1988, which is known from several middle Miocene Pisco Formation localities in the Pisco Basin (de Muizon, 1988). Overall, the preponderance of biostratigraphic evidence points to middle Miocene age for MUSM 1453, between 11–16 Mya (i.e., potentially coeval with *Pa. hutchisoni* material from USA).

**Pacifichelys hutchisoni** (Lynch and Parham, 2003) n. comb.

**Euclastes hutchisoni** **Lynch** AND **Parham, 2003, p. 22** (original description).
Occurrence.—The type locality of *Pa. hutchisoni* is LACM locality 3162, from the Round Mountain Silt Formation, in Kern County, California, USA (Fig. 4). This type locality and the localities of all paratype material derive from the Sharktooth Hill bonebed. Recent work using both biostratigraphic and magnetostratigraphic evidence places the age of the Sharktooth Hill bonebed between 15.9–15.2 Mya (Pyenson et al., 2009).

DESCRIPTION OF PACIFICHELYS URBINAI

Material.—The following description of *Pacifichelys urbinai* is based on seven specimens (UNMSM 1447–1453; Figs. 5–7). Three of these specimens consist of or include partial skulls (UNMSM 1447–1449), the other four are isolated jaws (UNMSM 1450–1453). USNMSM 1448 is the most nearly complete specimen, preserving some elements of the skull, jaw, neck vertebrae, forelimbs, coracoids, carapace, and plastron. This suite of elements might seem to make USNMSM 1448 a logical choice for the holotype, except for the fact that the lower jaw of this taxon is cemented to the palate. The alpha nomenclature and specific identity of durophagous stem cheloniids, especially *Pa. urbinai*, is largely dependent on palatal characters. UNMSM 1447 has the best-preserved palate of the three pan-cheloniid skulls known from Pisco Formation at the time of this writing. For this reason, we choose UNMSM 1447 as the holotype of *Pa. urbinai*. In the description below, we denote descriptive text that refers to characters that are coded in our matrix (Appendices) by listing the relevant characters in parentheses.

Holotype.—UNMSM 1447 (Figs. 5.1, 5.4, 6.1) is the largest of the three pan-cheloniid skulls known from the Pisco Formation. Its total length is 18.3 cm and the estimated length from the occiput (not preserved) to the tip of the snout is ~13.4 cm. The greatest width of the skull is ~13.6 cm, although the right otic and quadrate region have been crushed toward the midline of the skull (Fig. 5.4) making this measurement less than it would have been in life. In lateral view, the skull is vaulted, although not as high as that of *G. planimentum*. The anterior portion of UNMSM 1447 is well preserved, but the posterior skull roof is mostly missing. Aside from the left otic region and both quadrates, the posterior portion of the skull is either crushed or still covered in matrix. The preserved morphology of UNMSM 1447 allows for the coding of eight characters (1, 3, 4, 7, 9, 11–13).

Palatal elements of holotype.—The triturating surface of the palate is largely complete with some of the sutures visible (Fig. 5.1). Like all other durophagous stem cheloniids, it has a broad secondary palate (1) made up of the premaxillae, maxillae, vomer, and palatines. There are no foramina palatinum posterius (3). The lateral and anterior boundaries of the triturating surface are characterized by a very low, almost entirely lacking, tomial ridge (7). The tomial ridge of UNMSM 1447 is lower than that of the smaller paratype specimens (UNMSM 1448, 1449) as well as that of *Pa. hutchisoni* (Lynch and Parham, 2003, figs. 2, 3). The triturating surface is very slightly concave, and there are no
ridges or incised areas that would occlude with the horny ramphotheca of the lower jaw.

In ventral view, the premaxillae widen anteriorly. They are divided by a clear suture (13) and have a broad contact with vomer posteriorly (4). The vomer is irregularly shaped, but the lateral sutures on the ventral surface are not parallel (9). The posterior portion of the triturating surface is not prepared and the matrix grades into the crushed basioccipital. The lateral portion of both pterygoids and their articulation with the quadrates are preserved. There is no evidence of a processus pterygoideus externus on either side (11).

**Skull roof and orbit region of holotype.**—The orbits face laterally (Figs. 5.4, 6.1) (12). The interorbital space has been fully prepared, revealing the foramen orbito-nasale. The sutures in this orbit and nasal region are not visible because of their fusion. Dorsally, parts of the frontal sutures are visible revealing that the frontals did not enter the orbit. There are no scale sulci visible on the skull roof. The parietals are largely missing, making it impossible to determine the degree of temporal emargination from this specimen.

**Basicranium of holotype.**—The left otic region is preserved (Fig. 5.4), including the dorsal juncture of the opisthotic, prootic, and quadrate. The foramen stapedio-temporale between the prootic and quadrate is clearly visible. Medially, the sutures become obscured, but a distinct crista supraoccipitalis protrudes posteriorly from this region. At the base of the crista supraoccipitalis is a distinct foramen magnum. The lateral bones of the basicranium (jugals, squamosals) are missing and the posterio-medial elements (exoccipitals, basi-sphenoid, basioccipital) are crushed beyond recognition.

**Paratype cranial material.**—Paratypes UNMSM 1448 and 1449 both include mostly complete skulls. Unfortunately, UNMSM 1448 is badly crushed and UNMSM 1448 remains only partially prepared. Nevertheless, these specimens provide substantial new insights into the morphology of this species, allowing for the confirmation of four characters seen in the holotype (1, 7, 11, 12) and the coding of five additional characters (2, 14–17). The different sizes of the skulls (UNMSM 1448 is 8.3 cm from occiput to snout, UNMSM 1449 is 9.4 cm, the holotype is ~13.4 cm) provide a small growth series, allowing us to make tentative claims about ontogenetic variation. For example, both the width and height of the skulls appear to increase with size and presumable age (Figs. 5, 6.1, 6.2), suggesting that a hyper-durophagous feeding ecology also increased with age, as known from extant carettines (Bjorndal, 1997). The lower jaws (UNMSM 1450–3) allow for the coding of two additional characters (6, 8).

**Palatal elements and pterygoids of paratypes.**—The skulls of UNMSM 1448 and 1449 show variation in the height of the tommial ridge (7). As in the holotype, both specimens show a low tommial ridge; however some variation is present. The tommial ridge of UNMSM 1448, the smallest skull, is the higher than that of UNMSM 1449 (Figs. 5.2, 5.3), and both are higher than that of the holotype (Fig. 5.1). The reduction in the height of the tommial ridge may correspond to ontogenetic variation, with larger/older individuals of this species having flatter triturating surfaces. Along with the general differences in skull proportions mentioned above, the aforementioned character would also coincide with an increase in dipharyngeal with ontogeny. Aside from the tommial ridge, the lower jaw obscures the triturating surface of UNMSM 1448. UNMSM 1449 is not prepared enough to confirm the sutural morphology described for the holotype, but it is possible to see that a secondary palate is definitely present (1). Furthermore, the internal narial opening shows the presence of a distinct vomerine pillar (Fig. 5.3) revealing morphological state similar to that shown in *Pa. hutchisoni* (Lynch and Parham, 2003, figs 2B, 3A) (2).

Posterior to the triturating surface, the lateral surfaces of the pterygoids are perfectly smooth (Fig. 5.3) indicating that the absence of a processus pterygoideus externus (11). Postero-medially, the pterygoids meet in a low ventral ridge (Figs. 5.2, 5.3), showing a character state that is present in all known Cenozoic pan-cheloniods except for *Ch. mydas* (14).

**Dermal roofing elements of paratypes.**—The skull roof of UNMSM 1448 and 1449 are similar to that of the holotype, with all three skulls showing a frontal that does not reach the orbits (i.e., a prefrontal-postorbital contact is present). Lynch and Parham (2003) tentatively hypothesized the possible presence of nasals in *Pa. hutchisoni*. The sutures of UNMSM 1448, the smallest specimen, are clearly visible and show that no nasals are present in *Pa. urbinai*. The orbits of both UNMSM 1448 and 1449 face laterally as in the holotype (12), which is distinct from all *Euclastes* and other Cretaceous pan-cheloniods considered here (*Toxochelys*, *Lophocheleyinae*, *Mex. coahuilensis*). UNMSM 1449 shows an arrangement of the jugal, postorbital, and quadratojugal (Fig. 6.2) that is typically pan-chelonid. The otic regions of both UNMSM 1448 and 1449 are either missing or obscured. In UNMSM 1448, the squamosals have been deflected ventrally and medially onto the otic region thereby crushing or covering the morphology. In UNMSM 1449 both otic regions are filled with matrix. The posterior skull roof is intact only in UNMSM 1449, and this specimen shows that temporal emargination was weak to non-existent (17). Scale sulci are not visible on either UNMSM 1448 or 1449.

**Basicranium of paratypes.**—UNMSM 1448 and 1449 both show a v-shaped crest on the ventral surface of the basioccipitum. Posterior to this feature is a basicapital depression and anterior is midline ventral crest of the pterygoids. With some small amount of variation, morphology is typical of all definitive stem chelonoid and the crown as well as the erstwhile pan-chelonoids *Toxochelys* and the Lophocheleyinae.

Neither UNMSM 1448 nor 1449 show the osteology associated with the carotid arteries. In both specimens, the posterior entrance of the carotids may be discovered with additional preparation. The braincase of UNMSM 1449 is still fully encased in matrix and may be accessible through additional preparation or even CT scanning. The dorsal surface of the basioccipitum of UNMSM 1448 is partially preserved (Fig. 6.4) but has been damaged, perhaps during or after excavation. One processus clinoideus (left) is intact, but the other is completely missing. Posterior to the processus clinoideus the dorsum sellae is crushed. Both trabeculae of the rostrum basioccipitale are missing, but the medial ridge that lies posterior to the sella turcica is preserved. This feature is seen in extant Cheloniiidae and serves to separate the sella turcica from the dorsum sellae (16). The presence of the medial ridge also indicates that a rod-like rostrum basioccipitale was present (15).

**Lower jaws.**—Five specimens represent the lower jaw of *Pa. urbinai*. The most complete lower jaw is associated with UNMSM 1448, presently cemented to the ventral surface of the skull. The right ramus of the jaw is mostly missing (all except for its base). In addition to the dentary, the angular and surangular are visible on the left side. The surangular does not extend onto the dentary as it does in all extant chelonoids (8). UNMSM 1451 also includes a right ramus, but it is highly damaged and does not reveal any significant morphology.
Four specimens (UNMSM 1450–1453; Fig. 7) show a flat triturating surface of the dentary (6). None of these specimens show evidence of symphyseal ridges, even to the modest degree shown be some referred specimens of Pa. hutchisoni (Lynch and Parham, 2003, figs. 5A, D). Among the five known jaws, there is some variation in the proportions of the triturating surface. These can be attributed to the differential preservation. For example, the anterior portions of UNMSM 1450 and 1451 (Figs. 7.1, 7.2) are not preserved, giving these specimens a more blunt appearance. Even accounting for this morphology, UNMSM 1452 (Fig. 7.3) does appear to have a more elongate triturating surface. We do not consider these differences to be significant and therefore refer all specimens to Pa. urbaini.

Postcranial material (UNMSM 1448).—The postcranium of Pa. urbaini is known solely from a single specimen, UNMSM 1448. The preserved elements allow for six of the 18 postcranial characters of our matrix to be coded for Pa. urbaini (18, 23, 25, 26, 30, 34).

Cervical vertebrae (UNMSM 1448).—Seven partial or complete cervical vertebrae are preserved (Figs. 5.2, 8.1–3). The first cervical vertebra is fused to the occipital condyle of the skull (Fig. 5.2). The first cervical vertebra is mostly complete and has a distinctly concave posterior articulation. The rest of the preserved cervical series are preserved in articulation. Vertebræ two through six are complete, but the seventh cervical is missing its entire centrum. Vertebræ one through three are opisthocoelous, four is biconvex (Fig. 8.2), five and six are procoelous, and there were a platycoelous articulation between the sixth and the seventh vertebrae (23). Vertebræ two through six show strong ventral keels, and the height of the neural arch increases posteriorly. The eighth cervical vertebra is completely missing, so it cannot be compared to that described for Pa. hutchisoni (Lynch and Parham, 2003, fig. 5). Combining data from Pa. urbaini and Pa. hutchisoni, the composite Walther’s formula for the genus is 1(2)(3)(45)6(7)8; a common condition in Cheloniidae (Williams, 1950).

Pectoral apparatus (UNMSM 1448).—The humeri and pectoral girdles are preserved on both sides (Fig. 8.4–8.7). The humeri show the distally shifted lateral process and high angle between the shaft and capitum that is common to all chelonioid turtles (Parham, 2005). However, the lateral process is not as distally shifted and v-shaped (25) as in Cheloniidae. The coracoids (Fig. 7.6) are 7.4 cm long, making them longer than the humeri (7.2 cm) (26). The scapulae (Fig. 7.7) are 8.8 cm to the glenoid neck and form a wide angle with acromion (18). The radius and ulna of the right side are preserved. The radius (3.9 cm) is significantly longer than the ulna (3.4 cm) and shows two distinct rugosities. One rugosity is mid-shaft, marking the insertion of the musculus biceps superficialis, a primary flexor of the forelimb (Walker, 1973). The other rugosity is on the medial surface of the distal end and marks a strong attachment to the ulna. Both features are common to extant Cheloniidae, a clade that has rigid flippers and relies on forelimb flexion as their primary means to locomote. The presence of these radial rugosities may have phylogenetic significance, but their distribution among fossil forms is not documented.

Shell (UNMSM 1448).—The shell is represented by a partial carapace and a few non-descript plastron fragments, including a heavily damaged epiplastron fragment (not figured). The preserved carapace (Fig. 8.10) includes a nearly complete nuchal, a partial right first costal, and three peripherals on each side. There is no distinct sculpturing (34). The nuchal lacks post-nuchal fontanelles (3). A distinct rugosity on the ventral surface indicates an attachment for the eighth cervical vertebra. The three peripherals on the right side are articulated to the nuchal whereas the left side are articulated to one another but separate from the rest of the carapace (not figured). The third peripheral shows an insertion for the first costal rib, indicating that there are no supernumerary peripherals as in carettnes (31).

**Phylogenetic Analysis**

We performed a phylogenetic analysis of pan-cheloniid taxa, with an emphasis on stem cheloniids. The taxon-character data
matrix for this study (Appendices) is based on Brinkman et al. (2009), which was based on Lynch and Parham (2003), which was based on Parham and Fastovsky (1997), which was based, in part, on Hirayama (1994). We only exclude one character ("shape of skull") from Lynch and Parham (2003). Although there are obvious differences between narrow-skulled forms such as \textit{Pu. camperi}, \textit{Ere. imbricata}, and \textit{S. aegyptiacus} (Lydekker, 1889a) and broad skulled forms such as \textit{G. planimentum} (Owen, 1842) and \textit{Erq. gosseleti}, it is impossible to define the intermediate state in any explicit or repeatable way. In the process of checking the matrix from Brinkman et al. (2009), we also noted several changes from the codings given by Lynch and Parham (2003), which we mostly follow here. In some cases, but not all, Brinkman et al. (2009) provide an explanation for changing the coding of a character from Lynch and Parham (2003). In the present paper we provide alterations to the matrix of Brinkman et al. (2009) and, for the sake of explicitness, we justify changes by referring to specific references, figures, and even specimens. We hope that future researchers on pan-chelonioid phylogeny will follow suit and explicitly state and justify (with evidence) any changes to this matrix.

The phylogeny of the crown group Cheloniidae is well established by genetic analyses (Naro-Maciel et al., 2008), and so we use a backbone constraint tree to force the relationships in our analysis to conform to that phylogeny (Fig. 1). The effect of this constraint is small because, as shown by Parham and Fastovsky (1997), the morphological and genetic assessments of cheloniid phylogeny largely agree. Until recently, the only lingering uncertainty was on the placement of \textit{Natator depressus} (Garman, 1880). In contrast to the claim that Parham and Fastovsky (1997) hypothesized that \textit{N. depressus} shares a close affinity with carettnises (Naro-Maciel et al., 2008), the aforementioned authors did not resolve the position of \textit{N. depressus} with morphological characters. Recent studies place \textit{N. depressus} as either sister to the rest of the crown (Lynch and Parham, 2003; unconstrained analysis of the present study, not shown) or else in a polytomy with \textit{Ch. mydas} and the fossil species \textit{Syllomus aegyptiacus} (Brinkman et al., 2009). Naro-Maciel et al. (2008) confidently resolve \textit{N. depressus} as sister to \textit{Ch. mydas} and so that relationship is constrained in the present analysis.

Our matrix of 14 Operational Taxonomic Units (OTUs) and 35 characters (Appendix 2) was analyzed using the parsimony algorithm of PAUP* 4.0b10 (Swofford, 2002). Statistical support was calculated with 1000 bootstrap replicates and manually determining decay indices by searching for successively longer trees.

\textbf{Results.---}The result of our cladistic analysis is shown in Fig. 3. Our analysis retrieved three equally parsimonious trees of 65 steps. The only differences in the trees were among the relationships of \textit{Ar. cuneiceps} and \textit{Eochelone brabantica} Dollo, 1903. In our three trees, these two taxa were resolved as alternating successive outgroups to other Cenozoic forms or sister taxa. Our analysis confirms the placement of \textit{Mex. coahuilensis} as basal to the Lophochelyidae as postulated by Brinkman et al. (2009). The other fossil durophagous pan-cheloniids, including the former "Euclastes" \textit{Erq. gosseleti} and \textit{Pacifichelys}, are placed in a more crownward position. The relationships of these durophagous stem cheloniids (\textit{Erq. gosseleti}, \textit{Pacifichelys}) to other stem cheloniids (\textit{Ar. cuneiceps}, \textit{Eo. brabantica}, \textit{Pu. camperi}) remain poorly established, receiving no substantive decay index or bootstrap support. This uncertainty reflects an overall poor resolution of stem cheloniid phylogeny; the relationship among stem cheloniids has changed in every published analysis to date (e.g., Parham and Fastovsky, 1997; Lynch and Parham, 2006; Brinkman et al., 2009; this study). \textit{Erquelimesia gosseleti} and \textit{Pacifichelys} are hypothesized to be sister taxa based on their similar coding for characters directly and obviously correlated to durophagy (6, 7). The removal of either character results in \textit{Erq. gosseleti} and \textit{Pacifichelys} being placed as part of the stem-cheloniid
polytomy with Ar. cuneiceps and Eo. brabantica. Finally, previous studies (Lynch and Parham, 2003; Brinkman et al., 2009) placed S. aegyptiacus in a polytomy at the base of Cheloniidae, rendering its placement within or outside of the crown uncertain. In contrast to those studies, our analysis places S. aegyptiacus within the crown group Cheloniidae as sister to the extant flatback sea turtle, N. depressus. The exact position of S. aegyptiacus within the crown remains unstable, but its placement as a member of the crown group Cheloniidae garners relatively strong support.
that is why we recommend against lumping them all into the gous stem cheloniids cannot be accepted at face value, and pattern of homoplasy recovered by our analysis. Because of 2004) and can even be plastic within a single species independently within closely related turtle lineages (Claude, feeding ecology and correlated skull characters can evolve to tease apart convergent lineages. The fact that a durophagous similarity of their feeding apparatus. Because all other species of durophagous stem cheloniids are known only from cranial material, we cannot realistically expect cladistic analyses to indicate the hypothesized loss of this morphology. A, Assuming delayed transformation, shearing evolved two times; B, Assuming accelerated transformation, shearing evolved once and was lost in N. depressus.

FIGURE 9—Two equally parsimonious hypotheses about the evolution of a shearing feeding apparatus in cheloniid sea turtles. Circles with (+) indicate a hypothesized gain of this morphology whereas circles with (−) indicate the hypothesized loss of this morphology. A, Assuming delayed transformation, shearing evolved two times; B, Assuming accelerated transformation, shearing evolved once and was lost in N. depressus.

DISCUSSION

Naro-Maciel et al. (2008) reconstruct the evolution of dietary specialization in sea turtles by optimizing dietary data on their molecular phylogeny. They report that a specialized diet evolved independently three times within Chelonioida: in D. coriacea (cnidivory), in Ch. mydas (herbivory), and Ere. imbricata (spongivory). These three species each have uniquely specialized diets and were never considered to be sister taxa; therefore the conclusion that these diets were independently derived is not novel. However, by examining the morphology and phylogeny of extant and extinct species, it is possible to shed light on less obvious patterns of diet evolution in sea turtles. Spongivory and cnidivory have no reported osteological correlates, so their presence cannot be studied in fossil taxa. However, the optimization of crushing and shearing ecomorphs onto a phylogeny of pan-chelonioids (Fig. 3) helps show that these phenotypes evolved from a more generalized morphology at least seven times (three crushing, four shearing).

Three independent origins of durophagous specializations in pan-chelonioids is a minimum estimate because, as noted by Jalil et al. (2009), most durophagous stem-cheloniids are not well preserved enough to include in cladistic analyses. Furthermore, even the monophyly of the best-known forms, Erq. gosseleti and Pacificichelys, rests solely on the shared similarity of their feeding apparatus. Because all other species of durophagous stem-cheloniids are known only from cranial material, we cannot realistically expect cladistic analyses to tease apart convergent lineages. The fact that a durophagous feeding ecology and correlated skull characters can evolve independently within closely related turtle lineages (Claude, 2004) and can even be plastic within a single species (Dalrymple, 1977; Lindeman, 2000) further emphasizes the pattern of homoplasy recovered by our analysis. Because of this homoplasy, the monophyly of poorly known durophagous stem cheloniids cannot be accepted at face value, and that is why we recommend against lumping them all into the genus Euclastes.

The best way to further test the relationships of this complex is to provide more detailed descriptions of relevant material, especially those with preserved anatomy that evolved independently from diet (e.g., the postcranial skeleton and braincase). The Erq. gosseleti postcrania at the IRSReN and unpublished Eu. wielandi postcranial fossils from Morocco are two examples begging for additional study. Furthermore, even though Pa. urbinai is now one of the better-known durophagous stem cheloniids, nine of 35 characters are still coded as unknown (Appendix 1). It is possible to collect more material of this species from the Pisco Formation of Peru (Urbina and Lambert, pers. comm.), and so additional fieldwork could provide even more details of its morphology.

Setting the problematic stem cheloniid complex aside, it remains feasible to infer the timing of the origin of durophagy in stem cheloniid phylogeny. The first durophagous pan-chelonioid (Mex. coahuilensis, late Campanian) appears after the extinction of protostegids, which had previously diversified in the Early Cretaceous (Fig. 3; early Campanian; Hirayama, 1997). The timing of this origin, as well as the rapid diversification of pan-chelonioids in the Late Cretaceous in general, may correspond to the opening of ecological opportunities previously held by protostegids. By the Maastrichtian, Mex. coahuilensis was replaced by the durophagous stem cheloniids which survived into the middle Miocene.

In the modern sea turtle fauna, the carettines occupy the durophagous niche. The timing of caretteine origin bears on the pattern of ecological replacement established by the extinction and origin of protostegids, Mex. coahuilensis, and stem cheloniids in the Late Cretaceous. The evidence for the oldest diagnosable caretteines derives from dentaries reported from the middle Miocene (Serravalian, 13.6–11.6 mya) of the southeastern USA (Fort Green Mine, Hookers Prairie Mine; Dodd and Morgan, 1992; Figs. 3.8, 3.9). The first appearance of this durophagous lineage may just postdate Pacificichelys; Pa. hutchisoni is well constrained at 15.9–15.2 mya (see Systematic Paleontology), whereas estimates for the occurrence of Pa. urbinai lack chronostatigraphic precision (~16–11 mya). Additional stratigraphic study of the basal units of the Pisco Formation in Peru will help elucidate this temporal pattern.

At the present time, the occurrence of coeval crushing ecomorphs (2 spp. of Pacificichelys in the middle Miocene, 3 spp. of extant caretteines) can only be attributed to speciation within durophagous lineages, rather than the independent evolution of lineages into an occupied durophage niche. A similar pattern holds for shearing ecomorphs. According to our analysis, there were at least four independent origins of shearing ecomorphs among pan-chelonioids (Fig. 3). The only extant pan-chelonioid with this morphology, Ch. mydas, feeds almost exclusively on seagrass (Bjorndal, 1997). Sea grasses first appear in the Campanian, then proliferate in the Maastrichtian (van der Ham et al., 2007). This pattern generally coincides with the appearance and proliferation of this morphology in non-protostegid sea turtles. It is interesting to note that protostegids were already in decline by this time (Hirayama, 1994) and rarely evolved shearing ecomorphs (but see Bouliuchelys suteri Kear and Lee, 2006).

By the Maastrichtian, the pan-chelonioids Allopleuron hofmanni (Gray, 1831) and Mesodermochelys undulatus Hirayama and Chitoku, 1996 also exhibited shearing jaws. Mesodermochelys undulatus is the oldest dermochelyid, but the affinities of A. hofmanni remain controversial. Because our analysis does not include dermochelyid taxa or characters (see Phylogenetic Analysis: Cretaceous pan-chelonioids), we cannot discriminate whether these taxa evolved this morphology independently from one another or inherited it from a common ancestor. Nevertheless, the evolution of a shearing morphology in these forms does bolster the connection
between this morphology and the evolution of seagrass communities. For one, by the Maastrichtian, seagrasses are more common, thereby providing a more abundant and exploitable resource for sea turtles. Second, van der Ham et al. (2007) also note that within the Maastricht type section, *A. hofmanni* is always found closely associated with evidence of fossil seagrasses.

Following a short gap in the Paleocene during which no herbivorous sea turtles are yet reported (Fig. 3), the stem cheloniid *Ar. caneiceps* and its presumed close relative *Argillochelys antiqua* (König, 1825; Fig. 3.4) from the early Eocene represent a third iteration of the shearing ecomorphs. Following these taxa is a significant gap in the evidence, including an overall poor record for sea turtles in general (see “lack of integrated taxa” in Fig. 3).

The lack of relatively complete, well-described sea turtle fossils from the Oligocene makes it difficult to determine the polarity of some chelonian characters, including shearing specializations. Two taxa within Cheloniidae (*Ch. mydas, S. aegyptiacus*) have a highly ridged feeding apparatus, but the optimization of this feature onto the phylogeny is ambiguous. If one accepts a delayed transformation of this character state within the Cheloniidae (Fig. 9.1). If one accepts a rapid transformation for this state within the Cheloniidae, then *N. depressus* likely evolved from a shearing-specialized ancestor (Fig. 9.2). In this case, *N. depressus* would not retain the plesiomorphic, generalized, state as hypothesized by Naroc-Macid et al. (2008) but instead represents a secondary reversal. The ultimate resolution of this optimization is important, because the coeval occurrence of *Ch. mydas* lineage and *S. aegyptiacus* in the late Miocene impacts the proposed pattern of ecological replacement. A delayed optimization (Fig. 9.1) would suggest that the *Ch. mydas* lineage represents the evolution of a non-specialized form into an occupied herbivorous ecological niche rather than phylogenetic splitting within an already specialized lineage as proposed for other taxa. This ambiguity presents an incentive to collect and describe more sea turtle fossils from this time.

CONCLUSIONS

The emerging pattern of repeated ecomorph evolution in pan-chelonioids may represent ecological replacement following extincion, since the appearance of independently derived ecomorphs generally follows the disappearance of similarly adapted forms (Fig. 3). As shown in other taxa (Van Valkenburgh, 2007), the evolution of convergent ecomorphs is most clear among feeding extensions such as the crushing and shearing ecomorphs studied here. This convergent evolution occurs because turtles in general, and pan-chelonioaid sea turtles especially, have highly constrained bauplans. For pan-chelonioaid, we hypothesize that the structural constraints (e.g., those turtles in general, and pan-chelonioaid sea turtles especially, have highly constrained bauplans). For pan-chelonioaid, we hypothesize that the structural constraints of the turtle bauplan combined with the selective pressures of a marine environment provide limited channels for morphological evolution and ecological specialization.

The extinction and re-evolution of distinctive ecomorphs is termed “iterative evolution.” In sea turtles, the iterative evolution of feeding specializations occurs alongside a trend of increasing postcranial specialization through time, including the changes to the forelimb and shell. In the past, these patterns were obscured through the comparison of polyphyletic groups (e.g., Zangerl, 1980). But recent studies on sea turtle origins (Joyce, 2007) and specimen-based revisions of key/problematic taxa (Parham, 2005) are starting to reveal these patterns. Further teasing apart the morphological homoplasy associated with these macroevolutionary trends requires the description of relatively complete specimens. This necessity primarily results from the fact that most feeding specializations are restricted to the cranium, but postcranial morphology accounts for over half of the characters used in phylogenetic analysis. New discoveries and descriptions from middle Cenozoic taxa (Oligocene and Miocene; see “lack of integrated taxa” in Fig. 3) are sorely needed to bolster or refute the patterns presented here.

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following the example set by Joyce (2007). The only composite fossil taxa therefore potentially inappropriately chimeric OTUs. In doing so, we try to limit the assumptions associated with the construction of OTUs following the example set by Joyce (2007). The only composite fossil taxa in our study are Pacificichelys and the Cretaceous pan-cheloniods from the Western Interior Seaway of North America (Toxochelys and the Lophochelyinae, see below). We are confident in assuming monophyly for the genus Pacificichelys given the very strong phyletic similarity, temporal coincidence, and geographical proximity of Pa. huberti and Pa. urbini. The composite nature of the Cretaceous pan-cheloniod OTUs reflects the fact that the taxonomy of Toxochelys and the lophochelyids are in need of revision (Hirayama, 1997; Brinkman et al., 2009).

We are forced to exclude potentially relevant pan-cheloniod taxa known only from skulls (e.g., Nolichnemys baeri Brinkman, Hart, Janiszewski, and Colbert, 2008), which are somewhat different from known composite OTUs like Lophochelys and the pangochelyids. In general, descriptions of both cranial and postcranial material are required to phylogenetically place a taxon with any confidence. Future researchers ought to consider such a need when faced with the potential to collect complete or associated specimens from the field.

Outgroup.—The tree is rooted with a hypothetical outgroup constructed using predicted primitive states. These predictions are based upon comparison to the “macrobaenid” grade (sensu Parham and Hutchison, 2003) and other cryptodires that approximate the ancestral condition (see Joyce, 2007). Given the strong consistency of the hypothesis of Lepidochelyidae as the early crown group cryptodires and the specialized morphology of pan-cheloniods, we are confident in our polarity assessments even though the relationship of pan-cheloniods to a precise cryptodiran lineage or other fossil sea turtle clades (e.g., Protostegidae) remains unclear.

Cretaceous pan-cheloniods.—The recognition of Cretaceous pan-cheloniods Toxochelys and Clenchochelys Zangerl, 1953 as pan-cheloniods (i.e., closest to Chelonioidea that are stem to Cheloniidae) is supported by several morphologies (i.e., sister to the Chelonioidea plus D. coriacea) has varied among authors (Fig. 1). For example, Hirayama (1994, 1997, 1998) and Parham and Fastovsky (1997) consider them as within Chelonioidea, on the stem of Chelonioidea (i.e., pan-cheloniods). Other workers (Gaffney and Meylan, 1988; Kear and Lee, 2006) place these taxa outside crown group marine turtles, i.e., as stem cheloniods. The present matrix is not constructed to resolve this issue, which would require the inclusion of D. coriacea, other dermochelyids, various non-cheloniod cryptodires, and additional characters. The only study to include pan-cheloniods and a significant diversity of other cryptodires in a computer-assisted cladistic analysis is Joyce (2007). The preferred phylogenetic analysis of that study (Joyce, 2007:62) places T. latissimus Cope, 1873 as a stem cheloniod, supporting the hypotheses of Gaffney and Meylan (1988) and Kear and Lee (2006). Further resolution of this issue will require a re-analysis of Joyce (2007) to include additional characters and pan-cheloniod OTUs (e.g., a lophochelyine). Given the lingering uncertainty, we refrain from assigning our Toxochelys and Lophochelyinae (includes Ctenochelyidae) OTUs to the stem of Chelonioidea or Cheloniidae and refer to them as pan-cheloniods. We include three Cretaceous pan-cheloniod OTUs in our analysis of pan-cheloniods: Toxochelys, Lophochelyinae, and Mex. coahuilaensis. The codings for Toxochelys are based largely on the type species, T. latissimus, as described by Zangerl (1953) and Nicholls (1988). However, hindlimb characters (21–23) are based on Toxochelys moorevillensis Zangerl, 1953. The morphology of species assigned to the genus Toxochelys is rather homogenous, but see comments under character 1. The codings for Lophochelyinae are based several species, mostly assigned to the genus Ctenochelys. The alpha taxonomy of lophochelyine turtles has come under question by Hirayama (1997) and Brinkman et al. (2009) who speculated that the genus Lophochelys Zangerl, 1953 may simply represent juvenile specimens of other pan-cheloniods. The ultimate resolution of the nomenclatural issues surrounding lophochelyines will require careful examination and consideration of the type material; it is unclear whether Lophochelys or Ctenochelys or neither will end up being considered valid. But whatever the case, we consider the lophochelyine assemblage to be monophyletic and justify its inclusion in our analysis as a composite OTU. Ctenochelys stenoporus (Hay, 1905) was used to code characters 1–4, 6–9, 11–15, 18, 23, and 27 by reference to FMNH material, Zangerl (1953) and Matzke (2007). The original description and material of Ctenochelys tenuiseta Zangerl, 1953 was used to code characters 19–22, 24, 26, 31–36. Character 27 is based on the type specimen of Lophochelys naturix Zangerl, 1953. The original description and material of Ctenochelys acriti Zangerl, 1953 was used to code character 28. Character 29 was coded as polymorphic because lophochelyines include species with long plastria and species with short, wide plastria and it is impossible to know what the primitive state for the group is without a resolution of a lophochelyine phylogeny and aforementioned alpha taxonomic issues.
Similarly, character 30 was coded as polymorphic because the condition in USNM 357166 (Matzke, 2007) differs from that shown by other lophochelyines (Zangerl, 1953).

The third, and final Cretaceous pan-chelonioid used in this study is *Mex. coahuilaensis*. The codings for *Mex. coahuilaensis* are based entirely on Brinkman et al. (2009).

**Paleogene stem-chelonians.—** Four relatively well-known taxa that have traditionally been placed on the stem of Cheloniidae are included in our study. In past matrices, these taxa have been listed at the genus level; however, in our analysis these taxa are coded at the species level. The source of coding for this taxon is based largely on Owen and Bell (1849) and Moody (1970). We are unable to confirm the codings of several characters that have persisted in the literature since Hirayama (1994) so we leave these characters as uncertain. For example, the internal braincase characters of any specimen referred to *Argillochelys* has never been described or mentioned in the literature, yet nearly all matrices include codings for such features.

The skull of *Eochelone brabantica* Dollo, 1903 was described in detail by Casier (1968) and additional postcranial information can be gleaned from Moody (1970). Moody (1974) gives a detailed description of *Pa. camperi*, allowing for all characters to be scored. Finally, Zangerl (1971) provided the only detailed description of *Eq. gosseleti* to date. It is likely that there is a difference in the collection specimen at the IRPC to score more characters for *Eq. gosseleti* than we do here, but until this material is figured or else specifically described, we conservatively leave those characters blank.

**Neogene pan-chelonids.—** Two Neogene taxa, *S. aegyptiacus* and *Pacifichelys* are also included in this matrix. *Syllomus aegyptiacus* is known from relatively complete material from Japan and the USA (Weems, 1974, 1980; Hasegawa et al., 2005). *Pacifichelys* is scored based on *Pa. urbaini* (21 characters listed in the description) and by *Pa. nicotianus* (Lynch and Parham, 2003). *Pacifichelys nicotianus* contributes five additional characters to the *Pacifichelys* OTU (20, 21, 27, 28, 35) and requires that two other characters (9, 14) be coded as polymorphic.

**Extant Chelonidae.—** The six extant cheloniids are included as five OTUs. *Lepidochelys olivacea* and *Lepidochelys kempii* (Garman, 1880) are combined into one OTU (*Lepidochelys*) because they are identical for all characters used in this study. The other four OTUs are *Ca. caretta*, *Ch. mydas*, *Eretmochelys imbricata*, and *N. depressus*.

**CHARACTERS**

**Cranial Characters.—**

1. Secondary palate: (0) absent; (1) present; a secondary palate is defined here as a structure that is present in extant turtles and that is absent in *Syllomus* and *Ctenochelys*. The palate is considered to be present if a single foramen is present or if the secondary palate is seen in ventral view. Previously, the primitive and derived states of this character were coded as (0) absent and (1) present, but in this study we conservatively use the derived state (1) for all specimens.

2. Vomerine pillar visible in ventral view: (0) present; (1) absent, obscured by posterior extension of the triturating surface of the vomer.

3. Processus pterygoideus posterior: (0) wide; (1) narrow or lost.

4. Contact of vomer and premaxilla: (0) broad; (1) reduced.

5. Foramen caroticum laterale larger than foramen anterior canalis carotic interni: (0) absent; (1) present.

6. Tomial ridge: (0) pronounced; (1) low.

7. Gape: (0) open; (1) closed.

8. Shape of the anterior portion of the vomer in ventral view: (0) constant width; (1) variable width.

9. Palatine processus postnumerus: (0) absent; (1) present.

10. Direction of orbits: (0) dorsolaterally facing; (1) laterally facing.

11. Postmaxilla: (0) absent; (1) present.

12. Proximal processus petrogyoides externus: (0) absent; (1) present.

13. Fused premaxillae: (0) absent; (1) present.

14. Mid-ventral ridge on pterygoids: (0) absent; (1) present.

15. Tomial ridge: (0) pronounced; (1) low.

16. Processus petrogyoides externus: (0) large; (1) reduced.

17. Mid-ventral ridge on pterygoids: (0) absent; (1) present.

18. Shape of the anterior portion of the vomer in ventral view: (0) constant width; (1) variable width.

19. Cranial sutures on the prefrontal: (0) one pair; (1) two pairs.

20. Processus pterygoideus externus: (0) large; (1) reduced.

21. Processus pterygoideus externus: (0) absent; (1) present.

22. Foramen caroticum laterale larger than foramen anterior canalis carotic interni: (0) absent; (1) present.

23. Processus pterygoideus externus: (0) absent; (1) present.

24. Foramen caroticum laterale larger than foramen anterior canalis carotic interni: (0) absent; (1) present.

25. Mid-ventral ridge on pterygoids: (0) absent; (1) present.

26. Processus pterygoideus externus: (0) large; (1) reduced.

27. Fused premaxillae: (0) absent; (1) present.

28. Processus pterygoideus externus: (0) absent; (1) present.

29. Mid-ventral ridge on pterygoids: (0) absent; (1) present.

30. Processus pterygoideus externus: (0) absent; (1) present.

31. Processus pterygoideus externus: (0) absent; (1) present.

32. Fused premaxillae: (0) absent; (1) present.

33. Mid-ventral ridge on pterygoids: (0) absent; (1) present.

34. Processus pterygoideus externus: (0) large; (1) reduced.

35. Processus pterygoideus externus: (0) absent; (1) present.

36. Foramen caroticum laterale larger than foramen anterior canalis carotic interni: (0) absent; (1) present.

37. Mid-ventral ridge on pterygoids: (0) absent; (1) present.

38. Processus pterygoideus externus: (0) absent; (1) present.

39. Mid-ventral ridge on pterygoids: (0) absent; (1) present.

40. Processus pterygoideus externus: (0) large; (1) reduced.

41. Processus pterygoideus externus: (0) absent; (1) present.

42. Processus pterygoideus externus: (0) absent; (1) present.

43. Processus pterygoideus externus: (0) absent; (1) present.

44. Processus pterygoideus externus: (0) absent; (1) present.

45. Processus pterygoideus externus: (0) absent; (1) present.

46. Processus pterygoideus externus: (0) absent; (1) present.

47. Processus pterygoideus externus: (0) absent; (1) present.

48. Processus pterygoideus externus: (0) absent; (1) present.

49. Processus pterygoideus externus: (0) absent; (1) present.

50. Processus pterygoideus externus: (0) absent; (1) present.

51. Processus pterygoideus externus: (0) absent; (1) present.

52. Processus pterygoideus externus: (0) absent; (1) present.
19) Metischial process: (0) pronounced; (1) reduced; Brinkman et al. (2009) changed the coding for *Argillochelys* from the primitive state (0) to uncertain. We agree with this assessment for *Eo. cuineceps* as we can provide no evidence to the contrary. In most taxa, the difference between these two character states is obvious, with the crown group exhibiting the derived state of having very reduced metischial processes. The condition in *Pu. camperi*, however, is intermediate, and so we code it as such. As more material of stem chelonids is described, this character may require additional clarification and/or quantification.

20) Femoral trochanters: (0) separated by a fossa; (1) fossa obliterated; the coding for this femoral character and character 21 was reversed in Brinkman et al. (2009). This error is actually attributable to Lynch and Parham (2003) who reversed their characters 16 and 17. Brinkman et al. (2009) did not catch this error because the taxon they were using the matrix to place, *Mexit. coahuilensis*, does not have preserved femora.

21) Femoral trochanter ridge: (0) not complete; (1) complete, without a notch; the coding for this femoral character and character 20 was reversed in Brinkman et al. (2009). This error is actually attributable to Lynch and Parham (2003) who reversed their characters 16 and 17. Again, Brinkman et al. (2009) did not catch this error because the taxon they were using the matrix to place, *Mexit. coahuilensis*, does not have preserved femora.

22) Tibial pit for pubotibialis and flexor tibialis internus muscles: (0) absent; (1) present.

23) Centrum of seventh cervical vertebra: (0) procoelous; (1) platycoelous.

24) Articulations of first and second digits: (0) movable; (1) immovable; Brinkman et al. (2009) change the coding of the *Argillochelys* and *Sylloma* OTUs from uncertain (?) to the derived state (1) of having immoveable articulations of the first and second digits. As far as we know, specimens that show these characters have not been described. We further change the coding for *Eochelone* to (?). Moody (1970) described and figures the manus associated with the holotype of *Eo. brabantica*, but either the material or the description make a definitive decision on the articular surfaces impossible. As far as we know there are known other manus of stems referred to *Eochelone* known.

25) Humerus with v-shaped or triangular lateral process: (0) absent; (1) present.

26) Coracoid length in relation to humerus: (0) shorter; (1) longer; Hirayama (1994) coded *Ctenochelys* as being primitive for this feature, and this has been followed by all subsequent authors. We are unaware of any *Ctenochelys* specimens that have well preserved humeri and coracoids. However, the type specimen of *Lophochelys natatrix*, a taxon may be based on a juvenile (alluded to in Hirayama, 1997), does show a primitive state for this character and so we code the Lophochelyinae OTU as having the primitive state.

27) Seventh to eighth centrum articulation of the cervical vertebra: (0) single; (1) doubled; Brinkman et al. (2009) changed the coding of *Toxochelys* from derived (1) in Lynch and Parham (2003) to the primitive state (0). We agree with this assessment following the argumentation of Zangerl (1953:153). Brinkman et al. (2009) also change the coding for *Argillochelys* from primitive (0) to uncertain (?), but Moody (1970) states that a specimen *Ar. cuineceps* (SMC 10937) shows the primitive state (0).

**Appendix 2—Data matrix for phylogenetic analysis. Missing data are coded as "-". Polymorphic data (0 and 1) are coded as "&."**

<table>
<thead>
<tr>
<th>Outgroup</th>
<th>1</th>
<th>10</th>
<th>20</th>
<th>30</th>
</tr>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
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<td>0</td>
<td>0</td>
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<td>0</td>
</tr>
<tr>
<td><em>Ar. cuineceps</em></td>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Pacificichelys</em></td>
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<td>0</td>
</tr>
<tr>
<td><em>Pu. camperi</em></td>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
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<td>0</td>
</tr>
<tr>
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</tr>
<tr>
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</tr>
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</tr>
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