

# 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 urbinai* 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 (Cheloniodea Baur, 1893; Fig. 1) are divided into two clades, the Dermochelyidae Gray, 1825 and the Cheloniidae Bonaparte, 1832. Dermochelyids are represented by a single extant species, *Dermochelys coriacea* (Vandellius, 1761), a highly specialized, deep-diving, gigantothermic cnidivore 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 chelonids (six extant species of “hardshell” sea turtles) possess a carapace much more like other turtles. Chelonids possess morphological and physiological adaptations to a pelagic lifestyle, like *D. coriacea*, but some species also show feeding specializations that correspond to different diets (Bjorndal, 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 extant chelonids, as well as on macroevolutionary trends for the entire lineage (Pan-Cheloniodea).

In this study, we describe a new genus and species of a durophagous stem-chelonid 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-chelonids 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 Carettini 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 as a long-established molecular signal of monophyly (Dutton et al., 1996). For these reasons, Parham and Fastovsky (1997) proposed a phylogenetic definition for Carettini 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 Carettini more broadly, expanding it to include the related *Eretmochelys imbricata* (Linnaeus, 1766). This convention changes the traditional use of the name Carettini 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 Carettini as a clade that includes *Ca. caretta* and *Lepidochelys* and none of the other extant chelonids with the following definition: Carettini 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-Cheloniodea but rather an earlier, independent radiation of marine turtles. Consequently, the content of Cheloniodea in this paper differs from that of most previous authors (e.g., Hirayama, 1994, 1998). Understanding whether some

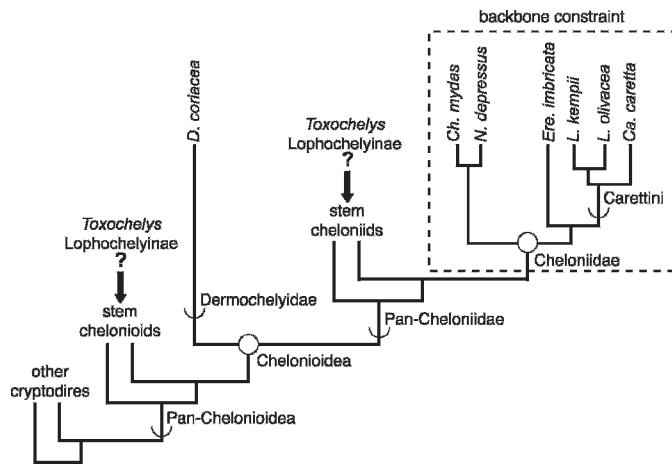


FIGURE 1—Diagram showing the phylogenetic taxonomy and cheloniid constraint tree used in this study. Full circles represent node-based definitions whereas semi-circles represent stem-based definitions. The controversial locations of *Toxochelys* and the Lophochelyiinae as either stem cheloniids or stem chelonioids are shown.

Cretaceous taxa are protostegids or pan-chelonioids, or where the dermochelyids fit within Pan-Chelonioidae, 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; IRScNB, 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, Aquillon-Martinez, de Leon Dávila, Jamniczky, 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 basishpenoid (14). Distinguished from early pan-chelonioids such as *Toxochelys* Cope, 1873 and the Lophochelyiinae Zangerl, 1953 by extensive secondary palate (1). Diagnosed from all pan-cheloniids by its lack of a rod-like rostrum basisphenoidale (15), a low dorsum sellae (16).

**Etymology.**—*Mexic-* for the country of Mexico, *-chelys* for turtle (Gr.).

**Discussion.**—In the original description of *Mex. coahuilaensis*, Brinkman et al. (2009) placed that species in the expanded concept of the genus *Euclastes* sensu Lynch and

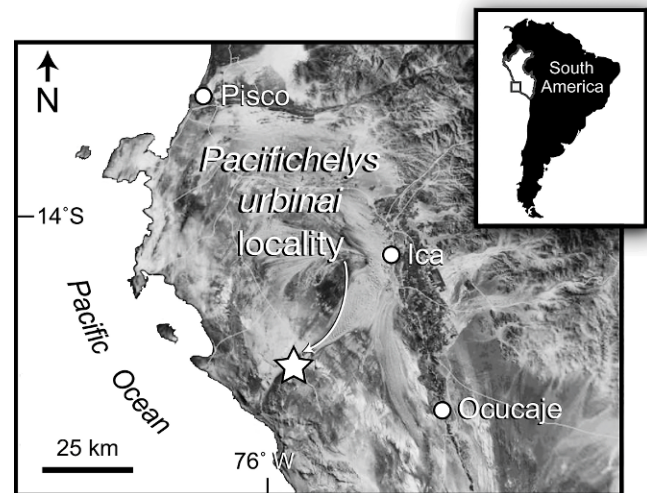


FIGURE 2—Type locality of *Pacificchelys urbinaei*, n. gen. n. sp., in the Pisco Basin of southern Peru.

Parham (2003), based on its secondary palate and overall similarity to 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*.

MEXICHELYS COAHUILENSIS (Brinkman, Aquillon-Martinez, De Leon Dávila, Jamniczky, Eberth, and Colbert, 2009)  
n. comb.

*Euclastes coahuilaensis* Brinkman, Carolina, Aquillon-Martinez, Dávila, Jamniczky, Eberth, and Colbert, 2009, p. 78 (original description).

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

CHELONIOIDEA Baur, 1893

PAN-CHELONIOIDAE Joyce, Parham, and Gauthier, 2004  
“DUROPHAGOUS STEM CHELONIIIDS”

*Osteopyginae* ZANGERL, 1953, p. 205.

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

“*Euclastes* group” JALIL, DE LAPPARENT DE BROIN, BARDET, VACANT, BOUYA, AMAGHZAZ, AND MESLOUH, 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*

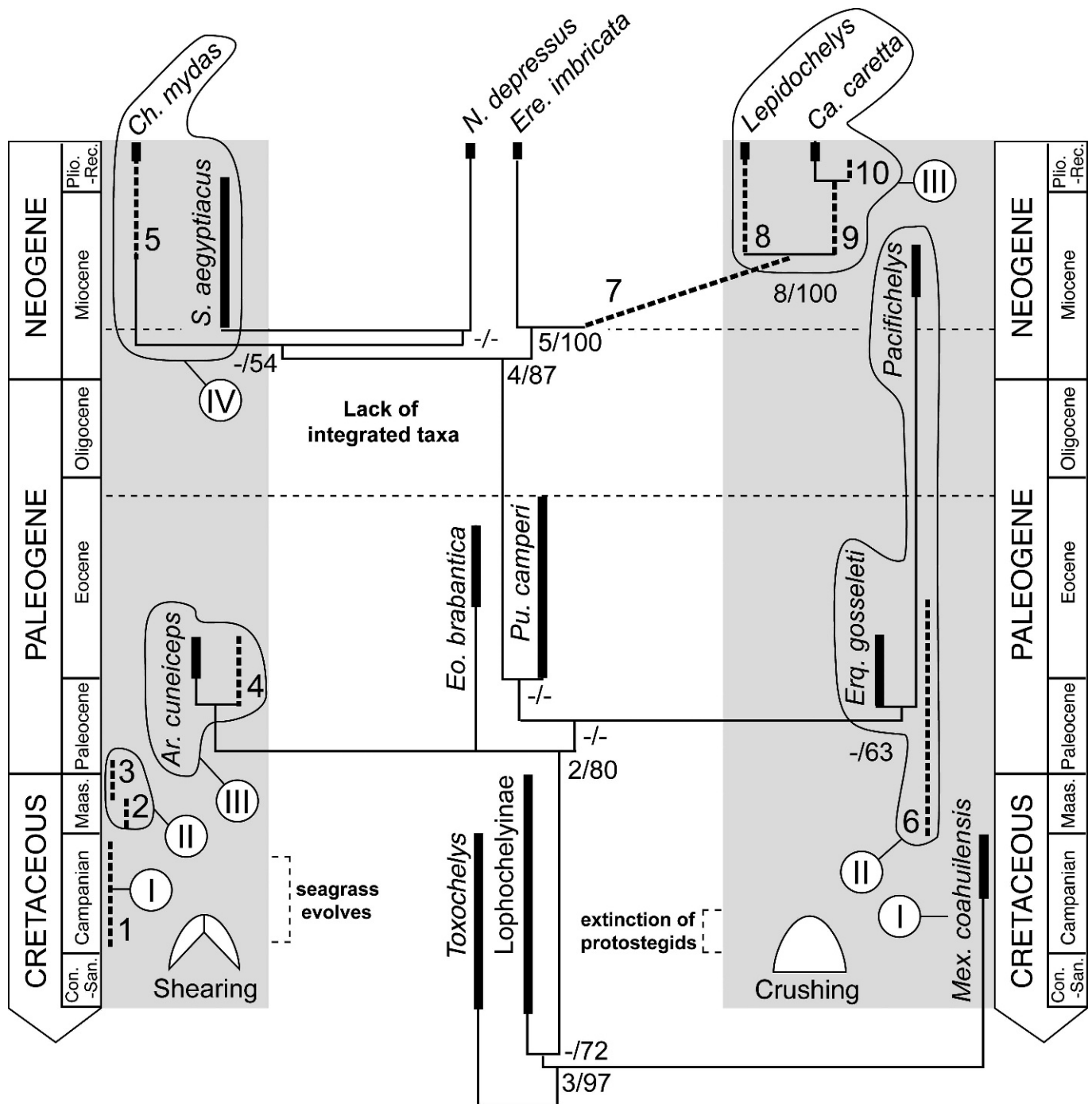


FIGURE 3—Phylogenetic hypothesis generated by this study. Numbers below nodes refer to support values (decay indices/bootstrap proportions). Values of “-” indicate decay indices of 1 or bootstraps of <50. Grey fields correspond to highly specialized feeders as indicated by thin dentaries with significant 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 cheloniids from *Eu. wielandi* to *G. planimentum*; 7, known range of pan-Carettini 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 cheloniids 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 cheloniid nor even a chelonioid, 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 Casadio, 2000). To resolve the status of “*Osteopygis*” skulls and perceived over-splitting, Lynch and Parham (2003) referred all assigned species of osteopygines to the oldest available genus name, *Euclastes*. Jalil et al. (2009) accepted the inappropriateness of using *Osteopygis* 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, of the eight species of hyper-durophagous stem cheloniids 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*.—*Erquelinnesia gosseleti*.

*Included species*.—*Erq. meridionalis* n. comb.

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

#### ERQUELINNESIA GOSSELETI (Dollo, 1886)

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

*Erquelinnesia gosseleti* DOLLO 1887, p. 393 (n. comb.).

*Euclastes gosseleti* DOLLO, 1888, p. 115 (n. comb.).

ERQUELINNESIA MERIDIONALIS (de la Fuente and Casadio, 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.).

*Erquelinnesia meridionalis* This study (n. comb.).

#### EUCLASTES Cope, 1867

*Rhetecheles* HAY, 1908, p. 162.

*Osteopygoides* KARL, TICHY, AND RUSCHAK, 1998, p. 332.

*Included species*.—*Euclastes* includes three species. The type species is *Eu. platyps*. There are two referred species, *Eu. acutirostris* Jalil, de Lapparent de Broin, Bardet, Vacant, Bouya, Amaghazaz, 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 platyps* Cope 1867 than to extant sea turtles or two relatively well-known Paleogene taxa. Unfortunately, the only known specimen of *Eu. platyps* (see Hay, 1908) is too incomplete to include in a phylogenetic analysis, and so its precise affinities to other pan-cheloniids remain cladistically untested. This situation could arguably discount the utility of this genus name; however, *Eu. platyps* is clearly a durophagous pan-cheloniid, and so it can be plausibly linked to phenetically similar, geographically proximal, and nearly contemporaneous durophagous pan-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, Amaghazaz, and Meslouh, 2009

#### EUCLASTES PLATYPS Cope, 1867

*Euclastes platyps* COPE, 1867, p. 41.

*Rhetecheles platyps* HAY, 1908, p. 162 (n. comb.).

#### EUCLASTES WIELANDI (Hay, 1908)

*Lytoloma angusta?* WIELAND, 1904, p. 183 (in part).

*Lytoloma wielandi* HAY, 1908, p. 157 (original description).

*Osteopygis borealis* HAY, 1908, p. 145 (in part).

*Erquelinnesia molaria* HAY, 1908, p. 160 (junior synonym).

*Osteopygis emarginatus* ZANGERL, 1953, p. 205 (in part)

*Osteopygis roundsi* WEEMS, 1988, p. 120 (junior synonym).

*Osteopygoides priscus* KARL, TICHY, AND RUSCHAK, 1998, p. 332 (junior synonym).

*Euclastes roundsi* LYNCH AND PARHAM, 2003, p. 23 (n. comb., junior synonym).

*Euclastes priscus* 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 crassicosata* OWEN AND BELL, 1849, p. 25 (in part)

*Thalassochelys planimentum* COPE, 1870, p. 146 (n. comb.).

*Puppigerus crassicosatus* COPE, 1870, p. 60 (in part).

*Glossochelys harvicensis* SEELEY, 1871, p. 227 (junior synonym).

*Pachyrhynchus planimentum* DOLLO, 1886, p. 138 (n. comb.).

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

*Glossochelys planimenta* 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-cheloniid, it lacks the dorsally directed orbits of *Euclastes* and the elongated secondary palate of *Erquelinnesia*. 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 urbinae* n. sp.

**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-chelonioid 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-chelonioids 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 tomial ridge (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-cheloniids by its wide skull and flat triturating surfaces (6, 7). Diagnosed from *Euclastes*, *Erquelinnesia*, and caretines by a vomerine pillar that is visible in ventral view (2). Further diagnosed from caretines by having a broad vomer-premaxillae contact on the palate (4), a low tomial 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 *Erquelinnesia* 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 cheloniid 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-cheloniids that otherwise had been replaced by the crown group.

#### PACIFICHELYS URBINAE 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 un-fused 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 ramphotheca.

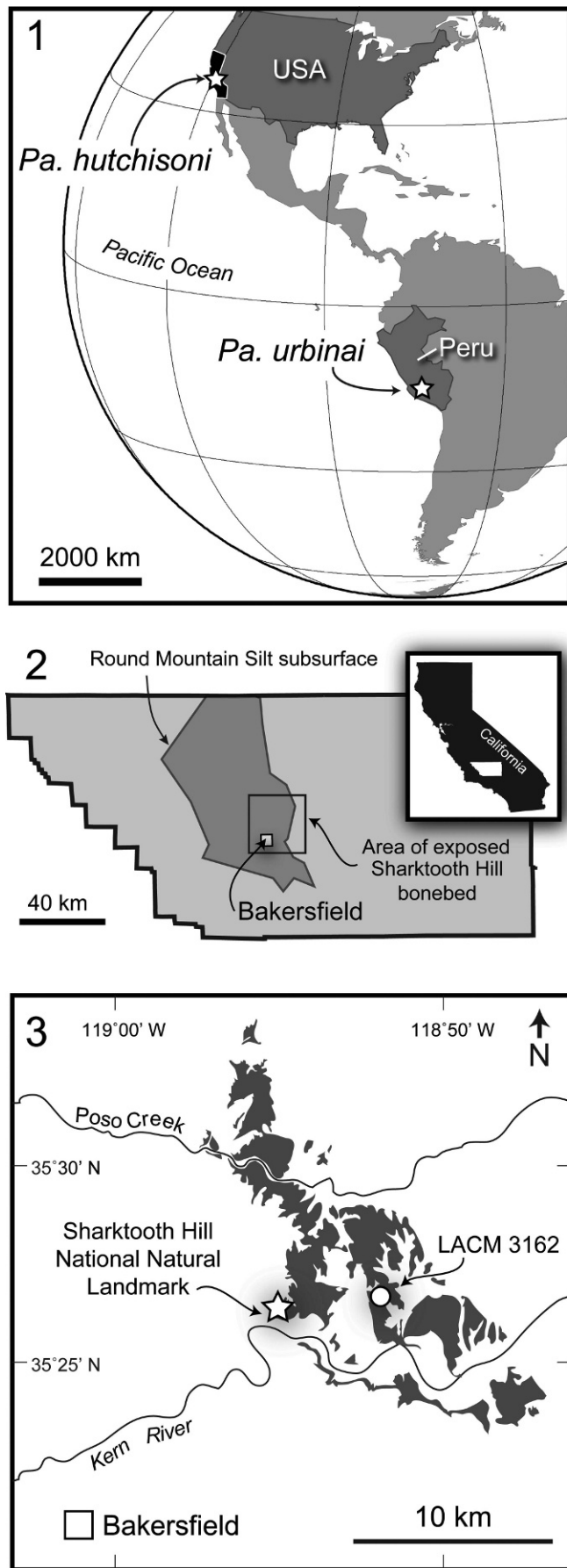
**Description.**—Broad skull in adults, secondary palate (1) with vomerine visible in ventral view (2), foramina palatinum posterius lost (3), broad contact of vomer with premaxillae (4), un-fused premaxillae (13), anterior width of vomer variable (9), low tomial ridge (7), processus pterygoideus externus 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 urbinae*” 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 *Incatella 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 *Pacificichelys 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). UNMSM 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 UNMSM 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

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FIGURE 4—1, Mercator plot of North and South America, showing localities of *Pacificichelys*; 2, Kern County, California, U.S.A., showing exposures of the Sharktooth Hill bonebed. Data on subsurface extent of the Round Mountain Silt from Pyenson et al. (2009); 3, detailed map for the type locality of *Pacificichelys hutchisoni*. Darkened outlines indicate mapped outcrop (see Pyenson et al., 2009).



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 basicranium. 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 postero-medial elements (exoccipitals, basisphenoid, 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 1449 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 caretines (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 tomial ridge (7). As in the holotype, both specimens show a low tomial ridge; however some variation is present. The tomial 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 tomial 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 durophagy with ontogeny. Aside from the tomial 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). Posteromedially, 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-cheloniids 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-chelonioids considered here (*Toxochelys*, *Lophochelyinae*, *Mex. coahuilensis*). UNMSM 1449 shows an arrangement of the jugal, postorbital, and quadratojugal (Fig. 6.2) that is typically pan-cheloniid. 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.

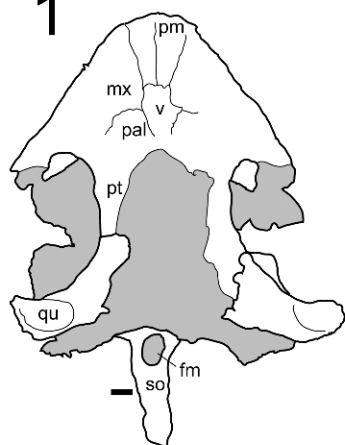
*Basicranium of paratypes.*—UNMSM 1448 and 1449 both show a v-shaped crest on the ventral surface of the basisphenoid. Posterior to this feature is a basioccipital depression and anterior is midline ventral crest of the pterygoids. With some small amount of variation, morphology is typical of all definitive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

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 basisphenoid of UNMSM 1448 is partially preserved (Fig. 6.4) but has been damaged, perhaps during or after excavation. One processus clinioideus (left) is intact, but the other is completely missing. Posterior to the processus clinioideus the dorsum sellae is crushed. Both trabeculae of the rostrum basisphenoidale are missing, but the medial ridge that lies posterior to the sella turcica is preserved. This feature is seen in extant Cheloniidae 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 basisphenoidale was present (15).

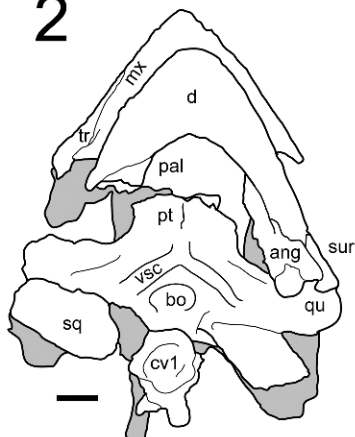
*Lower jaws.*—Five specimens represent the lower jaw of *Pa. urbinai*. The most complete lower jaw is associated with UNMSM 1448, presently cemented to the ventral surface of the skull. The right ramus of the jaw is mostly missing (all except for its base). In addition to the dentary, the angular and surangular are visible on the left side. The surangular does not extend onto the dentary as it does in all extant cheloniids (8). UNMSM 1451 also includes a right ramus, but it is highly damaged and does not reveal any significant morphology.



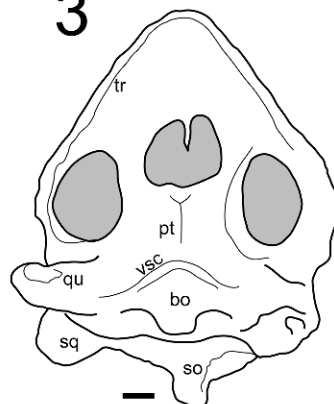
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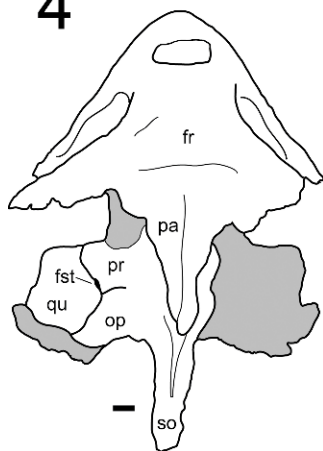
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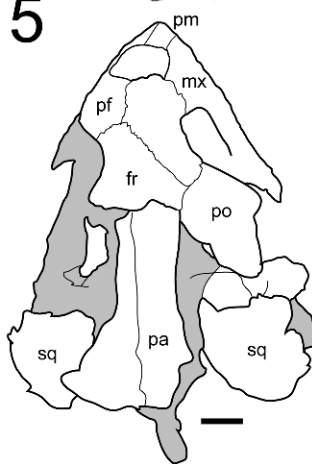
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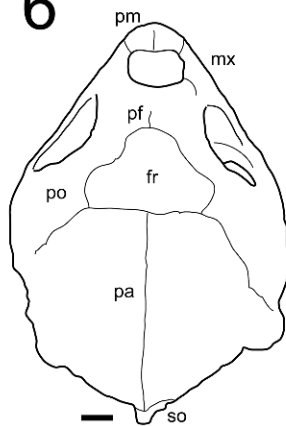
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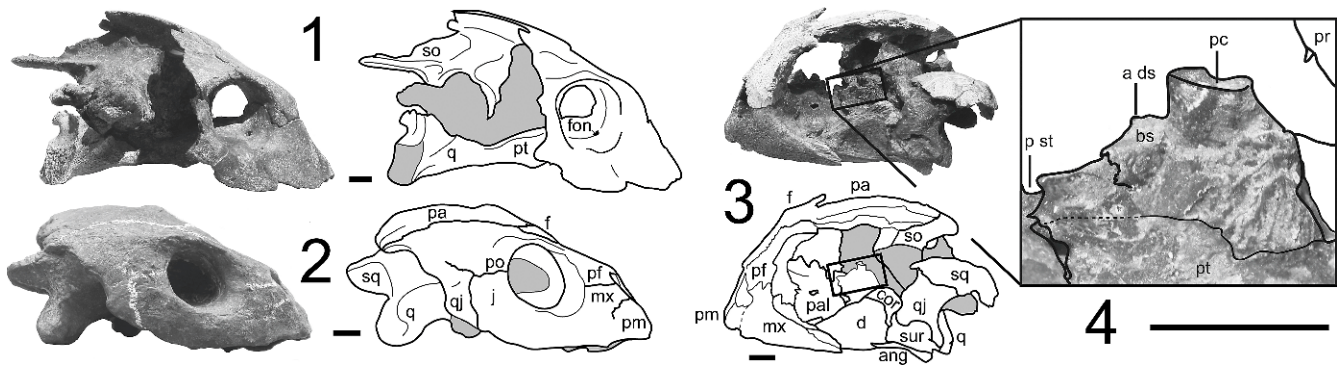


FIGURE 6—Referred skulls of *Pacifichelys urbinai* n. gen. n. sp. All scale bars = 1 cm. 1, UNMSM 1447 (holotype) in right lateral view; 2, UNMSM 1449 in right lateral view; 3, UNMSM 1448 in left lateral view; 4, enlarged view of the basisphenoid in oblique view. Abbreviations: a ds, anterior edge of dorsum sellae; ang, angular; bs, basisphenoid; d, dentary; fon, foramen oribito-nasale; j, jugal; mx, maxilla; p st, posterior edge of sella turcica; pa, parietal; pal, palatine; pc, processus clinoideus; pf, prefrontal; pm, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; su, surangular.

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 by 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. urbinai*.

**Postcranial material (UNMSM 1448).**—The postcranium of *Pa. urbinai* 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. urbinai* (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. Vertebrae two through six are complete, but the seventh cervical is missing its entire centrum. Vertebrae one through three are opisthocelous, four is biconvex (Fig. 8.2), five and six are procelous, and there was a platycoelous articulation between the sixth and the seventh vertebrae (23). Vertebrae 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. urbinai* and *Pa. hutchisoni*, the composite Walther's formula for the genus is (1(2(3(4)5)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 caput that is common to all chelonioid turtles (Parham, 2005). However, the lateral process is not as distally shifted or 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 forearm (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 forearm 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 caretines (31).

#### PHYLOGENETIC ANALYSIS

We performed a phylogenetic analysis of pan-chelonioid taxa, with an emphasis on stem cheloniids. The taxon-character data

FIGURE 5—Skulls of *Pacifichelys urbinai* n. gen. n. sp. All scale bars = 1 cm. 1, UNMSM 1447 (holotype) in ventral view; 2, UNMSM 1448 in ventral view; 3, UNMSM 1449 in ventral view; 4, UNMSM 1447 (holotype) in dorsal view; 5, UNMSM 1448 in dorsal view; 6, UNMSM 1449 in dorsal view. Abbreviations: ang, angular; bo, basioccipital; cv1, first cervical vertebrae; d, dentary; fm, foramen magnum; fr, frontal; fst, foramen stapediotemporal; mx, maxilla; op, opisthotic; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; qu, quadrate; so, supraoccipital; sq, squamosal; su, surangular; tr, tomial ridge; v, vomer; vsc, v-shaped crest of the basisphenoid.



FIGURE 7—Lower jaws referred to *Pacifichelys urbinai* n. gen. n. sp. Scale bar = 1 cm. 1, UNMSM 1451 in dorsal view; 2, UNMSM 1450 in dorsal view; 3, UNMSM 1452 in dorsal view; 4, UNMSM 1453 in dorsal view.

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 *Pu. camperi*, *Ere. imbricata*, and *S. aegyptiacus* (Lydekker, 1889a) and broad skulled forms such as *G. planimentum* (Owen, 1842) and *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 *Natator depressus* (Garman, 1880). In contrast to the claim that Parham and Fastovsky (1997) hypothesized that *N. depressus* shares a close affinity with caretines (Naro-Maciel et al., 2008), the aforementioned authors did not resolve the position of *N. depressus* with morphological characters. Recent studies place *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 *Ch. mydas* and the fossil species *Syllomus aegyptiacus* (Brinkman et al., 2009). Naro-Maciel et al. (2008) confidently resolve *N. depressus* as sister to *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.

**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 *Ar. cuneiceps* and *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 *Mex. coahuilensis* as basal to the Lophochelyiinae as postulated by Brinkman et al. (2009). The other fossil durophagous pan-cheloniids, including the former “*Eucastes*” *Erq. gosseleti* and *Pacifichelys*, are placed in a more crownward position. The relationships of these durophagous stem cheloniids (*Erq. gosseleti*, *Pacifichelys*) to other stem cheloniids (*Ar. cuneiceps*, *Eo. brabantica*, *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). *Erquelinnesia gosseleti* and *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 *Erq. gosseleti* and *Pacifichelys* being placed as part of the stem-cheloniid



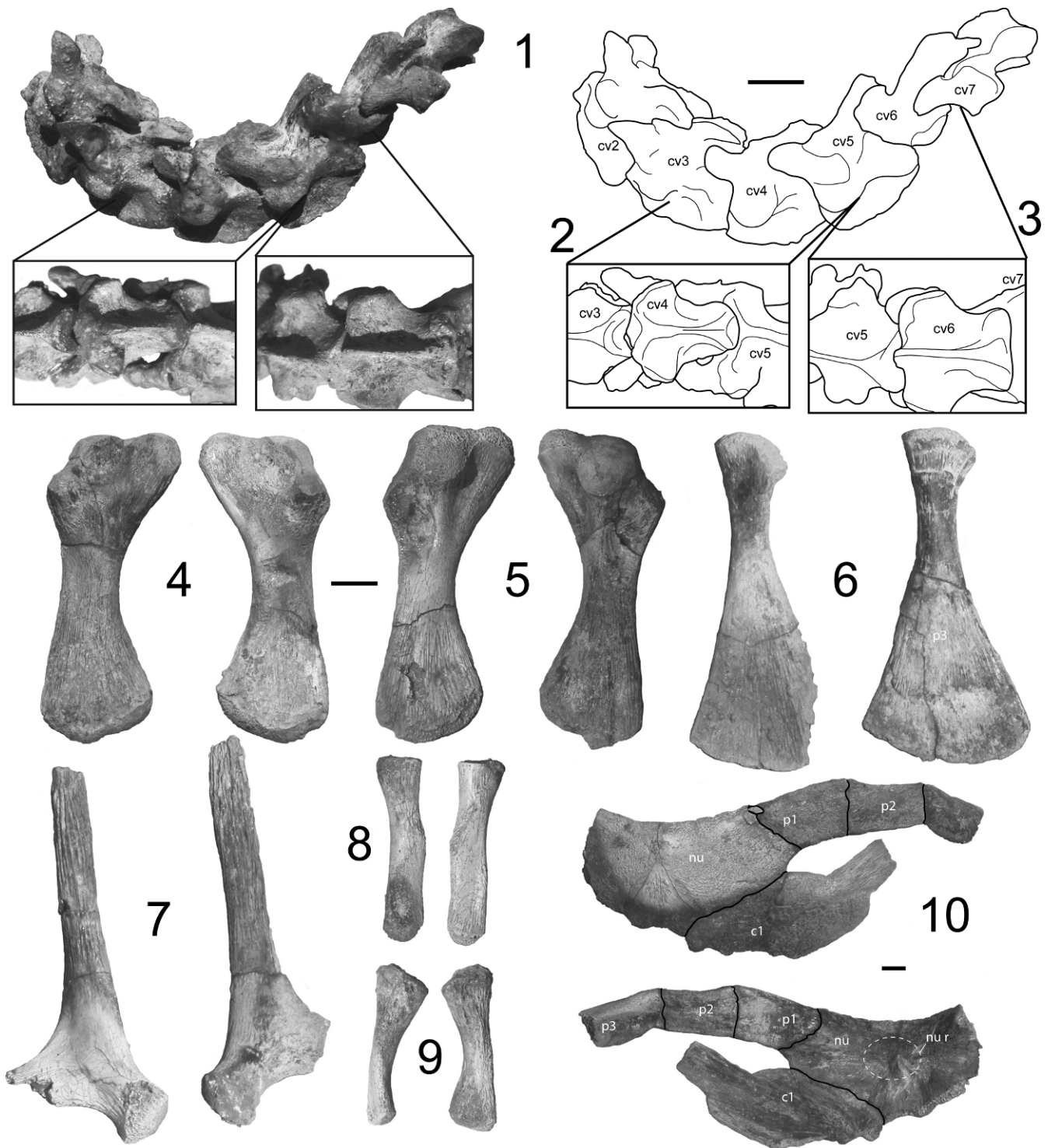


FIGURE 8—UNMSM 1448, postcranial material referred to *Pacificchelys urbinai* n. gen. n. sp. All scale bars = 1 cm. 1, cervical vertebrae 2–7 in right lateral view; 2, cervical vertebrae 3–5 in ventral view showing biconvex vertebra 4; 3, cervical vertebrae 5–7 in ventral view showing platycoelous articulation between 6 and 7; 4, left and right humeri in ventral view; 5, left and right humeri in dorsal view; 6, left and right coracoid in ventral and dorsal views respectively; 7, right and left scapulae in posterior view; 8, right radius, proximal side down; 9, right ulna, proximal side down; 10, anterior carapace in dorsal and ventral views. Abbreviations: c1, first costal; cv2–7, second to seventh cervical vertebrae; nu, nuchal; nu r, nuchal rugosity; p1–3, peripherals one through three.

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.



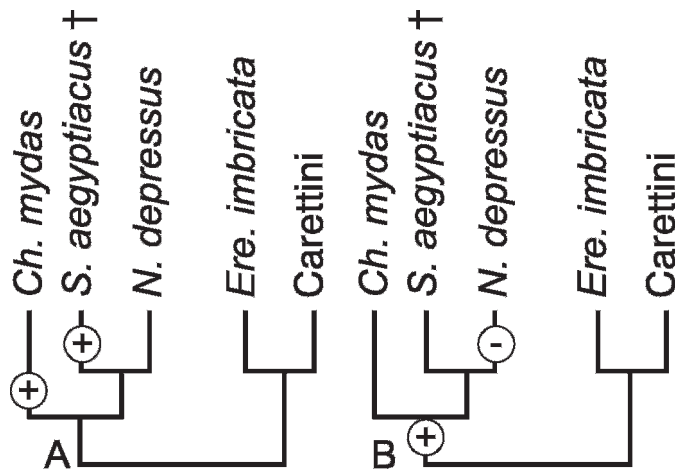


FIGURE 9—Two equally parsimonious hypotheses about the evolution of a shearing feeding apparatus in cheloniid sea turtles. Circles with (+) indicate a hypothesized gain of this morphology whereas circles with (-) indicate the hypothesized loss of this morphology. A, Assuming delayed transformation, shearing 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 Chelonioidae: 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-chelonioids are not well preserved enough to include in cladistic analyses. Furthermore, even the monophyly of the best-known forms, *Erq. gosseleti* and *Pacifichelys*, rests solely on the shared similarity of their feeding apparatus. Because all other species of durophagous stem-chelonioids 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 chelonioids 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 IRSNB 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 chelonioids, 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. coahuilaensis*, 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. coahuilaensis* was replaced by the durophagous stem chelonioids which survived into the middle Miocene.

In the modern sea turtle fauna, the caretines occupy the durophagous niche. The timing of caretine origin bears on the pattern of ecological replacement established by the extinction and origin of protostegids, *Mex. coahuilaensis*, and stem chelonioids in the Late Cretaceous. The evidence for the oldest diagnosable caretines derives from dentaries reported from the middle Miocene (Serravallo, 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 *Pacifichelys*; *Pa. hutchisoni* is well constrained at 15.9–15.2 mya (see Systematic Paleontology), whereas estimates for the occurrence of *Pa. urbinai* lack chronostratigraphic 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 *Pacifichelys* in the middle Miocene, 3 spp. of extant caretines) 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 *Bouliachelys 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. cuneiceps* 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 cheloniid 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, there would be two independent evolutions of shearing specializations within 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 Naro-Maciel 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 extinction, 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 extremes such as the crushing and shearing ecomorphs studied here. This convergent evolution occurs because turtles in general, and pan-chelonioid sea turtles especially, have highly constrained bauplans. For pan-chelonioids, 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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- Western Interior Seaway of North America (*Toxochelys* and the Lophochelyinae, see below). We are confident in assuming monophyly for the genus *Pacificchelys* given the very strong phenetic similarity, temporal coincidence, and geographic proximity of *Pa. hutchisoni* and *Pa. urbinai*. The composite nature of the Cretaceous pan-chelonoid OTUs reflects the fact that the taxonomy of *Toxochelys* and the lophochelyines are in need of revision (Hirayama, 1997; Brinkman et al., 2009).
- We are forced to exclude potentially relevant pan-chelonoid taxa known only from skulls (e.g., *Nichollssemys baeiri* Brinkman, Hart, Jamniczky, and Colbert, 2006, all three species of *Eucastes*) because their inclusion results in an unresolved polytomy. The necessity of this action highlights the fact that fossil sea turtles exhibit many homoplastic characters. 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 (often even vexing) morphological homogeneity of early crown group cryptodires and the specialized morphology of pan-chelonoids, we are confident in our polarity assessments even though the relationship of pan-chelonoids to a precise cryptodiran lineage or other fossil sea turtle clades (e.g., Protostegidae) remains unclear.
- Cretaceous pan-chelonoids.**—The recognition of Cretaceous pan-chelonoids *Toxochelys* and *Ctenochelys* Zangerl, 1953 as pan-chelonoids (i.e., closer to Cheloniidae than to *Dermochelys coriacea*) or stem chelonoids (i.e., sister to the Cheloniidae plus *D. coriacea*) has varied among authors (Fig. 1). For example, Hirayama (1994, 1997, 1998) and Parham and Fastovsky (1997) consider them as within Cheloniodea, on the stem of Cheloniidae (i.e., pan-chelonoids). Other workers (Gaffney and Meylan, 1988; Kear and Lee, 2006) place these taxa outside crown group marine turtles, i.e., as stem chelonoids. The present matrix is not constructed to resolve this issue, which would require the inclusion of *D. coriacea*, other dermochelyids, various non-chelonoid cryptodires, and additional characters. The only study to include pan-chelonoids 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. latiremis* Cope, 1873 as a stem chelonoid, 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-chelonoid OTUs (e.g., a lophochelyine). Given the lingering uncertainty, we refrain from assigning our *Toxochelys* and Lophochelyinae (includes *Ctenochelys*) OTUs to the stem of Cheloniodea or Cheloniidae and refer to them plainly as pan-chelonoids. We include three Cretaceous pan-chelonoid OTUs in our analysis of pan-chelonoids: *Toxochelys*, Lophochelyinae, and *Mex. coahuilaensis*.
- The codings for *Toxochelys* are based largely on the type species, *T. latiremis*, 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-chelonoids. 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 tenuitesta* Zangerl, 1953 was used to code characters 19–22, 24, 26, 31–36. Character 27 is based on the type specimen of *Lophochelys natatrix* Zangerl, 1953. The original description and material of *Ctenochelys acris* Zangerl, 1953 was used to code character 28. Character 29 was coded as polymorphic because lophochelyines include species with long plastra and species with short, wide plastra 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.

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#### APPENDIX 1

Discussion of operational taxonomic units and characters used in the phylogenetic analysis

#### OPERATIONAL TAXONOMIC UNITS

In this version of the matrix, we decrease the number of composite and 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 *Pacificchelys* and the Cretaceous pan-chelonoids from the

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-chelonoid used in this study is *Mex. coahuilaensis*. The codings for *Mex. coahuilaensis* are based entirely on Brinkman et al. (2009).

**Paleogene stem-cheloniids.**—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, which is adequate for monotypic genera such as *Puppigerus* Cope, 1870 and *Eochelone* Dollo, 1903. However, polytypic genera such as *Argillochelys* Lydekker, 1889b or *Euclastes*, may not be monophyletic. Therefore, it is important to state which species and citations exhibit the relevant characters as part of the documentation for the character matrix.

In this study we use the best-known species of *Argillochelys*, *Argillochelys cuneiceps* (Owen, 1849) instead of a composite OTU. Our 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 *Pu. camperi*, allowing for all characters to be scored. Finally, Zangerl (1971) provided the only detailed description of *Erq. gosseleti* to date. It is likely that there is sufficient material in the collections at the IRScNB to score more characters for *Erq. gosseleti* than we do here, but until this material is figured or else specifically described, we conservatively leave those characters blank.

**Neogene pan-cheloniids.**—Two Neogene taxa, *S. aegyptiacus* and *Pacificchelys* 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). *Pacificchelys* is scored based on *Pa. urbinai* (21 characters listed in the description) and by *Pa. hutchisoni* (Lynch and Parham, 2003). *Pacificchelys hutchisoni* contributes five additional characters to the *Pacificchelys* OTU (20, 21, 27, 28, 35) and requires that two other characters (9, 14) be coded as polymorphic.

**Extant Cheloniidae.**—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 by the (in this case bony) separation of the narial cavity from the oral cavity. For the purpose of most sea turtle matrices (Hirayama, 1994; Parham and Fastovsky, 1997; Lynch and Parham, 2003), the distinction between primitive and derived states is based on the presence or absence of distinct narial openings into the oral cavity. Taxa or OTUs that do not show distinct narial openings in ventral (palatal) view are traditionally coded as exhibiting the derived state.

Brinkman et al. (2009:87) code *Ctenochelys* as lacking a secondary palate based on the observation that the “relative position of the internal narial opening differs little from that of *Toxochelys*.” As defined above, the derived state (absence of narial openings in ventral view) is clearly present in specimens of *Ctenochelys* such as *Ctenochelys procax* (Hay, 1908) (CNHM UC 614; Zangerl, 1953:Pl. 19) and *Ctenochelys stenopora* (Hay, 1908) (AMNH 6137; Zangerl, 1953:Pl. 17). Along with AMNH 6137, Brinkman et al. (2009) cite USNM 391920 as evidence for the lack of a secondary palate. In addition to disagreeing with this characterization for AMNH 6137, we point out that USNM 391920 (described by Matzke, 2007) is a crushed juvenile specimen that is difficult to interpret. Matzke (2007) even characterizes this specimen as having an “incipient secondary palate” and notes that the development of the secondary palate is likely correlated to ontogeny.

The matter is further complicated by an important observation, reported by Brinkman et al. (2009), that a well-preserved specimen of *Toxochelys latiremis* (ROM 28563, described by Nicholls, 1988) has a palate that is similar to that described by specimens referred to *Ctenochelys*. This feature of ROM 28563 has not yet been illustrated, but if correct, would clearly prompt a reassessment of the distribution and

coding of this character. Other specimens referred to *Toxochelys latiremis* (AMNH 1497, AMNH 5118, YPM 3604, YPM 3609; Figured by Zangerl, 1953:pls.12, 13) show that a secondary palate (as defined here) is lacking and these specimens exhibit a different character state than in aforementioned specimens of *Ctenochelys*. Therefore, we submit that the condition in ROM 28563 may necessitate a polymorphic coding for *Toxochelys* rather than a reinterpretation of this character away from its traditional and accepted definition. We retain the coding of the derived state (1, secondary palate present) for *Ctenochelys*. And until the condition in ROM 28563 can be confirmed, we conservatively retain the primitive state (0, secondary palate absent) for *Toxochelys*.

As an additional clarification, we note that, whereas Brinkman et al. (2009:87) argued that *Ctenochelys* should be coded as having the primitive state (0) in the text, in their matrix (Brinkman et al., 2009, table 2) this taxon is coded as having the derived state (1). We agree with the coding in their matrix, but not coding they argued for in the text.

Brinkman et al. (2009) note that *Argillochelys* should “coded as being without a secondary palate based on illustrations from Owen and Bell (1849:Pl. XV, fig. 3) that show that the relative position of the internal narial opening are similar to those of *Eochelys*.” First, we think that Brinkman et al. (2009) actually mean *Eochelone*, the only Cenozoic stem chelonoid that is coded as having a primary palate, and not *Eochelys* Moody, 1968, an objective junior synonym of *Puppigerus* (a taxon with one of the more extensive secondary palates among pan-cheloniids). But when we compare *Ar. cuneiceps* (the type specimen, BMNH 41636, is figured by Owen and Bell [1849:pl. XVI] to *Eo. brabantica* (well figured by Casier, 1968), we cannot confirm this assessment. Whereas *Eo. brabantica* shows two distinct narial openings, the condition figured by Owen and Bell (1849) shows one irregularly shaped foramen, a condition that is not only different from *Eo. brabantica*, but also from any other panchelonoid. Additional illustration given by Moody (1970, fig. 35) does not show this single foramen and we think that the condition shown by Owen and Bell (1849) is not natural and may demonstrate a lack of preparation at that time. Furthermore, both the illustration given by Owen and Bell (1849) and Moody (1970) show a significant contribution to the secondary palate by the palatines. In this respect, *Ar. cuneiceps* differs significantly from *Eo. brabantica*. Pending additional description and figuring of BMNH 41636 or other specimens referred to *Ar. cuneiceps*, we conservatively retain the assumption that *Ar. cuneiceps* exhibits the derived state of a secondary palate.

2) Vomerine pillar visible in ventral view: (0) present; (1) absent, obscured by posterior extension of the triturating surface of the vomer; this character was created to accommodate the state seen in *Pacificchelys*. In both species of *Pacificchelys*, the vomerine pillar is visible in ventral view. Previously the primitive and derived states of this character coincided with those of the previous character.

3) Foramen palatinum posterius: (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 carotici interni: (0) absent; (1) present.

6) Dentary: (0) flat triturating surface; (1) lingual ridge present.

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

8) Surangular extending anteriorly onto dentary: (0) absent; (1) present.

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

10) Cranial scutes on the prefrontal: (0) one pair; (1) two pairs.

11) Processus pterygoideus externus: (0) large; (1) reduced; our coding for *Syllomus* differs from that of Brinkman et al. (2009). Hirayama (2005) shows that, whereas the posterior pterygoids are constricted in *Syllomus aegyptiacus*, there is no evidence for distinct processes in the anterior region. Instead, the condition of *Syllomus* is like the derived state shown by *Pu. camperi* and the crown clade (minus *Natator depressus*).

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

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

14) Mid-ventral ridge on pterygoids: (0) absent; (1) present; this character refers to the medial crest of the pterygoids that extends anteriorly from the v-shaped basisphenoid. Brinkman et al. (2009) refers to this as a crest on the “palate.”

15) Rod-like rostrum basisphenoidale: (0) absent; (1) present.

16) Dorsum sellae: (0) low; (1) high.

17) Temporal emargination: (0) distinct (reaching foramen stapedia-temporale); (1) weak.

### Non-shell Postcranial Characters.—

18) Dorsal process of scapula forming relatively wide angle with acromion: (0) absent; (1) present; in this character, “relatively wide angle” refers to an angle of over 110°. In most panchelonoids the angle is near 90°.

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

35) Shape of pygal: (0) notched posteriorly; (1) not notched—Brinkman et al. (2009) change the coding for *Argillochelys* from Lynch and Parham (2003) from uncertain (?) to derived (1). We are not sure what specimens or references this coding is from so we conservatively revert the coding for *Ar. cuineiceps* to uncertain (?).

[illegible]