TERLINGUACHELYS FISCHBECKI, A NEW GENUS AND SPECIES OF SEA TURTLE (CHELONIOIDEA: PROTOSTEGIDAE) FROM THE UPPER CRETACEOUS OF TEXAS

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ABSTRACT—Remains of a large sea turtle, *Terlinguachelys fischbecki* n. gen. and sp., were recovered from paralic deposits of the Upper Cretaceous (Campanian) Aguja Formation in Big Bend National Park, Texas. *T. fischbecki* is a primitive protostegid that retains a constricted humerus, well ossified plastron and costals, prominent retroarticular process on the lower jaw, and long slender femora; however, it has some features, such as a prominent tubercle at the base of the scapular acromion process, found elsewhere only in derived leatherback sea turtles. The unique combination of primitive and derived traits in *T. fischbecki* illustrates further diversity among Cretaceous sea turtles and another case of parallelism common in sea turtle phylogeny.

INTRODUCTION

SEA TURTLES (superfamily Chelonioidea) were diverse and abundant during Late Cretaceous time, and likely reached their peak diversity during the Campanian stage (Weems, 1988; Hirayama, 1997). They were the only major group of marine reptiles to survive the terminal Cretaceous mass extinction relatively unscathed. Remains of sea turtles are commonly preserved in the pelagic marine shale and chalk deposits that accumulated in the Late Cretaceous interior epeiric sea of North America. Most of these remains pertain to the extinct family Protostegidae. It is therefore of interest to report an unusual and previously unknown sea turtle from paralic Upper Cretaceous (Campanian) strata that accumulated along the western shore of the epeiric sea in Texas. The single and as yet only known specimen of this turtle is here designated the type of *Terlinguachelys fischbecki* n. gen. and sp. Recognition of this new species further increases the known diversity of Cretaceous sea turtles, and is of interest in examining the phylogeny of sea turtles. *T. fischbecki* is likely a primitive protostegid but has several features generally thought to be synapomorphic for more derived lineages, making its systematic placement uncertain. A brief description of this specimen was given previously by Tomlinson (1997).

Together, most marine turtles comprise a natural group (superfamily Chelonioidea). Of the six extant genera of sea turtles, five (*Caretta*, *Chelonia*, *Eretmochelys*, *Lepidochelys*, *Natator*) are allied together in family Cheloniidae, and one (*Dermochelys*) is the sole living representative of family Dermochelyidae. The extinct family Protostegidae is known only from Cretaceous strata. These three families of sea turtles are recognized by most authors and each comprises a relatively distinct and well-defined clade. However, some extinct taxa are hypothesized to represent near relatives or sister groups of one or several of these three families, and authors have interpreted such taxa alternatively as either constituting separate families (e.g., Toxochelyidae, Osteopygidae, Desmatochelyidae) or have included some or all within three more expansively defined conventional families. Retention of plesiomorphic features among their early representatives and parallel evolution in the separate lineages presents a problem of recognizing ''grades'' rather than clades, particularly among the least derived sea turtles. Nevertheless, in the following description and discussion, comparisons are made with other sea turtles, using the terms cheloniid, dermochelyid, and protostegid generally in a manner consistent with the phylogenetic hypothesis of Hirayama (1998), recognizing, however, that taxa included in each family vary among authors (see discussion of sea turtle relationships below).

GEOLOGIC SETTING

Stratigraphy.—The sea turtle specimen described in the present study was collected from the Aguja Formation, near the western border of Big Bend National Park in Brewster County, Texas. The Aguja Formation comprises an eastward-thinning wedge of paralic and marine sandstones interbedded to the west with mudstone and lignite deposited in coastal plain and fluvial environments (Fig. 1). The Aguja Formation is underlain by, and to the east intertongues with, marine shale of the Pen Formation. Two depositional sequences are represented in these deposits, the lower of which is present only in the western Big Bend region.

Lehman (1985) informally subdivided the Aguja Formation into several members. The basal sandstone member consists of progradational deltaic and littoral facies. It is overlain by the lower shale member, which consists of interbedded carbonaceous shale and lignite that accumulated in coastal marsh and swamps landward of the shoreline. A thin transgressive marine sandstone, the Rattlesnake Mountain sandstone member, overlies the lower shale disconformably and was deposited by landward retreat of a barrier island system and later submerged inner shelf shoals. The specimen described herein was collected from these paralic facies. A westward-thinning marine shale overlies the Rattlesnake Mountain sandstone. This marine shale unit, interposed within the Aguja, is informally referred to as the McKinney Springs tongue of the Pen Formation. Overlying this marine shale is the second depositional sequence of the Aguja, extensive over the entire Big Bend region. A progradational deltaic unit, the Terlingua Creek sandstone member, is overlain by the upper shale member which consists of mudstone, carbonaceous shale, and lenticular sandstone deposited in coastal plain and fluvial environments. Most of the known vertebrate fauna of the Aguja Formation has been collected from the upper shale member (Lehman, 1989; Rowe et al., 1992). The Aguja Formation is overlain by fluvial deposits of the Javelina Formation.

Institutional abbreviations.—The following institutional abbreviation is used: TMM, Texas Memorial Museum Vertebrate Paleontology Laboratory, Austin, Texas.

SYSTEMATIC PALEONTOLOGY

Superfamily CHELONIOIDEA Baur, 1893
Family PROTOSTEGIDAE Cope, 1872
Genus TERLINGUACHELYS new genus

Type species.—*Terlinguachelys fischbecki* n. sp., by monotypy.
Diagnosis.—As for the species, by monotypy.
Etymology.—After the town of Terlingua, Texas, and the creek of the same name that flows intermittently along the western border of Big Bend National Park, Texas. Folklore holds that the
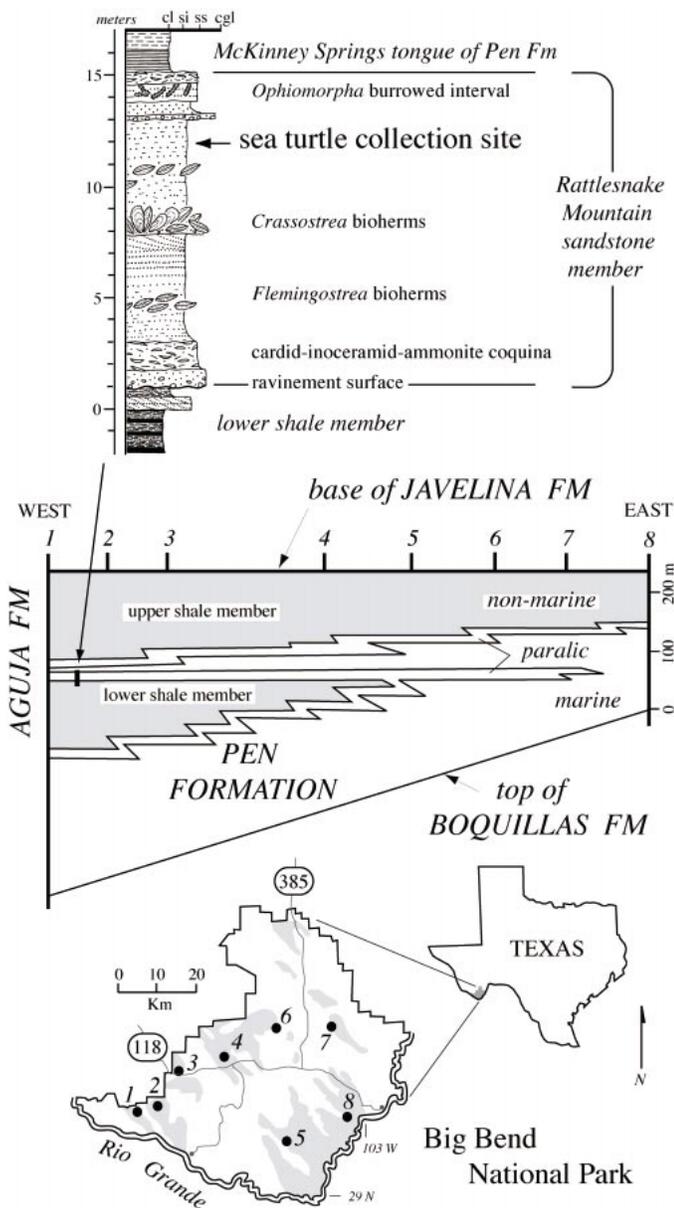
FIGURE *1*—Exposures of Upper Cretaceous sedimentary rocks in Big Bend National Park, Texas (below), and cross section showing stratigraphic relationships of the Aguja Formation, with details of the stratigraphy at the sea turtle collection site.

town of Terlingua derives its name from corruption of the Spanish *tres lenguas* for the three languages (Spanish, Apache, and English) originally spoken there. However, an alternative derivation is from the Apache word *tezlingo* which refers to a native plant, probably sotol, and the alcoholic drink made from it (Miles, 1993).

TERLINGUACHELYS FISCHBECKI new species
Figures 3–11

Diagnosis.—Large sea turtle (estimated carapace length 150 cm), with slender epiplastra having digitate anterior projection, high plastral index (length of bridge 103 percent of plastron half width), long hyo-hypoplastral suture with small lateral fontanelle (five percent of plastron half width), long femur (107 percent

humerus length) with small major and minor trochanters of similar size and only weakly connected posteriorly, mandible with sagittal symphyseal trough, narrow flat triturating surface with labial denticulations, mediolaterally expanded mandibular articulation, and large retroarticular process; scapula with short unconstricted glenoid neck and well-developed tubercle on the acromial process. Distinguished from other chelonioids by its unreduced posterior jaw elements and retroarticular process, large scapular acromion tubercle, and long femur retaining an intertrochanteric fossa.

Etymology.—After Mr. George R. Fischbeck, a science teacher who appeared on public television in New Mexico during the 1960s and inspired many children with an appreciation for science, including at that time the authors.

Type.—TMM 43072–1, a large, incomplete specimen consisting of the mandible and hyoid bone, fragmentary nuchal, neurals and costals, several segments of co-ossified peripherals, pygal and suprapygal, a large part of the plastron including the right epiplastron, hyoplastron, and hypoplastron, left hyoplastron, complete left scapula, complete right and left humeri, right and left ulnae, right radius, part of the left flipper including carpals, metacarpals, and phalanges, parts of the left ilium and ischium, right femur, and additional fragments of indeterminate nature or position.

The large size of this individual, the fully enclosed ectepicondylar foramen in the humerus, the thorough co-ossification of hyo- and hypoplastra, some of the peripheral bones, as well as the completely ossified and sharply delineated articular surfaces on limb elements all indicate that this was an old adult individual at the time of its death.

Occurrence.—TMM 43072–1 was collected by T. Lehman, W. Langston, E. Yarmer, and R. Rainey for the Texas Memorial Museum in 1987 (field designation WL-475). The collection site is in Big Bend National Park, north of the Castolon Road about 1.5 km east of the mouth of Santa Elena Canyon. Exact locality information is available from the Vertebrate Paleontology Laboratory at the Texas Memorial Museum in Austin, Texas. The specimen was collected from near the top of the Rattlesnake Mountain sandstone member of the Aguja Formation (Fig. 1). At the collection site, the Rattlesnake Mountain sandstone is 15 m thick; the specimen was found 12 m above the base of this unit (see Macon, 1994; his locality L3 on geologic map, fig. 1.5; and measured section A.6). Macon (1994) conducted a detailed study of the sedimentology of the Rattlesnake Mountain sandstone. The turtle was collected from ''yellow friable sandstone facies'' interpreted by Macon (1994) as middle and upper shoreface deposits that accumulated during landward retreat of a barrier island complex. The paleoshoreline trended roughly northwest-southeast through the Big Bend region at that time (Lehman, 1985; Macon, 1994). Fragmentary undiagnostic remains of sea turtles had previously been reported from this unit (e.g., TMM 41838–17, centrum of a shell vertebra; Lehman, 1985), and it is possible that these also pertain to *Terlinguachelys fischbecki.*

Age.—Dating of the Aguja Formation is based entirely on biostratigraphic correlation of its marine invertebrate fauna and terrestrial vertebrate fauna (Rowe et al., 1992; Cifelli, 1994; Lehman, 1997). No radiometric age determinations are yet available for this section. Collectively, the available biostratigraphic data indicate that the Aguja Formation ranges from middle to late Campanian in age. The upper part of the upper shale member probably extends into the early Maastrichtian (Lehman, 1985). The Rattlesnake Mountain sandstone member has yielded biostratigraphically significant inoceramid and ostreid bivalves, and the ammonites *Pachydiscus paulsoni*, *Baculites mclearni*, and *Hoplitoplacenticeras* cf. *H. plasticum*. These strongly suggest a middle Campanian age assignment for this unit (e.g., Cobban and Kennedy, 1992, 1993).
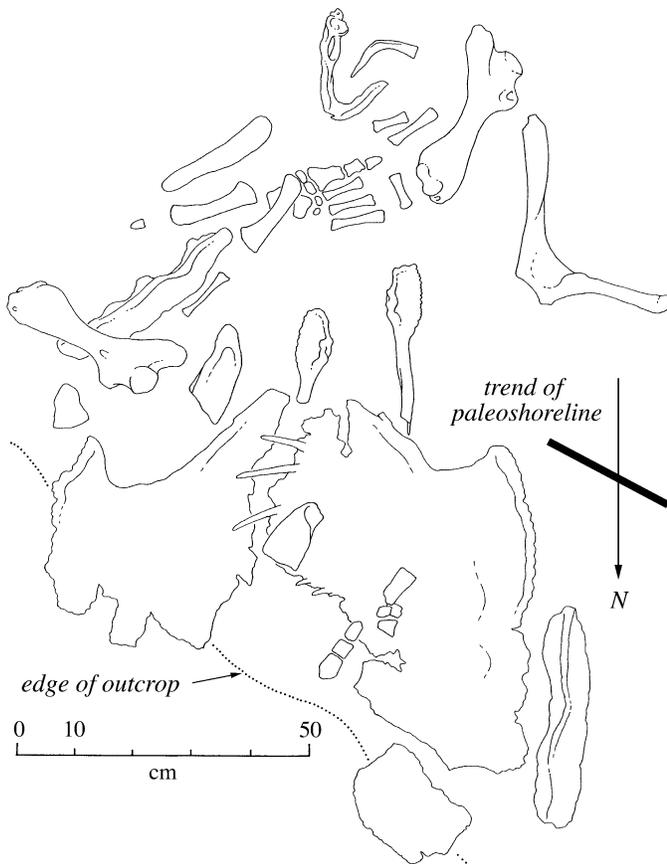
FIGURE 2—Diagram showing the positions of in situ skeletal elements of *Terlinguachelys fischbecki* n. gen. and sp. (TMM 43072-1) as preserved. Anterior limb elements were transported to the southwest (toward the paleoshoreline) relative to the plastron prior to burial.

Taphonomy.—When discovered, the rear end of the plastron was exposed and fragmented by erosion. Parts of the right femur were collected as surface float, but no other hindlimb elements were preserved. The carcass was resting on its plastron; the anterior end of the specimen had completely disarticulated but remained associated prior to burial (Fig. 2). Forelimb elements had been reoriented and aligned by wave or current action, but not far displaced. Part of one flipper remained articulated, perhaps still bound in connective tissue prior to burial. The skull, vertebrae, and many of the distal forelimb elements are missing, presumably transported away from the rest of the carcass. Most of the bones are well preserved, unabraded, and with fine surface detail; however, some (e.g., femur, pelvic bones) had deteriorated and lost much of the cortical bone prior to burial. These had perhaps been exposed at the sediment surface for a longer period. All of the bones suffered from relatively recent precipitation of a surficial gypsum crystal crust, probably due to alteration of pyrite when exposed in the modern soil environment. No obvious evidence for predation or scavenging of the carcass is evident. However, a few shark teeth (*Scapanorhynchus texanus*) were found, along with a layer of clay galls and carbonized plant debris associated with the skeleton. The sediment matrix of the specimen consists of crudely bedded very fine sandstone with *Ophiomorpha* burrows. These sediments accumulated in a shallow marine shoreface environment associated with ostreid (*Flemingostrea subspatulata* and *Crassostrea cusseta*), gastrochaenid, and cardid bivalves suggestive of normal marine salinities (Lehman, 1985;

Macon, 1994). The occurrence of this specimen in nearshore beach deposits is somewhat unusual, as articulated or associated remains of Cretaceous sea turtles are more commonly encountered in lagoonal or offshore marine shale and chalk (e.g., Meyer, 1991). However, all sea turtles return to beaches to nest.

DESCRIPTION

Lower jaw.—The right ramus of the lower jaw is preserved completely; the left ramus is broken through the dentary (Fig. 3). Although the bone surface is not well preserved, sutures between elements appear to be thoroughly co-ossified and are difficult to delineate. Strong longitudinal ridges follow the anterior external curvature of the dentary where the horny rhamphotheca would have been attached. Overall, the mandible is relatively small and slender considering the great size of the animal's shell. In dorsal view, the general form of the mandible is broad and U-shaped, rather than a tight ''V'' with the rami meeting at an acute angle, as for example in *Eretmochelys* (Carr, 1952). The rami meet at an angle of about 40 degrees. This is comparable to the average value found in extant cheloniids, where the range is from 35 degrees (*Eretmochelys*; Carr, 1952) to 50 degrees (*Natator*; Zangerl et al., 1988). Lower values are found in some protostegids (e.g., 25 degrees in *Archelon*, 32 degrees in *Protostega*; Nicholls et al., 1990) and higher values in some dermochelyids (e.g., 68 degrees in *Dermochelys*; Gaffney, 1979) and in *Toxochelys* (up to 85 degrees; Zangerl, 1953). The rami are narrow along their length up to the symphysis, and lack the wide triturating surface found in some modern cheloniids (e.g., *Lepidochelys*, *Caretta*; Carr, 1952).

The mandibular symphysis is completely fused and very short, only about 15 percent of the sagittal length of the mandible. Among extant cheloniids, this value ranges from 20 percent (*Chelonia*) to 33 percent (*Caretta*; Carr, 1952) and is as high as 41–58 percent in some fossil taxa (*Osteopygis* and *Erquelinnesia*, respectively; Foster, 1980). Low values are also found in dermochelyids (15 percent in *Dermochelys*; Gaffney, 1979). The symphysis in *Terlinguachelys* n. gen. is, however, almost twice the width of the triturating surface. Hence, this surface is also relatively very narrow. A sagittally extended triturating surface is in many chelonioids associated with development of a secondary palate, and is a prominent characteristic of osteopygines, but one also found to a lesser degree in other Cheloniidae (e.g., *Catapleura*, *Puppigerus*; Weems, 1988) and some Protostegidae (*Protostega*; Nicholls et al., 1990). The very narrow symphysis and triturating surface in *Terlinguachelys* suggests that it may have lacked a secondary palate; although the lower jaw is in many cases not a reliable indicator of palatal condition (Zangerl, 1980). In *Terlinguachelys*, the ventral border of the symphysis is slightly drawn posteriorly to form a small knob on the midline, as in many chelonioids.

The triturating surface in *Terlinguachelys* is of uniform width along its length, with labial and lingual ridges parallel to one another and of approximately equal height. The lingual ridge diminishes in height approaching the symphysis where it is absent, producing a narrow symphyseal trough. This contrasts with the condition in many sea turtles where the lingual ridge is raised and prominent, or forms a forward projection at the symphysis (e.g., *Natator*; Zangerl et al., 1988) but is similar to that in *Mesodermochelys* (Hirayama and Chitoku, 1996). In *Terlinguachelys*, there is no sagittal ridge on the triturating surface along the symphysis, as there is in many living and fossil chelonioids. A prominent sagittal ridge is found in some protostegids (e.g., *Desmatochelys*, *Calcarichelys*, *Chelosphargis*, *Rhinochelys*; Hooks, 1998; Nicholls, 1992; Collins, 1970), a weaker ridge occurs in many cheloniids (*Natator*, *Chelonia*, *Syllomus*; Carr, 1952; Zangerl et al., 1988), some species of *Toxochelys* (*T. moorevillensis*;
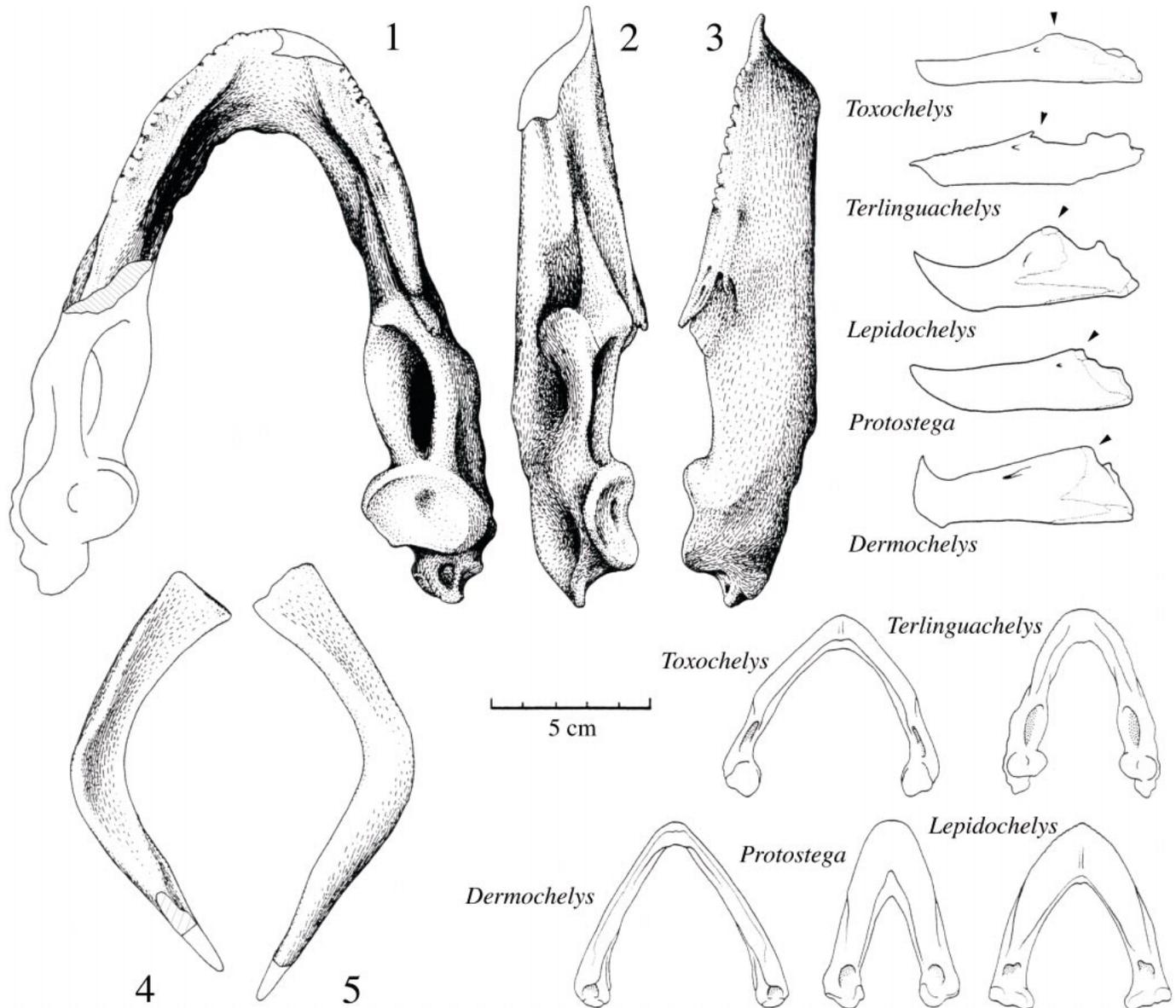
FIGURE 3—*Terlinguachelys fischbecki* n. gen. and sp. (TMM 43072-1) lower jaw in *1,* dorsal; *2,* medial; and *3,* lateral views; left first ceratobranchial in *4,* dorsal; and *5,* ventral views. Drawings compare sea turtle jaws in lateral and dorsal views, scaled to equal length (modified from Carr, 1952; Gaffney, 1979; Hirayama, 1994). Arrows indicate position of coronoid process.

Nicholls et al., 1990), and some dermochelyids (*Mesodermochelys*; Hirayama and Chitoku, 1996). The triturating surface itself is relatively flat, not concave as in most sea turtles (e.g., *Toxochelys* Nicholls et al., 1990). Faint ridges cross the triturating surface obliquely and merge to form coarse denticulations along the anterior three-fourths of the labial ridge. This contrasts with the condition in some chelonids where denticulations are instead found on the lingual ridge (*Chelonia*, *Natator*; Hirayama and Chitoku, 1996). The labial denticulations in *Terlinguachelys* are more pronounced than in *Eretmochelys* (Carr, 1952), but much weaker than the ''pseudodont'' denticulations in *Syllomus* (Weems, 1988). In *Terlinguachelys*, the coronoid does not appear to form any part of the triturating surface.

The articular region of the jaw is broad and well developed, in contrast to most chelonioids where the posterior section of the jaw is extremely reduced (e.g., Hirayama, 1994; Fig. 3). The dorsal opening of the fossa meckelii is very large, and the mandibular articulation is broad mediolaterally and inclined medially. There is a distinct retroarticular process with a shallow fossa on its dorsal surface pierced by a tiny foramen (the foramen posterius chorda tympani; Gaffney, 1979).

The lateral profile of the mandible is long and low, with the coronoid process at midlength, rather than shifted posteriorly as is typical in advanced chelonioids (Fig. 3.3). The posterodorsal end of the dentary is drawn upward to form a distinct dorsal ''spur'' marking the former posterior limit of the rhamphotheca, and a small opening (foramen dentofaciale majus; Gaffney, 1979) penetrates the lateral surface of the dentary directly below this. The posterior margin of the dentary appears to be nearly flush with the lateral face of the jaw, and does not expose a section of
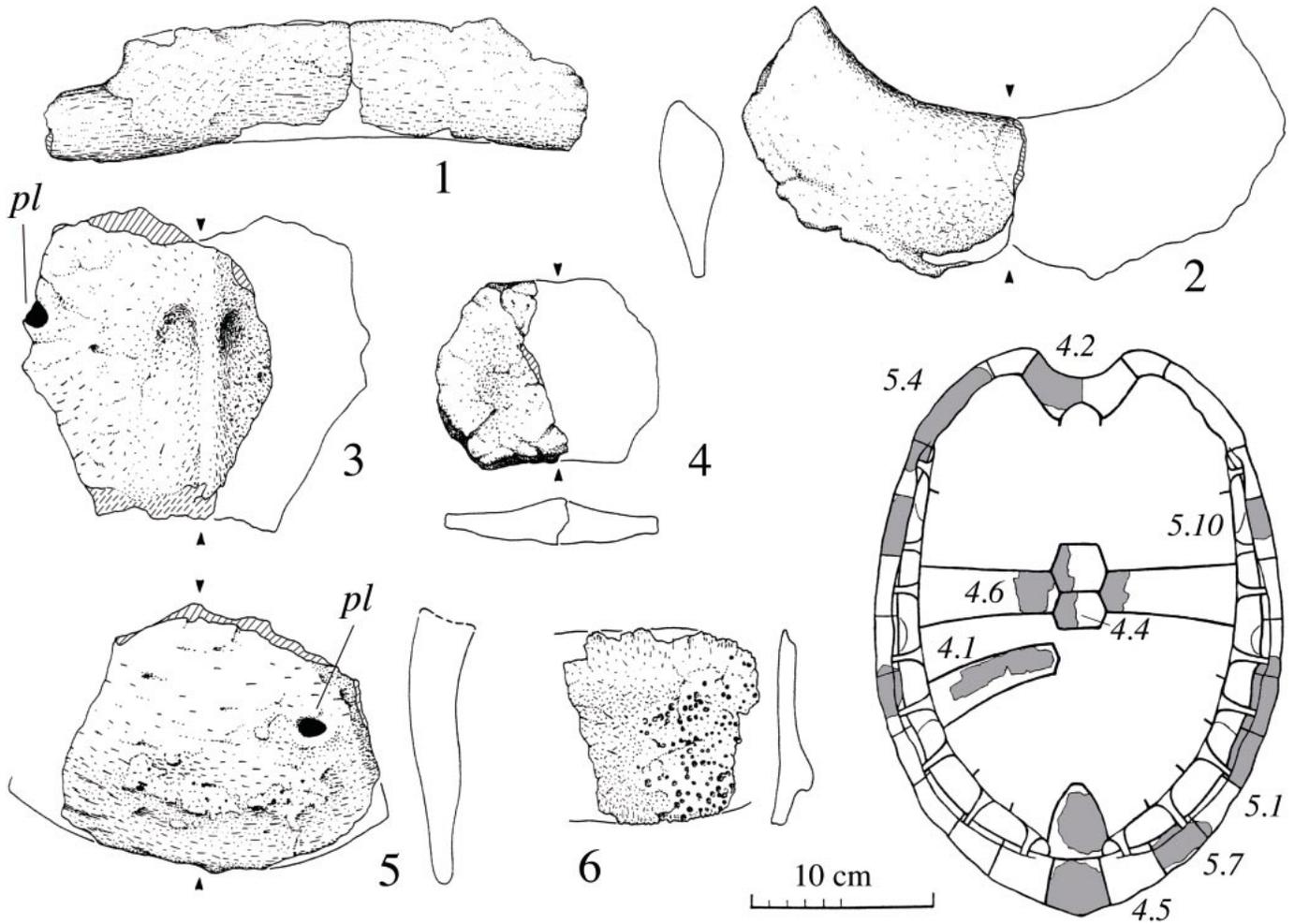
FIGURE *4*—*Terlinguachelys fischbecki* n. gen. and sp. (TMM 43072-1) fragments of carapace, including *1,* part of left posterior costal; *2,* left part of nuchal; *3,* ?suprapygal; *4,* part of neural; *5,* pygal; and *6,* proximal end of midcostal, with cross sections. Arrows indicate midline, pl = parasitic lesions. Diagrammatic reconstruction gives interpreted positions of preserved carapace fragments (shaded areas) with numbers corresponding to those in Figures 4 and 5.

the underlying surangular as in most modern cheloniids (Zangerl et al., 1988). The coronoid process is not elevated above the level of the dorsal spur of the dentary. This may be due in part to post-mortem distortion; both the coronoid and prearticular appear to be slightly displaced ventrally. Nevertheless, the mandible is not so dorsoventrally flattened as in *Puppigerus* or *Tasbacka* (Tong and Hirayama, 2002). The anterior end of the dentary does not form an elevated or recurved dorsal ''hook'' (e.g., *Dermochelys*; Gaffney, 1979); instead, the labial ridge curls forward to form a thin anteriorly projecting ''lip.''

A shallow groove (sulcus cartilaginis meckelii; Gaffney, 1979) passes along the medial surface of the dentary (Fig. 3.2). The splenial is missing, probably due to postmortem loss. There appear to be contact surfaces for the splenial between the anterior processes of the coronoid and prearticular. An opening (foramen intermandibularis caudalis; Gaffney, 1979) is present along the contact between the prearticular and angular, although the thin bone in this area is broken and the original limits of the foramen are uncertain.

Hyoid apparatus.—The first ceratobranchial of the left side was preserved lying between the rami of the lower jaw; it is well preserved though missing a small piece of the distal (posterior)

tip (Fig. 3.4, 3.5). It is very well ossified throughout. The antero-medial process for articulation with the hyoid body is wide, flattened, and mildly concave on its dorsal face. The bone narrows posterolaterally and is curved and twisted longitudinally. In relative length, width, and curvature, this element compares favorably with that in *Natator depressus* (Zangerl et al., 1988). It is broader, shorter, and more strongly curved than in *Chelonia mydas* and *Caretta caretta* (Zangerl et al., 1988), or in *Desmatochelys lowi* (Elliot et al., 1997).

Carapace.—Little of the carapace is preserved (Figs. 4, 5). There are parts of several neurals (none preserved completely), parts of three costals, half of the nuchal, three large sections of co-ossified peripherals and parts of several others, the pygal and suprapygal, as well as parts not determinable as to their position. All parts of the carapace are mildly to severely weathered. Where preserved, the external bone surface texture consists of low irregular rounded nodes separated by scattered tiny pits (''nutrient foramina'' of authors) and thin discontinuous grooves over a finely ''cross-hatched'' bone tissue. Clusters of larger circular pits, reminiscent of those in trionychid turtles, are present on the proximal parts of the costals (Fig. 4.6), but the preserved elements lack
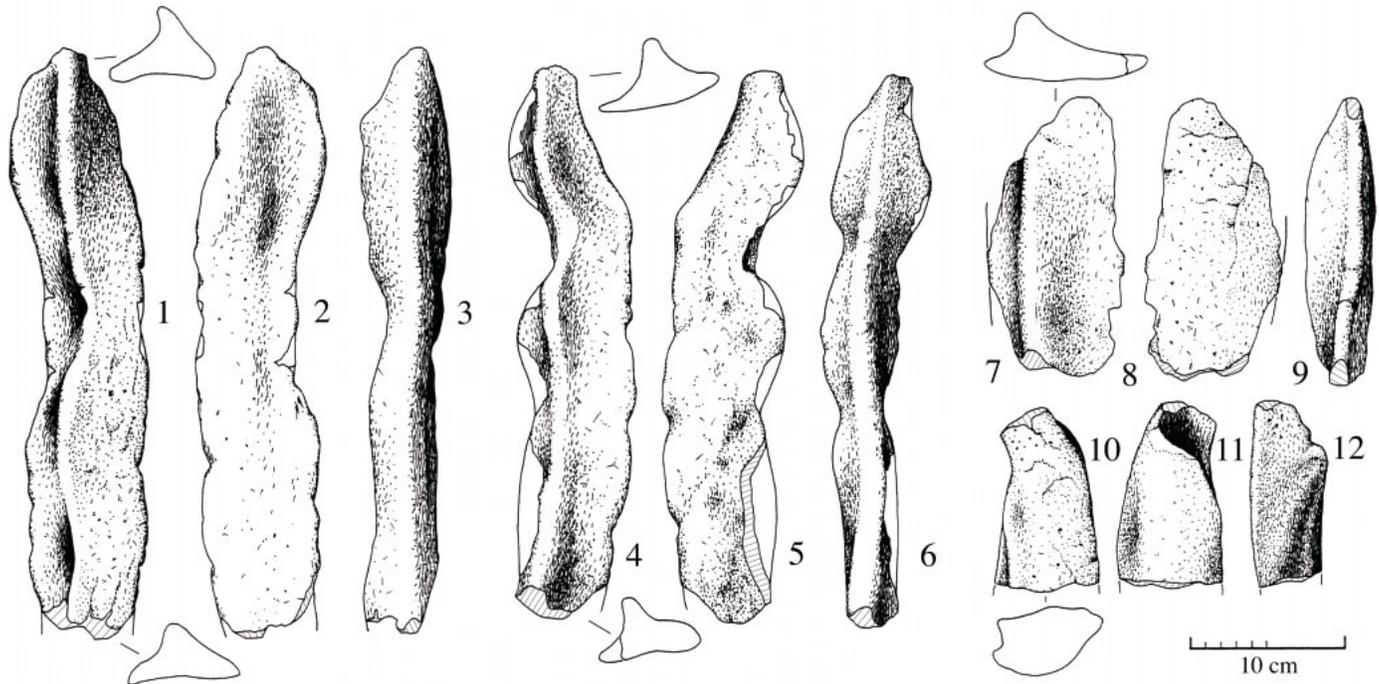
FIGURE 5—*Terlinguachelys fischbecki* n. gen. and sp. (TMM 43072-1) parts of co-ossified right ?sixth through eighth peripherals in *1,* dorsal; *2,* ventral; and *3,* lateral views; parts of ?second and third peripherals in *4,* dorsal; *5,* ventral; and *6,* lateral views; right ?tenth peripheral in *7,* dorsal; *8,* ventral; and *9,* lateral views; part of right ?fourth peripheral in *10,* dorsal; *11,* ventral; and *12,* lateral views. Interpreted positions are shown on reconstruction of carapace in Figure 4.

coarsely pitted or corrugated surface ornament (e.g., as in *Syllomus*; Weems, 1974).

Together the preserved parts are sufficient to indicate that ossification of the carapace was reduced in *Terlinguachelys*, though certainly not to the extent seen in derived protostegids and dermochelyids. The peripherals are relatively very narrow compared to the great width of the shell (as determined from the plastron), and judging from the very thin medial edges of the peripherals, where preserved, there likely were continuous well-developed costoperipheral fontanelles. None of the preserved peripherals is sutured to a costal, and this specimen is an aged individual. The restoration of the carapace given here assumes that 11 pairs of peripherals and eight pairs of costals were present, as is typical in cheloniids (Fig. 4).

The neurals appear to be broad and hexagonal in outline, as in cheloniids, rather than narrow and rectangular as in protostegids and dermochelyids (Hirayama, 1994), although their exact shape is uncertain. The neurals are thick (up to 30 mm) with an elevated keel along the midline, and thin abruptly to 10 mm along their edges. There are no traces of scute sulci on the preserved neural fragments. The proximal ends of two midcostals are at least 110 mm in width, and typically about 10 mm in thickness, although none of their edges is fully preserved. A larger segment of a posterior costal has most of its surface dermal bone covering abraded, but is at least 300 mm long, with the free distal end of the rib 40 mm in width (Fig. 4.1). The left half of the nuchal is preserved, and indicates that the shell margin was deeply indented along the midline, as in many chelonioids. There is no evidence for a ventral knob on the preserved part of the nuchal. The anterior margin of the nuchal is thick (40 mm) and rounded, but the bone thins abruptly along its posterior edge (Fig. 4.2). Along the midline, the posterior edge appears to be indented (although this may be due to breakage) where it would have met the first neural.

Three segments of co-ossified peripherals, and parts of several others, are each from a different part of the carapace and together provide a general indication of the form of the shell margin. These segments appear to represent the second and third (Fig. 5.4–5.6), fourth (Fig. 5.10–5.12), sixth through eighth (Fig. 5.1–5.3), and tenth (Fig. 5.7–5.9); with their position interpreted by a gradual increase in width posteriorly and change in cross-sectional form. Each segment seems to retain its natural curvature. No scute sulci are apparent and the sutures between peripherals are difficult to discern. The medial faces of the peripherals are shallowly, not deeply, indented. There are only broad depressions, not well defined or deep sockets for articulation with the ribs, as are found in some basal cheloniids (e.g., *Toxochelys*, *Osteopygis*). The ventral faces of the peripherals are wider, extend farther medially, and are mildly concave, particularly from sixth through tenth. The dorsal faces are flat or weakly concave. Where preserved, the medial margins of both dorsal and ventral faces are irregularly scalloped. The angle of divergence between dorsal and ventral faces of the peripherals (45–50 degrees in the midperipherals) suggests a highly arched, rather than compressed shell form (e.g., compared with 10–20 degree angle of divergence in posterior peripherals of *Osteopygis*; Hay, 1908). Where the lateral edges of the peripherals are preserved, there is a slight indication of a weakly scalloped shell margin.

The third peripheral has a medial bend that corresponds to a slight inflection in the anterior margin of the carapace, as observed in many modern cheloniids. The fourth peripheral is substantially thicker than the others, and has a rectangular cross section with a socket for articulation with the axillary buttress of the plastron. The pygal (Fig. 4.5) preserves its general arcuate form, but is abraded on all edges. It does not appear to be either extended or indented along the midline as in many chelonioids. A thick, irregularly triangular abraded bone, here interpreted as part
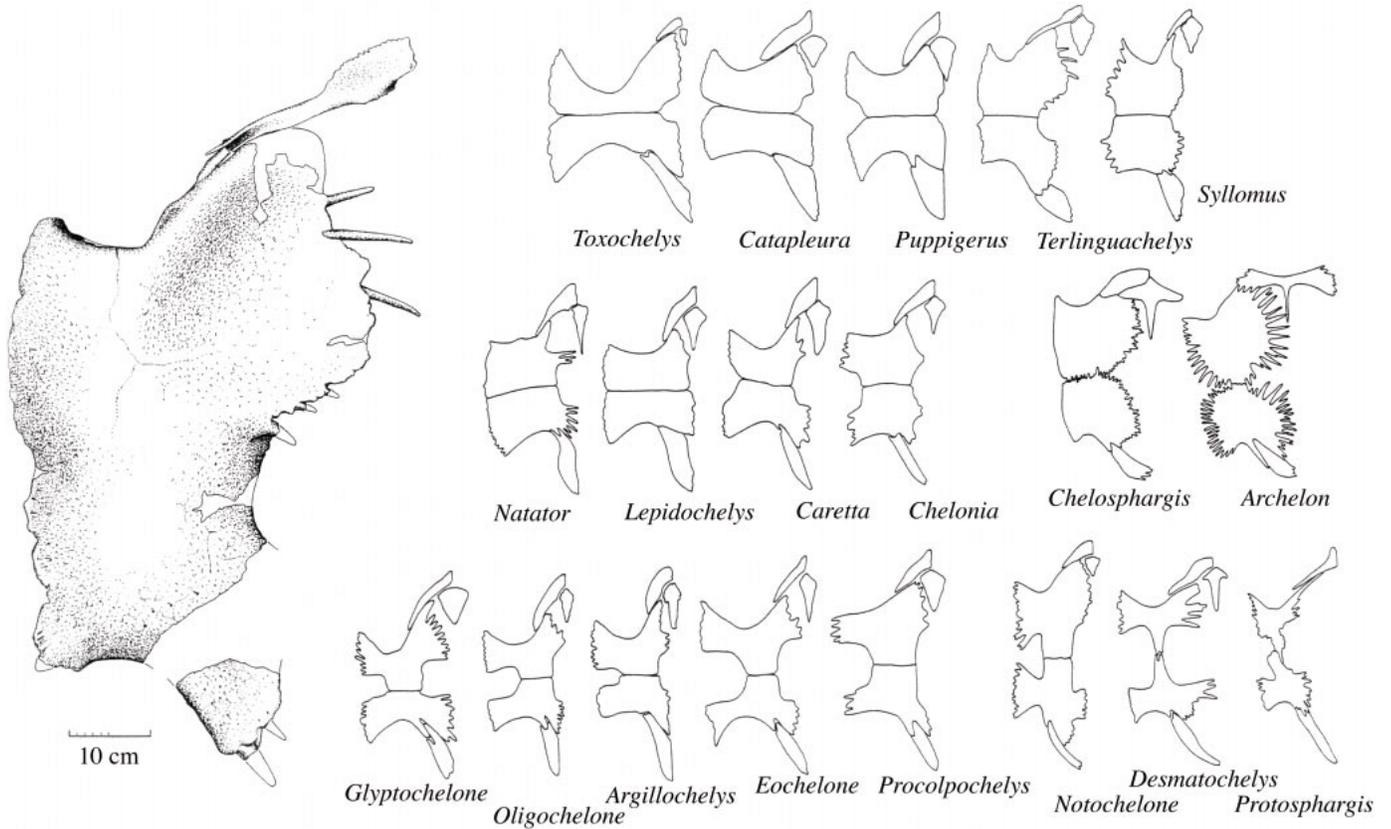
FIGURE 6—*Terlinguachelys fischbecki* n. gen. and sp. (TMM 43072-1) right half of plastron in ventral view, and comparison with plastra in other cheloniid, protostegid, and dermochelyid sea turtles, scaled to equal length (modified from Hay, 1908; Zangerl, 1958, 1980; Hirayama, 1994, 1997).

of a suprapygal (Fig. 4.3), has a longitudinal ridge along the midline. Both the pygal and suprapygal have large circular lesions in the bone, probably parasite attachment sites, very similar in form and size to those described in *Corsochelys* (Zangerl, 1960).

Plastron.—Much of the plastron is preserved. The right epiplaston, hyoplastron, and hypoplastron are preserved in articulation, though the posteromedial part of the hypoplastron is fragmented (Fig. 6). The left hyoplastron is nearly complete. The remaining preserved parts of the plastron are of uncertain position. In contrast to the condition in many sea turtles, the plastron is very well ossified. The plastron is strongly arched along its lateral margins, slightly flattened to concave anteromedially, and somewhat less so posteromedially. The cylindrical axillary buttress is robust; the inguinal buttress slightly less so. In general, the bones are very thick, 25–35 mm along the axillary and inguinal borders, 10–15 mm over much of the central parts of the hyo-hypoplastra, thinning to a few millimeters along the preserved medial borders. The external surface texture is similar to that of the carapace, and consists of subtle low, rounded bosses with scattered small pits and thin grooves. Scute sulci are either poorly developed or absent entirely. A vague possible sulcus extends posteriorly from the axillary notch and occupies a position comparable to that between the pectoral and abdominal scutes in modern cheloniids. Also in contrast to the condition typical in sea turtles, the sutures between hyo- and hypoplastra are so firmly co-ossified they are difficult to locate. Although the actual borders of the lateral and medial fontanelles are not well preserved, judging from the areas of thinning in the hyo- and hypoplastra, both fontanelles were present, though relatively small. Their shape cannot be precisely determined. The lateral fontanelle was extremely

small, its width could be no more than five percent of the estimated half width of the plastron. Among modern and fossil cheloniids, the transverse width of the lateral fontanelle is typically 20–50 percent of the half width of the plastron. Only in *Lepidochelys* and *Natator* is this value less than 10 percent (measurements as indicated by Zangerl et al., 1988). In *Terlinguachelys* the length of the hyo-hypoplastron suture is at least 57 percent of the estimated half width of the plastron; the range in modern and fossil cheloniids is from about 30 to nearly 90 percent (measurements taken as indicated by Zangerl et al., 1988). Hence, the medial fontanelle in *Terlinguachelys* is of moderate size.

The plastron is also relatively elongate anteroposteriorly. The axillo-inguinal distance (or minimum length of the "bridge") is 103 percent of the estimated half width of the plastron. This value (the "plastral bridge index" of Zangerl, 1953) ranges from about 60 to 100 percent in modern and fossil cheloniids (measurements as indicated by Zangerl et al., 1988). The plastral indices in living forms *Chelonia*, *Eretmochelys*, and *Natator* are in the range of 90–100, approaching that in *Terlinguachelys*. The plastral index is high in *Desmatochelys* (105; Zangerl and Sloan, 1960), *Corsochelys* (106; Zangerl, 1960), and *Mesodermochelys* (110–120; Hirayama and Chitoku, 1996) and in Cenozoic dermochelyids, but these also have very large lateral and medial fontanelles as well as overall reduction of all bones in the plastron. By contrast, *Toxochelys* and osteopygines are characterized by a dramatically constricted "waist" between the axillary and inguinal notches (Zangerl, 1953). The plastron in *Terlinguachelys* is not reduced as in either of the two hypothetical modes described by Weems (1988): by anteroposterior constriction toward a transverse midline axis, as exemplified by *Toxochelys* and osteopygines, or by

lateral constriction toward two parallel anteroposterior axes, as in typical Protostegidae and Dermochelyidae.

Terlinguachelys clearly lacks the marked axillo-inguinal constriction of the plastron that typifies basal Cheloniidae. It also lacks the circular stellate pattern with fingerlike projections typical of advanced protostegids, and the extreme medial and lateral reduction typical of dermochelyids. Among living cheloniids, the plastron in *Terlinguachelys* is very much like that in *Natator depressus* (Zangerl et al., 1988) except that both anterior and posterior lobes are slightly larger, medial and lateral fontanelles are larger, and the epiplastra are more slender in *Terlinguachelys*. The plastron of the Miocene cheloniid *Syllomus*, which has hyo-hypoplastra sutured along nearly their entire length is also similar, as is *Procolpochelys*, except that it has much wider lateral fontanelles and a shorter anterior lobe (Weems, 1974). Primitive cheloniids (e.g., *Catapleura*, *Glyptochelone*) have relatively much larger epi- and xiphiplastra; and primitive protostegids or dermochelyids (e.g., *Notochelone*, *Mesodermochelys*) show greater fontanellization. However, the degree of fontanellization is subject to individual, particularly ontogenetic variation in sea turtles (e.g., Zangerl, 1958, 1980). Because the type specimen is the only known representative of *Terlinguachelys*, such comparisons are therefore of limited value, although this specimen is certainly an old adult individual.

The hyo-hypoplastra have digitations (plastral "teeth" or "prongs" of authors) apparently only along their medial borders. Some of these are preserved entirely, while others are broken at their bases. Those along the anteromedial border are very slender and long. Those along the posteromedial border are stouter and flattened.

The right epiplaston is complete and co-ossified at its posterolateral end with the hyoplastron (Figs. 6, 7). The anterior part of the left epiplastron is also preserved. The general form of the epiplastron is similar to that in *Desmatochelys* (Zangerl and Sloan, 1960), but it is relatively more slender than in most cheloniids and has a sharp forward projection (Fig. 7). The posterior end of the epiplastron is a slender rod with a flat medial face for articulation with the hyoplastron and a rounded free lateral face. The bone flattens and expands abruptly anteriorly to form a dorsally concave plate and is thickened along the short midline symphysis for the opposite epiplastron. The free anterolateral edge is coarsely denticulate, as in the "suture-like rugosities" found in *Procolpochelys* (Zangerl and Turnbull, 1955, p. 357). The epiplastra were not co-ossified with the entoplastron, which is not preserved. There are distinct knobs on the dorsomedial articulation facets for the entoplastron. These articulation surfaces show that the entoplastron was relatively small; however, the suture between epiplastra indicates that the medial gap between right and left plastral elements was large.

Scapula.—The left scapula is preserved completely, and retains much of its natural curvature and longitudinally striated surface texture (Fig. 8.9–8.12). The blade of the scapula (dorsal process) and acromion (ventral process) are of slender construction and nearly the same length, unlike in most protostegids for example, where the acromion is typically much shorter (e.g., *Desmatochelys* and *Protostega*; Williston, 1898; Wieland, 1906). The scapular blade and acromion diverge at an angle of 101 degrees directly above the glenoid cavity. As in some dermochelyids (e.g., *Psephophorus* Weems, 1974) there is no extended or constricted "neck" separating the glenoid from the diverging scapular limbs as is typical of cheloniids, for example.

The glenoid cavity is narrow and elongate dorsoventrally in the same plane as the limbs of the scapula. The articular surface itself is concave, not convex as in many chelonioids (e.g., *Corsochelys* Zangerl, 1960). The facet for articulation with the coracoid is small and indistinct. The blade of the scapula (dorsal process) is
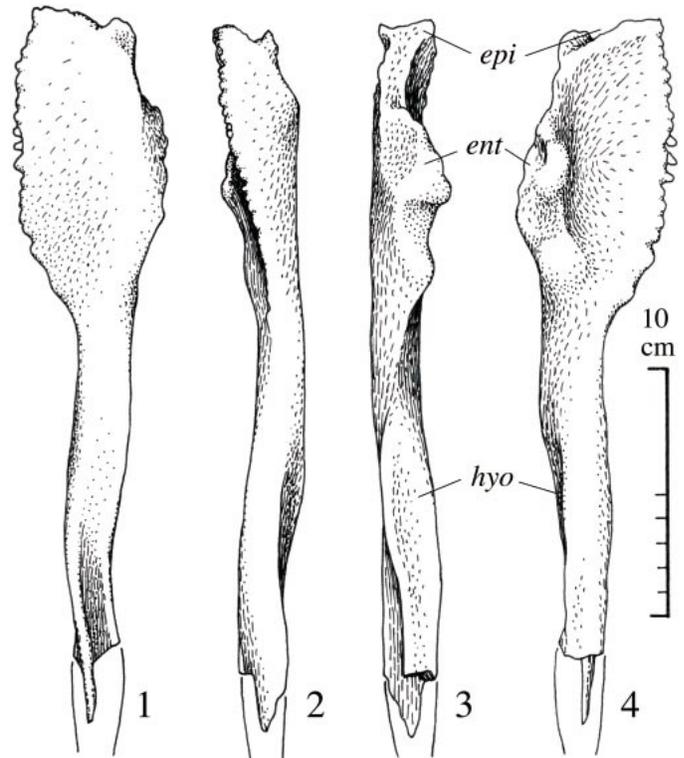

FIGURE *7—Terlinguachelys fischbecki* n. gen. and sp. (TMM 43072-1) right epiplastron in *1,* ventral; *2,* anterolateral; *3,* ventromedial; and *4,* dorsal views; showing contacts for hyoplastron (hyo), entoplastron (ent), and opposite epiplastron (epi).

oval in cross section near its base, but is thin and flattened distally, ending in delicate unfinished medial and lateral edges (originally covered in suprascapular cartilage). A low ridge crosses the posterior surface of the blade from its medial edge to the dorsal lip of the glenoid cavity. In contrast, the acromion (ventral process) is stout and circular in cross section, ending in a bluntly rounded triangular articulation surface. There is a prominent tubercle, elevated 20 mm above the surface of the shaft, on the posterior face of the acromion near its base. This feature is similar to, but developed to a extent greater than in *Dermochelys coriacea* (Walker, 1973; Wieland, 1906, pl. 33).

Coracoid.—The proximal ends of both coracoids are preserved, although neither is very informative. The shaft of the coracoid is constricted abruptly below the proximal end (Fig. 8.13).

Humerus.—Both left and right humeri are preserved completely; they are uncrushed and retain their natural curvature (Fig. 8.1–8.3). The articular surfaces and tuberosities are fully formed and well ossified, although the end of the medial process on the right element has been mildly abraded. The shaft of the humerus has a surface texture of coarse longitudinal striations. The bone is stout, but relatively slender with the shaft constricted at midlength to form a prominent "waist." The sigmoidal curvature of the shaft in anterior view, and strong waist, produce a general form distinct from the dorsoventrally flattened shape typical of advanced protostegids and dermochelyids (Hirayama, 1994).

The medial (ulnar) process is very elongate proximally and extends well posterior of the articular surface of the head. The angle between the axis of the shaft and plane of movement of the humerus (angle β as measured by Zangerl, 1953) is 27 degrees. This angle is relatively low, as in *Toxochelys* (29 degrees), compared with 50–70 degrees typical of modern cheloniids (Zangerl,
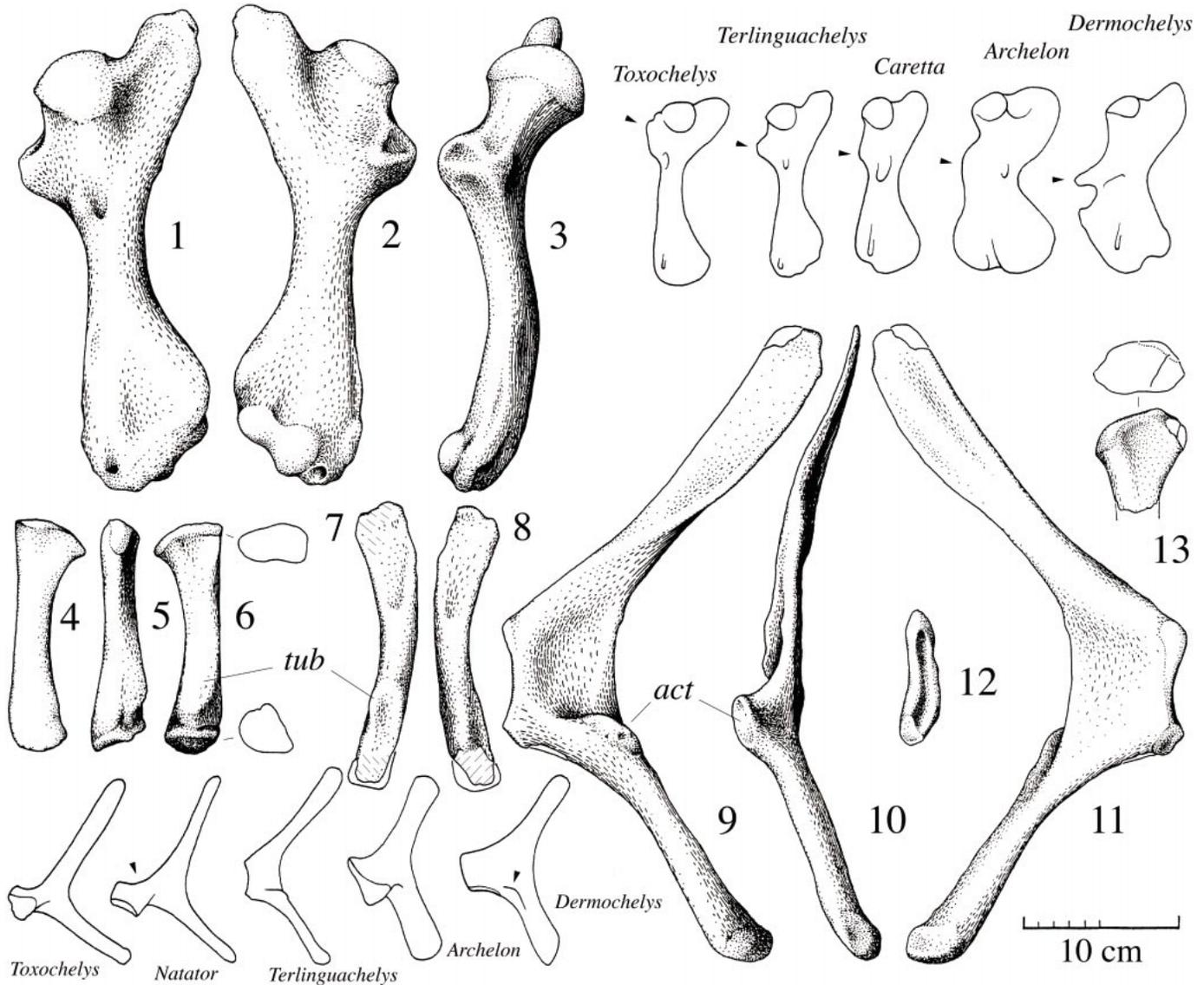
FIGURE 8—*Terlinguachelys fischbecki* n. gen. and sp. (TMM 43072-1) left humerus in *1,* dorsal; *2,* ventral; and *3,* anterior views; left ulna in *4,* dorsal; *5,* posterior; and *6,* ventral views with outlines of proximal and distal articulation surfaces; right radius in *7,* ventral; and *8,* dorsal views; left scapula in *9,* posterior; *10,* medial; and *11,* anterior views; with *12,* glenoid surface; *13,* proximal end of left coracoid in dorsal view, with outline of proximal end. Drawings compare humeri and scapulae in other sea turtles, scaled to equal length (modified from Hay, 1908; Zangerl et al., 1988; Hirayama, 1994); arrows indicate position of humeral lateral process, constricted glenoid neck, and acromion tubercle of scapula; act = acromion tubercle, tub = tuberosity for articulation of ulna and radius, both are shown with proximal end down.

1953, 1960). The head is hemispherical with a distinctly delineated articular surface and is set at an angle of 130 degrees relative to the shaft (angle $\propto$ of Zangerl, 1953). This angle is comparable to that in other chelonioids (120–140 degrees; Zangerl, 1953). The articular surface of the head extends only slightly onto the ventral surface of the bone. The lateral (radial) process is strongly developed, peaked and pyramidal, with distinct facets facing proximally and distally separated by a subtle ridge, and with a pronounced triangular pit on the proximal surface. The lateral process arises from the shaft at a point distal to the head, more distinctly so than in *Toxochelys* and osteopygines, but not so far displaced distally as is typical of dermochelyids. The lateral process projects only slightly anteriorly. There is a small shallow fossa on the dorsal surface of the humeral shaft adjacent to the base of the lateral process and a small tuberosity on the shaft next

to the fossa. This area is the tendon attachment site for insertion of the latissimus dorsi-teres major. A fossa, usually of larger diameter and depth, or a deep double pit (*Natator*), occurs at this position on the shaft of the humerus in Tertiary and modern cheloniids (Zangerl, 1958; Zangerl et al., 1988).

The distal end of the shaft is markedly expanded mediolaterally. The distal articular condyle is very well delineated, unlike in many chelonioids, and lies nearly entirely on the ventral surface of the bone. This suggests that *Terlinguachelys* had more flexibility of the elbow joint than is typical of most chelonioids (see Zangerl, 1953). The articular surface has a distinct saddle-shaped trochlea and elevated hemispherical radial capitellum. The radial epicondyle is relatively small; hence the ectepicondylar foramen passes very near the lateral edge of the bone. This foramen is distinctly defined and fully enclosed, and is not set at the distal

end of a groove on the dorsal surface of the humerus, as in some chelonioids. Indeed, there is no indication whatsoever of such a groove in *Terlinguachelys*. The fully enclosed foramen likely reflects the old age of this individual at the time of its death.

Zangerl (1958) illustrated the humeri of many modern and fossil cheloniids, and a detailed comparison of chelonioid humeri was given by Hirayama (1992, 1994). *Terlinguachelys* has a humerus similar to those of "cheloniid grade" (Hirayama, 1992). It retains a strong sigmoidal curvature, and has a triangular lateral process with a pronounced ridge. Its general form is most like those in the Tertiary cheloniids *Eochelone, Carolinochelys,* and *Procolopochelys* (Weems, 1974). However, the lateral process in *T. fischbecki* also has a distinct median concavity as found in humeri of "protostegid grade" (Hirayama, 1992). Interestingly, the fragmentary humerus of *Atlantochelys mortoni* (Hay, 1908; see illustrations given by Leidy, 1865, pl. 8, figs. 3–5) is quite similar in general form and in its narrow waist, but is twice as large as that in *T. fischbecki*. The medial process projects from the axis of the shaft at a slightly lower angle, and so the plane of motion of the head lies at a greater angle to the shaft. *A. mortoni* was considered to be a protostegid by Hirayama (1997). Because TMM 43072-1 represents an aged adult, and is half the size of *A. mortoni*, it seems unlikely that the two could pertain to the same species. The type and only known specimen of *A. mortoni* is probably inadequate to diagnose the genus and species properly. Nevertheless, it was found in nearshore deposits in New Jersey that are correlative with the Aguja Formation, and it remains possible that additional material of *A. mortoni* could reveal a close relationship with *T. fischbecki*.

Ulna.—Both left and right ulnae are preserved, although the proximal end of the right element is weathered (Fig. 8.4–8.6). The shaft of the ulna is relatively straight and cylindrical, with a flat straight anterior edge and a curved concave posterior edge. The distal end is dorsoventrally flattened with a mildly convex and faintly bilobed articulation surface for the ulnare and intermedium. The proximal end is stouter and expanded dorsoventrally, with a slightly concave saddle-shaped articulation surface for the trochlear condyle of the humerus. There is a pronounced rugose surface on the ventral face of the shaft inset from the proximal end for ligamentous attachment to the radius (Hirayama, 1994). As preserved, the left ulna was nearly in articulation with the carpus (Fig. 9). The ulna is short compared to the humerus, 47 percent its length; however, the ulna is typically 45–55 percent the length of the humerus in cheloniids (Zangerl and Sloan, 1960; Zangerl et al., 1988) and in protostegids (50 percent in *Archelon* and *Protostega*; Wieland, 1906), but is even shorter in dermochelyids (e.g., 39 percent in *Dermochelys*).

Radius.—The right radius is preserved, although its ventral surface and proximal end are deteriorated (Fig. 8.7, 8.8). As is usual in chelonioids, the radius is notably longer than the ulna. Its length relative to the humerus is also typical (60 percent of humerus length, usually 55–65 percent in cheloniids, as low as 50 percent in *Dermochelys*, as high as 70 percent in *Desmatochelys*; Zangerl and Sloan, 1960). The bone is thickest at its proximal end, semicircular in section at midlength, while the distal end is thin, flattened dorsoventrally, and expanded anteroposteriorly. The shaft is curved anteriorly along its length, though not forming a distinct angle as is usual in protostegids (Hirayama and Chitoku, 1996; Hirayama, 1998). The ventral surface has a facet for articulation with the ulna along the proximal third of its length. This articulation with the ulna indicates that in life position, the two bones did not lie entirely side by side in the same plane with the flipper (e.g., as in most protostegids), but the ulna overlapped the radius dorsally at its proximal end (e.g., as in *Dermochelys*). The two bones were not, however, united suturally at their distal ends as in cheloniids.
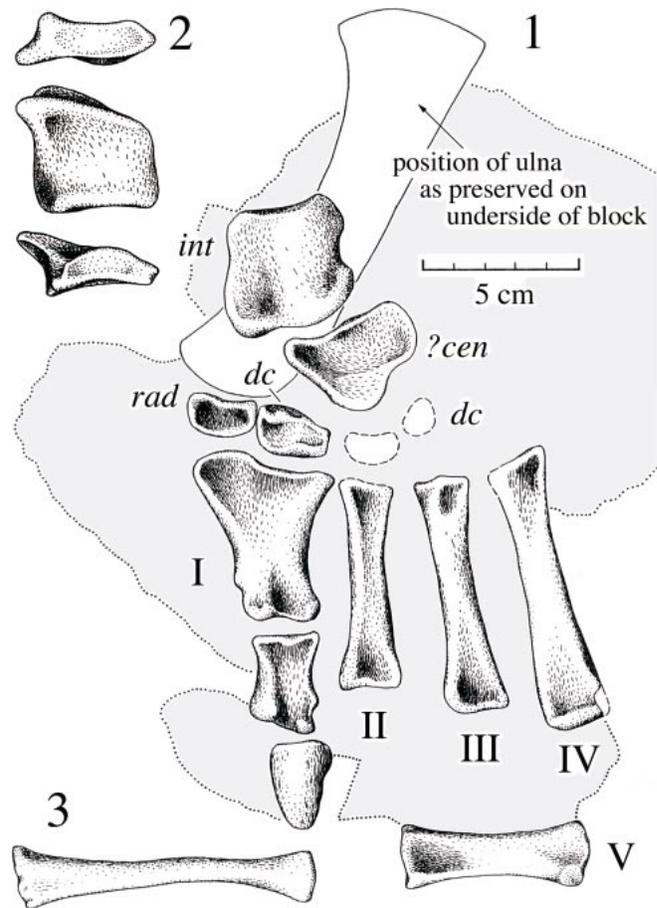

FIGURE *9—Terlinguachelys fischbecki* n. gen. and sp. (TMM 43072-1) part of left flipper in *1,* dorsal view, as preserved, partially articulated in matrix; showing intermedium (int), centrale (?cen), radiale (rad), distal carpals (dc, those shown in dashed outlines are visible on the underside of the matrix block), metacarpals I through V, and phalanges of first digit; *2,* detached ?ulnare in proximal, dorsal, and distal views; *3,* ?second phalanx of digit IV.

Carpus and manus.—Parts of the left flipper are preserved in articulation, and nearly in natural position relative to the ulna, as though partly bound together in connective tissue when buried. These were left in place, as they were preserved in a block of sandstone matrix (Fig. 9). The bones are mildly crushed dorsoventrally, particularly the ends of the metacarpals, suggesting that they were originally hollow or composed of open cancellous bone tissue. The radiale, intermedium, ?centrale, several distal carpalia, metacarpals I through IV, and phalanges of the first digit are all preserved in articulation or nearly so. The ?ulnare, metacarpal V, and additional phalanges are disarticulated and preserved nearby, but the positions of the remaining preserved phalanges are uncertain. Many additional fragments were retrieved but could not be restored to their positions. The absence of carpalia IV and V and the pisiforme suggests that these bones may have been fused together as a single plate, as in modern cheloniids.

In general, the form of the carpus and manus is similar to that in modern and Tertiary cheloniids (e.g., Zangerl, 1958). The intermedium is a large, stout, rectangular block. It is slightly twisted longitudinally, much thicker, and less flattened dorsoventrally than the other carpals. Nearly in articulation with the intermedium and the first three distal carpalia is the presumed centrale. It is an irregular triangular plate, strongly concave on its dorsal surface
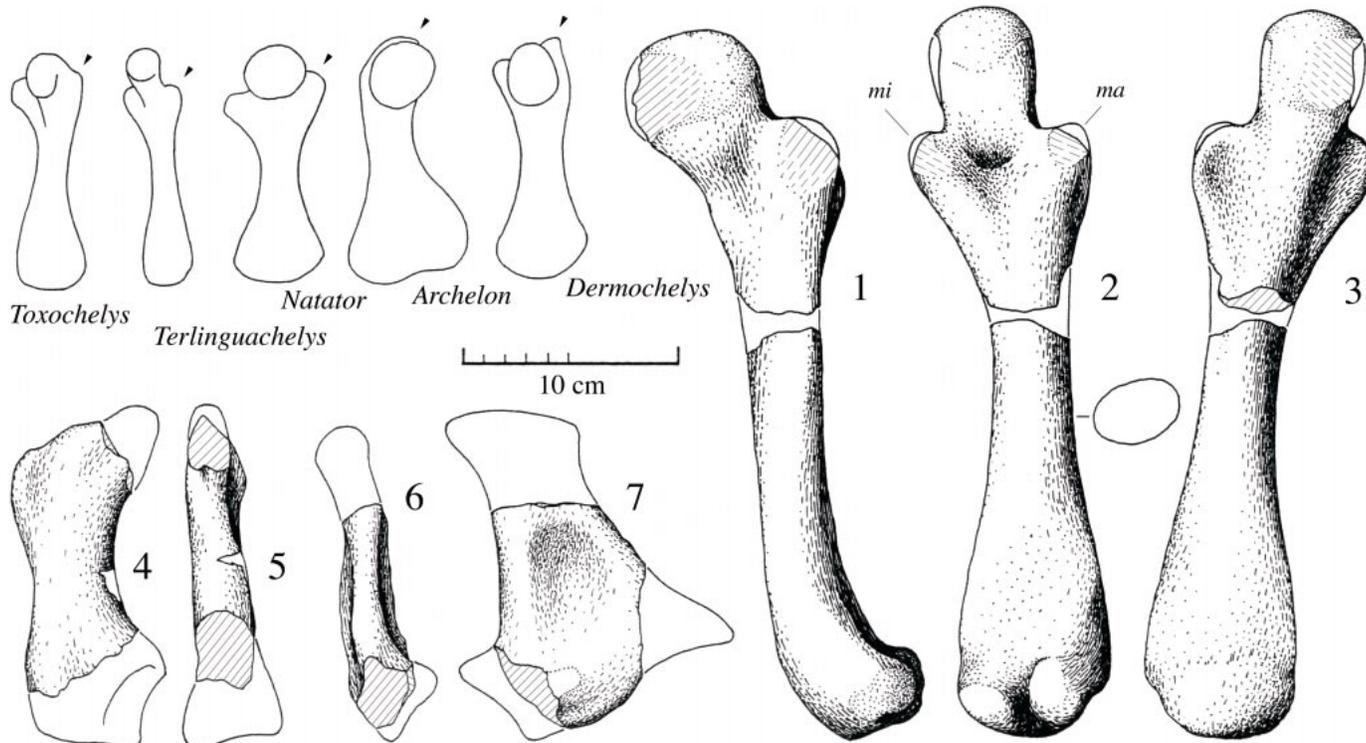
FIGURE 10—*Terlinguachelys fischbecki* n. gen. and sp. (TMM 43072-1) right femur in *1,* anterior (fibular); *2,* ventral; and *3,* dorsal views, with cross section of shaft at midlength; part of ?left ilium in *4,* lateral; and *5,* ventral views; part of left ischium in *6,* anterior; and *7,* dorsal views. Drawings compare femora in other sea turtles, scaled to comparable length (modified from Hay, 1908; Volker, 1913; Zangerl et al., 1988). Arrows indicate major trochanter, ma = major and mi = minor trochanters.

(partly a result of crushing). If correctly identified here, the centrale is very large relative to the intermedium and ulnare. In sea turtles other than *Toxochelys* the centrale is considerably smaller (Wieland, 1906). Another large carpal element was preserved separately. This unusual bone is interpreted as the ulnare, although it does not closely resemble this element in other sea turtles (Fig. 9.2). This flattened rectangular bone has joint surfaces on three sides. It is thickest at its presumed proximal end and is expanded medially to form an overlapping joint with the intermedium. Metacarpal I articulates proximally with two small reniform bones; one of these is certainly distal carpal I, the other may be the radiale. The two bones appear to be co-ossified along their ventral edges, but are separate on the dorsal surface. Two additional small ossicles (distal carpalia II and III) protrude from the ventral surface of the matrix block, but are barely exposed on the dorsal surface. Relative to the forearm bones in *Terlinguachelys* the carpus as a whole is smaller, the centrale larger, and the ulnare smaller than in advanced protostegids and dermochelyids (Wieland, 1902). Moreover, the radiale is apparently not ossified in the latter taxa.

The metacarpals are all dorsoventrally flattened; the minimum thickness of their shafts is about 60 percent their width. Metacarpals increase in length from I through IV, with V about equal in length to II. Metacarpal I is much shorter and broader than the others, as is typical in cheloniids and protostegids, and is not elongate as in *Dermochelys* (Volker, 1913). Metacarpal II is substantially shorter than III and IV, whereas in living cheloniids all three are more nearly the same length. In contrast to the metacarpals, the phalanges of digits II through V are narrow, elongate, and in some cases anteroposteriorly flattened. The articular surfaces of the phalanges are flat and lack distinct condyles, with the exception of those of digit I, which appear to have weak condyles,

and so were perhaps capable of some mobility. This is also the case in *Toxochelys*, *Santanachelys*, and some other protostegids that retained moveable articulations in the first and second digits (Case, 1898; Hirayama, 1994). The terminal claw phalanx of digit I is relatively short and broad, not narrow and elongate as in *Protostega* for example (Wieland, 1906). Another disarticulated terminal phalanx is also preserved, but it is so similar in form to that on digit I that it probably represents the same element from the right flipper.

Pelvic girdle.—Only parts of the left ilium and ischium are preserved (Fig. 10.4–10.7). Little more than their general form is discernible, because both elements are severely abraded and lack most of their lamellar cortical bone surface. The short, stout form of the ilium is much like that in *Corsochelys* (Zangerl, 1960) and it appears to lack an elongate postacetabular process. Similarly, the ischium appears to be relatively short, but both the lateral and medial processes are broken.

Femur.—The proximal end of the right femur, as well as its shaft and distal end, are preserved as two parts that cannot be confidently joined together due to mild weathering of the broken ends (Fig. 10.1–10.3). However, very little if any is missing between the two parts, and together they provide a nearly complete view of the form of the bone. The dorsal surface of the femur in particular is weathered and lacks the cortical bone surface. The femur is slender, not expanded distally, and retains a relatively strong dorsoventral curvature. The head is compressed anteroposteriorly and is not hemispherical as in most chelonioids, suggesting that the hind limb had a limited plane of movement in *Terlinguachelys*. The two trochanters are small and comparable in size; the major trochanter is not highly elevated compared to the femoral head, and has a relatively weakly developed muscle scar. The trochanters are separated by a shallow fossa proximally,

behind the femoral head, but weakly joined anteroposteriorly at their bases by a low ridge (e.g., as in *Desmatochelys*; Zangerl and Sloan, 1960). The shaft has an anteroposteriorly elongate oval cross section at midlength, and there is longitudinal torsion of the shaft such that the femoral head projects anteriorly (toward the fibular side) relative to the plane of the distal condyles. The tibial condyle is more bulbous, and is wider dorsoventrally, than the fibular condyle.

In contrast to typical sea turtles, the femur in *Terlinguachelys* is very long relative to the humerus, at least 107 percent its length. In modern and Tertiary cheloniids, as well as in *Dermochelys*, and protostegids for which data are available, the femur varies from 65 to 85 percent the length of the humerus, reaching a maximum of 90–95 percent in *Toxochelys* and *Desmatochelys* (Zangerl et al., 1988). In freshwater turtles, the femur typically exceeds the humerus in length. This seemingly reflects a major shift in the mode of aquatic locomotion. Whereas freshwater turtles utilize their hind limbs more fully in propulsion, the hind limbs in advanced sea turtles are modified for only a limited range of motion to serve as "rudders" (Zangerl, 1953; Zangerl and Sloan, 1960).

Tibia.—Only a fragment of the proximal end of the shaft of the ?right tibia is preserved. Although poorly preserved, it is a stout, triangular cross section, and appears to lack the tendon attachment pit found in Tertiary and modern cheloniids.

COMPARISON WITH OTHER SEA TURTLES

Apart from general hypotheses of evolutionary relationships among sea turtles (e.g., Zangerl, 1953; Zangerl and Sloan, 1960), several explicit phylogenetic analyses have been presented for Chelonioidea (Gaffney and Meylan, 1988; Weems, 1988; Hirayama, 1994, 1997, 1998; Hirayama and Chitoku, 1996; Moody, 1997) or for its constituent families (Zangerl, 1980; Zangerl et al., 1988; Parham and Fastovsky, 1997 for Cheloniidae; Wood et al., 1996 for Dermochelyidae; Hooks, 1998 for Protostegidae). Most of these analyses rely heavily on cranial and vertebral characters, and the lack of preservation of these elements in *Terlinguachelys* n. gen. makes it difficult to include it in a similar analysis. Nevertheless, it is possible to interpret the likely relationships of *Terlinguachelys* based on the material preserved.

The proposed sea turtle phylogenies, while differing in the placement of some taxa and in the nomenclature advocated, are all similar in their general structure and in recognizing the same basic clades (Fig. 12). For example, most phylogenetic analyses regard Cheloniidae as relatively primitive among sea turtle families, with *Toxochelys*, *Ctenochelys*, and Osteopyginae considered by some authors as either closely related sister taxa of Cheloniidae (e.g., Gaffney and Meylan, 1988) or as basal members of the family (e.g., Hirayama, 1998). Protostegidae and Dermochelyidae are each more derived, more closely related to each other than either is to Cheloniidae, and so comprise Dermochelyoidea (node 3 in the cladogram of Hirayama, 1998; or above node D10 in the cladogram of Gaffney and Meylan, 1988, fig. 5.9). Some sea turtles (e.g., *Desmatochelys*, *Notochelone*) are regarded as either sister taxa of Dermochelyoidea (Gaffney and Meylan, 1988) or as basal members of Protostegidae (Hirayama, 1998). In the following discussion, clades are referred to basically as advocated in the phylogenetic hypothesis of Hirayama (1998). Cheloniidae is used in the broad sense, while "derived" or "advanced" cheloniids here exclude *Toxochelys*, *Ctenochelys*, and Osteopyginae (above node C6 on the cladogram of Hirayama and Chitoku, 1996, or above D6 on the cladogram of Gaffney and Meylan, 1988, fig. 5.9). Similarly, "derived" Protostegidae here exclude *Santanachelys*; and "derived" dermochelyids exclude *Mesodermochelys* and *Corsochelys*.

Chelonioid phylogenetic trends that occurred in parallel in all three major sea turtle families include 1) increased fontanellization and elongation of the carapace and plastron, 2) reduction of the hind limbs and their modification as "rudders" (shortening of femur, fusion and elevation of trochanters), 3) enhancement of the forelimb "paddles" (divergence of scapular processes, straightening and flattening of the humerus, distal displacement of the humeral lateral process, immobilization of the digits), and 4) posterior shift in the mandibular coronoid process and reduction of posterior jaw elements. Retention of primitive traits is thought to be associated with a paralic or even "pre-paralic" lifestyle, while derived traits are largely associated with adaptation to a truly pelagic lifestyle (Zangerl, 1969, 1980; Zangerl et al., 1988). Zangerl (1969, 1980) observed that once the basic chelonioid design was established, there was limited potential for further morphological differentiation because of the constraints of their shell and aquatic "flying" mode of locomotion. As a result, many chelonioid species do not exhibit unique characters but instead unique *combinations* of character states, and cases of parallelism appear to be common (Zangerl and Turnbull, 1955). Evolutionary modifications involved basically the same features in all three lineages.

That *Terlinguachelys* clearly pertains to Chelonioidea is indicated by its forelimb, which is modified to form a "flipper" with a relatively straightened humerus having a distally displaced lateral (radial) process, elongate metacarpals and phalanges flattened into a single plane, and flattened carpals with restricted joint surfaces (Gaffney and Meylan, 1988).

Plesiomorphic character states.—*Terlinguachelys* retains many features that are seemingly primitive for sea turtles and it lacks the most conspicuous synapomorphies of Cheloniidae, Protostegidae, or Dermochelyidae. Retained presumably primitive features in *Terlinguachelys* include 1) its well-ossified plastron with a 2) long co-ossified hyo-hypoplastron suture and 3) only small lateral and medial fontanelles, 4) the long femur with 5) small major and minor trochanters of similar size and 6) retaining the intertrochanteric fossa, and 7) the narrow symphysis and triturating surface of the mandible, as well as its 8) coronoid process situated at midlength and 9) broad articular and retroarticular region. The first digit of the flipper also appears to 10) retain partly moveable articulations. Those fragments of neurals preserved appear to be 11) broad and hexagonal in outline, not narrow and rectangular. The humerus is 12) sigmoidal and narrow-waisted, not broad and flattened, and has a lateral process 13) only slightly displaced distally. The limb bone articular surfaces are 14) smooth and avascular.

Apomorphic character states.—Derived features in *Terlinguachelys* include 1) a short scapular glenoid neck, 2) the wide angle of divergence between scapular processes, 3) a prominent acromion tubercle, 4) a depression on the lateral humeral process, 5) a radius markedly longer than the ulna and 6) with pronounced anterior curvature, and 7) the elongate plastral bridge. *Terlinguachelys* also has 8) poor development of scute sulci on the carapace and plastron. Four of these eight apomorphic features are expressed to some degree in all three sea turtle lineages.

Summary of cranial features.—*Terlinguachelys* has a peculiar jaw structure with a low lateral profile, coronoid process at midlength, large dorsal opening for the fossa meckelii, broad mandibular articulation, and prominent retroarticular process. These features likely reflect retention of a primitive condition comparable to that in the basal cheloniid *Toxochelys*, but could be interpreted as unique apomorphies in *Terlinguachelys*. The very short mandibular symphysis and narrow triturating surface contrast markedly with the condition in Osteopyginae as well as in most derived cheloniids, and suggests that *Terlinguachelys* lacked an extensive secondary palate. The mandibular triturating surface also lacks the sagittal ridge typical of Protostegidae, and judging
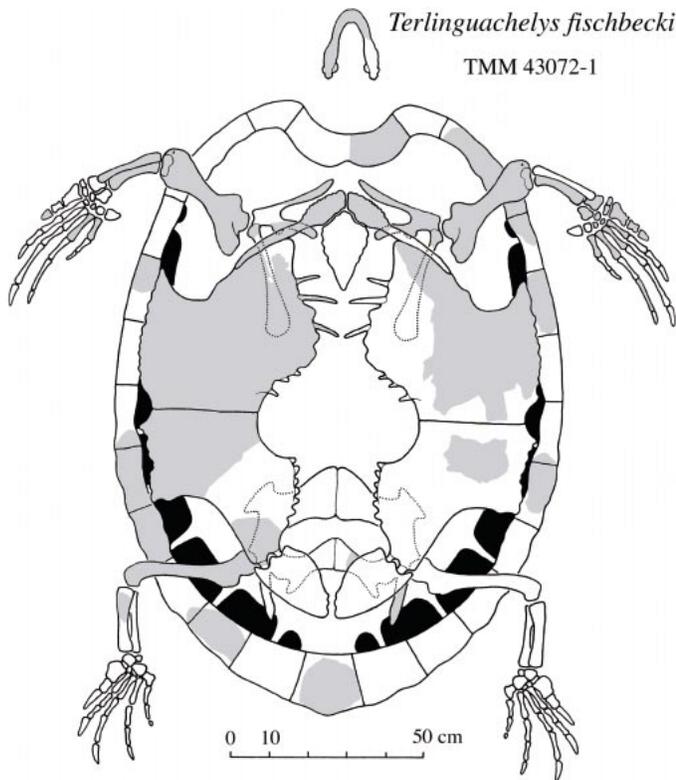
FIGURE *11*—*Terlinguachelys fischbecki* n. gen. and sp. (TMM 43072-1) reconstruction of skeleton with preserved parts indicated by shaded areas.

FIGURE *12*—Cladogram showing the hypothetical phylogenetic relationships among sea turtle families (simplified from Gaffney and Meylan, 1988; Parham and Fastovsky, 1997; Hirayama, 1998) and the likely phylogenetic position of *Terlinguachelys* n. gen. discussed in text.

from the size of the mandible, the skull was relatively quite small in *Terlinguachelys* compared to the huge skull in most Protostegidae (Fig. 11).

Summary of shell features.—A small plastron with narrow bridge is considered to be the primitive condition for Chelonioidea, and is associated with weak modification of the limbs and girdles for aquatic locomotion, as in *Toxochelys*, *Ctenochelys*, and osteopygines (Zangerl, 1953; Hirayama, 1997). *Terlinguachelys* clearly lacks the marked axillo-inguinal constriction of the plastron that typifies basal cheloniids (e.g., *Toxochelys* and Osteopyginae). The relatively elongate plastron (high plastral bridge index) in *Terlinguachelys*, as in dermochelyoids and derived cheloniids, is a trait associated with overall elongation and streamlining of the shell and adoption of a truly pelagic lifestyle (Hirayama, 1997). Hirayama (1998) suggested that a plastral index greater than 100 is synapomorphic for Dermochelyoidea. Some derived cheloniids (*Chelonia*, *Natator*) have indices of nearly 100, *Terlinguachelys* is about 103, while most dermochelyoids range from 105 to 120.

The well-ossified plastron in *Terlinguachelys* is very similar in form to that in advanced cheloniids (*Natator* Zangerl et al., 1988; *Syllomus* Weems, 1974). In typical Dermochelyoidea, even primitive species (e.g., *Desmatochelys*, *Mesodermochelys*), the plastron has large medial and peripheroplastral fontanelles and the hyo-hypoplastral contact is reduced to a narrow projection (e.g., Gaffney and Meylan, 1988). *Terlinguachelys* clearly lacks the extreme fontanellization considered synapomorphic for Dermochelyidae (Hirayama, 1998). The plastron in *Terlinguachelys* also lacks the circular stellate form with processes radiating from the centers of the hyo-hypoplastra that typifies advanced Protostegidae, and retains well-developed epiplastra that are lost in derived
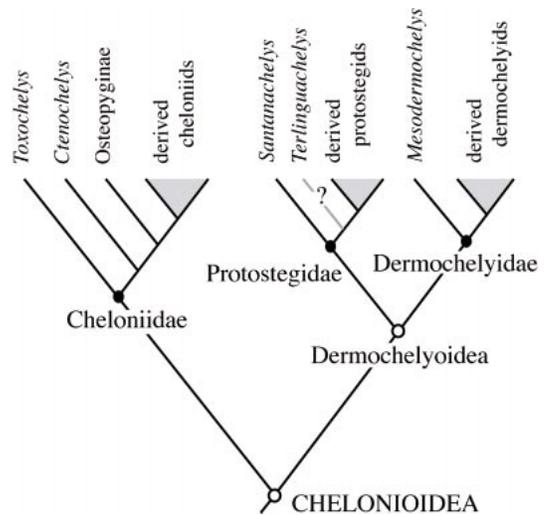
Protostegidae (Wieland, 1906, 1909). However, the basal protostegid *Santanachelys* (Hirayama, 1998) retains a well-ossified plastron with large epiplastra and is quite similar to that in *Terlinguachelys*.

The fragmentary neurals in *Terlinguachelys* appear to be broad and hexagonal in outline, a retention of the primitive condition (as in Cheloniidae), not narrow and rectangular (as in Protostegidae and Dermochelyidae; Hirayama and Chitoku, 1996). Advanced protostegids have reduced the costal plates of the carapace to vestiges on the proximal ends of the ribs. Both costal and peripheral plates are vestigial in advanced dermochelyids (Nielsen, 1964; Wood et al., 1996); as evident even in some Cretaceous forms (*Protosphargis*, Capellini, 1884). However, basal protostegids (e.g., *Santanachelys*) and basal dermochelyids (e.g., *Corsochelys*, *Mesodermochelys*) retain a carapace with only moderately reduced costal plates, comparable to that in many cheloniids. The poor development of scute sulci on the carapace and plastron in *Terlinguachelys* is found elsewhere in derived protostegids and in dermochelyids (Hirayama, 1994; Hirayama and Chitoku, 1996), but is also observed in a few ostensible cheloniids (e.g., *Allopleuron*).

Summary of limb and girdle features.—In dermochelyoids the forelimbs are typically very long in relation to the hind limbs and to the body as a whole. While this is evident even in basal dermochelyids (*Mesodermochelys*), some basal protostegids (*Santanachelys*) retain relatively short forelimbs. *Terlinguachelys* has short forelimbs comparable with those in most cheloniids. In *Terlinguachelys*, the humeral shaft retains a sigmoidal curvature and narrow waist, but the medial process is elevated above the head, and the triangular lateral process of the humerus is displaced distally compared to the condition in *Toxochelys* and osteopygines. This general morphology is similar to that in derived Cheloniidae. Basal protostegids and basal dermochelyids (*Rhinochelys*, *Desmatochelys*, *Mesodermochelys*) exhibit a comparable form; however, they may be distinguishable on the basis of the distinctive morphology of the lateral process (Hirayama, 1992). In *Terlinguachelys*, the lateral process is not so far distal or elongate, nor is the shaft flattened and widened to the extent seen in derived protostegids and dermochelyids (Hirayama, 1994). However, the depression on the lateral process of the humerus is a feature found

elsewhere only in advanced protostegids (more derived than *Santanachelys*), where this is thought to reflect a distinctive supracoracoideus muscle insertion (Hirayama, 1992, 1998). The marked anterior curvature of the radius is also regarded as a protostegid synapomorphy (Hirayama and Chitoku, 1996; Hirayama, 1998). Hence, these two details of the forelimb in *Terlinguachelys* are shared with Protostegidae.

The wide angle of divergence between scapular processes in *Terlinguachelys* is typical of dermochelyoids, but also found in a few advanced cheloniids (e.g., *Chelonia*). Hirayama (1998) proposed that an angle exceeding 110 degrees is synapomorphic for Dermochelyoidea. In *Terlinguachelys* this angle is 101 degrees. Two features of the scapula imply a close relationship with Dermochelyidae. The prominent tubercle near the base of the acromion process is a feature found elsewhere only in the modern leatherback *Dermochelys coriacea* (Wieland, 1906, pl. 33; Walker, 1973) and in isolated specimens referred to Dermochelyidae (Parham and Stidham, 1999). This feature has not been noted (though it may be present) in other members of the family (e.g., *Protosphargis*, *Eosphargis*, *Psephophorous*). Walker (1973) observed that the acromion tubercle reflects a unique lateral subdivision of the acromiocoracoid ligament and insertion of the testocoracoid muscle in *Dermochelys*. Parham and Stidham (1999) regarded this feature as synapomorphic for Dermochelyidae. Similarly, divergence of the limbs of the scapula immediately above the glenoid, with no elongate or constricted scapular neck is also regarded as a dermochelyid synapomorphy, and has been used to identify isolated specimens as pertaining to the family (Weems, 1974). These two features in *Terliguachelys* argue for dermochelyid affinity even though the shell and limbs lack any conspicuous dermochelyid specialization. For example, *Terlinguachelys* has an exceptionally long femur with small weakly connected trochanters, comparable to that in basal cheloniids. In advanced protostegids and dermochelyids, the femur is much shorter, trochanters are joined by a ridge, and the major trochanter projects proximal to the femoral head (Gaffney and Meylan, 1988). This derived condition is evident even in basal dermochelyids (e.g., *Mesodermochelys*), however, some basal protostegids (e.g., *Desmatochelys*) retain a form similar to that in *Terlinguachelys*. The limb bone articular surfaces in *Terliguachelys* also lack the large transphyseal vascular channels and rugose texture that characterize Dermochelyidae and Protostegidae, and presumed to be associated with their advanced metabolic physiology (Rhodin, 1985). Instead, the articular surfaces are smooth, avascular, and sharply defined, as in typical Cheloniidae.

Phylogenetic position of Terlinguachelys.—The meager preserved parts of the cranium convey little information regarding the affinities of *Terlinguachelys*. Its mandible expresses retained primitive attributes or unique apomorphies or both. The shell in *Terlinguachelys* exhibits features compatible with those of advanced cheloniids and basal protostegids but shares no traits with more derived sea turtles. The basic morphology of limb and girdle elements is also in agreement with the condition in derived cheloniids and basal protostegids, however, several details of the forelimb suggest affinity with both protostegids and dermochelyids.

Although collectively the preserved parts of *Terlinguachelys* agree in most ways with derived Cheloniidae, cheloniids as a group are regarded as relatively primitive among sea turtles and therefore many of their features reflect the retention of a primitive condition. Hence, the primitive features of *Terlinguachelys* do not necessarily indicate a close relationship with Cheloniidae. Several possible phylogenetic positions could be supported, depending on the weight one grants *Terlinguachelys* few apomorphies, and whether its primitive features are considered retained or instead reacquired through reversal. *Terlinguachelys* could be 1) a cheloniid convergent with dermochelyoids in a few details of the forelimb, 2) a sister taxon to Dermochelyoidea, 3) a very primitive protostegid, considering the curved radius and concavity on the lateral process of the humerus as unique synapomorphies for Protostegidae, or 4) a very primitive dermochelyid, considering the scapular acromion tubercle and short glenoid neck as unique synapomorphies for Dermochelyidae.

The first hypothesis has some support from precedence. Features generally associated with Dermochelyoidea were independently acquired in some highly derived cheloniids. For example, *Syllomus* is convergent with dermochelyoids in some ways (e.g., the elongate recurved form and medial position of the lateral process on the humerus, the elevated major trochanter of the femur above the level of the head, the extreme posterior position of the mandibular coronoid process and highly reduced posterior jaw section; Weems, 1980). The problematic cheloniid *Allopleuron* has strongly divergent scapular processes, a high plastral bridge index, reduced shell ossification, and loss of scute sulci in common with dermochelyoids (Hirayama, 1994). The hypothesis that *Terlinguachelys* is a derived cheloniid emphasizes its presumed retained primitive characters and regards its few derived features as effects of parallelism.

The latter three hypotheses instead emphasize *Terlinguachelys* few conspicuous apomorphies. These are presumed to reflect stable characters in the forelimb flipper structure that were resistant to modification once fixed. Some of its primitive features may therefore be considered reacquired through reversal. The hypothesis that *Terlinguachelys* is a sister taxon to Dermochelyoidea is plausible; a comparable phylogenetic position has been advocated for other problematic taxa (e.g., *Allopleuron*, *Desmatochelys*, *Notochelone*; Gaffney and Meylan, 1988). This would require, however, that the common ancestor of dermochelyoids possessed a few distinctly protostegid and dermochelyid derived forelimb features that were subsequently lost in each clade. The hypothesis that *Terlinguachelys* is a primitive protostegid is probably the most parsimonious. *Terlinguachelys* shares two purportedly unambiguous synapomorphies of Protostegidae, and many of its preserved parts resemble the basal protostegid *Santanachelys* (Hirayama, 1998). This hypothesis would require that the dermochelyid scapular acromion tubercle and short glenoid neck evolved independently in *Terlinguachelys*, a plausible scenario in view of the fact that both features are apparently lacking in the basal dermochelyid *Mesodermochelys* (Hirayama and Chitoku, 1996). The hypothesis that *Terlinguachelys* is a dermochelyid seems the least likely and would require retention or reacquisition of a much more primitive shell and limb morphology in *Terlinguachelys* compared to known basal dermochelyids, and the loss of otherwise typical protostegid features (pit on lateral humeral process and curved radius) in all more derived dermochelyids.

Terlinguachelys is herein regarded as a primitive member of Protostegidae. However, in having somewhat uncertain affinities it is certainly not alone among sea turtles. There has long been disagreement over the placement of some taxa (e.g., *Allopleuron*, *Desmatochelys*, *Notochelone*) and with the recent descriptions of basal representatives of each sea turtle lineage, the morphological boundaries between the three traditional clades have become less distinct.

CONCLUSIONS

Terlinguachelys n. gen. has a combination of retained primitive traits and some derived features that suggest possible affinities with several sea turtle lineages whose more derived members are easily separable. *Terlinguachelys* may be a primitive member of Protostegidae, and it is herein assigned to that family. It exhibits some features more primitive than the basal protostegid *Santanachelys* (e.g., long femur, small plastral fontanelles, broad neurals), and some features more derived (e.g., pit on lateral process

of humerus), but it certainly lacks the striking specializations of advanced protostegids, the most typical sea turtles of the Late Cretaceous interior of North America. The retention (or reacquisition) of many primitive features in *Terlinguachelys* may have been associated with a paralic lifestyle atypical for advanced Protostegidae. For example, the exceptionally long femur, and lack of fusion of the weak femoral trochanters, suggests that *Terlinguachelys* retained primitively long and mobile hind limbs, and lacked the specialized hind limb ''rudders'' of advanced chelonioids. *Terlinguachelys* may have retained a more primitive mode of aquatic propulsion, and utilized its hind limbs in the alternate lateral stroking manner of freshwater turtles (Zangerl, 1953). If *Terlinguachelys* is indeed a basal protostegid, then specialized hind limb rudders may have evolved independently in each of the three sea turtle families. Moreover, the smooth avascular articular surfaces of the limb elements in *Terlinguachelys* suggest that advanced metabolic physiology in protostegids (Rhodin, 1985) also arose independently in dermochelyids. The unusual conformation of the jaw in *Terlinguachelys*, with its flat anteriorly projecting triturating surface, symphyseal trough, low medial coronoid process, broad mandibular articulation, and pronounced retroarticular process, suggests a unique feeding specialization in *Terlinguachelys* also perhaps associated with a paralic habitat.

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APPENDIX *1*—Measurements of the type specimen of *Terlinguachelys fischbecki* (TMM 43072-1), in millimeters. For paired elements, the measurement given is that of the best-preserved specimen. Measurements were taken in the manner shown by Zangerl et al. (1988) and otherwise along the straight line distance (not along curvature). * = measurement is an estimate.

lower jaw, sagittal length	181
lower jaw, length along ramus	190
lower jaw, width of triturating surface	15
lower jaw, length of symphysis	28
plastron, axillo-inguinal distance	515
plastron, length of hyo-hypoplastron suture	285
plastron, width of lateral fontanelle	*25
plastron, half width	*500
plastron, length	*1100
scapula, greatest length of blade	310
scapula, greatest length of acromion process	270
scapula, length of glenoid	80
scapula, least width of glenoid	24
humerus, greatest length	301
humerus, least width of shaft	40
humerus, transverse width of distal end	95
humerus, transverse width of head	50
ulna, length	143
ulna, greatest width of proximal end	35
ulna, greatest width of distal end	44
metacarpal I, length	55
radius, length	180
radius, greatest width of proximal end	26
radius, greatest width of distal end	35
proximal phalanx, digit I, length	29
terminal phalanx, digit I, length	27
metacarpal II, length	70
metacarpal III, length	75
metacarpal IV, length	95
second phalanx, digit IV, length	100
metacarpal V, length	66
femur, length	*323
femur, width of distal end	70
femur, anteroposterior diameter of shaft	40
femur, dorsoventral diameter of shaft	24
femur, width of head	45
femur, width across trochanters	73