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Evolution and Phylogeny of Leatherback Turtles (Dermochelyidae), with Descriptions of New Fossil Taxa

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ABSTRACT. – **Recent discoveries of fossil leatherback turtles have permitted recognition of two new genera, *Egyptemys* from the Eocene of northern Egypt and *Natemys* from the Oligocene of coastal Peru. A review of the entire fossil record of dermochelyids allows, for the first time, the formulation of a phylogenetic hypothesis for this extremely divergent family of turtles. Until now, there has been a tendency to refer most fossil dermochelyid remains to the extinct genus *Psephophorus*, the implication being that some form of *Psephophorus* evolved, over some undefined span of time during the Tertiary, into the living genus *Dermochelys*. However, cladistic analysis clearly indicates that dermochelyid evolution has been considerably more complex. The earliest known leatherbacks in the Cretaceous had a shell morphology similar to other types of marine turtles. Subsequent evolution led to several distinct lineages, all but one of which became extinct. One of these is represented by forms having a smooth, unridged carapace characterized by unique "sunflower" shaped clusters of bony ossicles. One of the species in this lineage, *Natemys peruvianus* (sp. nov.), unlike typical dermochelyids, is characterized by a fully ossified plastral mosaic composed of large numbers of small bony ossicles. There are at least two (and perhaps more) other leatherback lineages typified by carapaces with various kinds of distinctive ridge morphologies and other associated osteological features. Most taxa previously referred to *Psephophorus* are not assignable to that genus, and *Psephophorus* is definitely not ancestral to *Dermochelys*. Features of shell evolution in the *Dermochelys* lineage include: 1) a progressive decrease in shell thickness; 2) a concomitant decrease in the size of individual ossicles (and therefore an overall increase in the number of ossicles forming the carapace); 3) a progressive increase in the prominence of the anteroposterior ridges, which are formed as flexures of the entire carapacial bony mosaic instead of being expressed only on the dorsal surface of the carapace; 4) the development of undulating crests on the ridges; and 5) an increase in the number of ossicles between adjacent ridges.**

KEY WORDS. – **Reptilia; Testudines; Dermochelyidae; *Egyptemys eocaenus*; *Natemys peruvianus*; *Psephophorus rupeliensis*; *Cosmochelys dolloi*; *Psephophorus polygonus*; *Dermochelys coriacea*; systematics; paleontology; phylogeny; Egypt; Peru; Belgium**

Dermochelys coriacea, the leatherback turtle, is a remarkable creature. Arguably the largest of all living reptiles, it certainly has the broadest geographic distribution of any extant reptilian species, occurring in tropical, temperate, and even subarctic marine waters. *Dermochelys* is an extraordinary migrator, routinely traversing, for example, the North Atlantic Ocean.

Unusual anatomical features abound in this unique turtle. So peculiar are dermochelyids in so many respects that they were at one time classified in a separate suborder (the "Athecae") from all other turtles. The carapace consists of thousands of tiny, irregularly sized and shaped ossicles joined together in mosaic fashion. Seven prominent, sharply peaked ridges extend along the anteroposterior axis of the carapace. Between these ridges, the bone of the carapace can be as little as 3–4 mm thick. Thus, the largest of all living turtles has one of the thinnest of all bony shells. When a beached leatherback dies, its shell does not long retain the rotund profile characteristic of live individuals. The carapace first sags and then quickly collapses into a jumble of disarticulated ossicles – a true paleontologist's nightmare.

The plastron, in contrast to the carapace, consists only of a fragile, narrow outer oval of bone. The area encompassed within this ring is not ossified, except for a few isolated lines of bony ossicles. All that covers the abdomen, therefore, is an expanse of thick, heavy fibrous tissue as much as several cm thick.

The large scutes that cover the shells of most turtles are absent on both carapace and plastron. Instead, the shell is covered by a thin veneer of scaleless skin, although hatchlings have numerous small bead-like scales covering the whole shell.

While we know a considerable amount about the anatomy, behavior, ecology, and physiology of living leatherback turtles, not much is yet known about their ancestry. The genus *Dermochelys* has virtually no fossil record. Fragments of shell mosaic, isolated limb bones, and some skull material have occasionally been described from fossil localities scattered around the world spanning most of the Tertiary. With relatively few exceptions, most of this material has been referred to the extinct dermochelyid genus *Psephophorus*. Thus, the prevailing view has been that some form of *Psephophorus* presumably gave rise to *Dermochelys* sometime during the latter part of the Tertiary. This view implies that leatherbacks have had a simple evolutionary history.

New discoveries suggest otherwise, however. Information provided by previously undescribed fossils, combined with first-hand examination of most dermochelyid type specimens and a review of the relevant literature, indicates that several different leatherback lineages existed at one time or another in the past, often concurrently.

The purpose of this paper is to identify these lineages as well as to suggest possible relationships within and between them wherever possible. Some major evolutionary trends within the dermochelyids can also be perceived. These results are based in part on descriptions of new fossil leatherback material from Egypt, Peru, and Belgium which follow below.

Abbreviations used in this paper are as follows: BMNH – British Museum (Natural History); CMNH – Carnegie Museum of Natural History; GMC – Geological Museum, Cairo, Egypt; IRSNB – Institut Royal des Sciences Naturelles de Belgique; MCZ – Museum of Comparative Zoology, Harvard University; MHNP – Museo de Historia Natural, Lima, Peru; NHV – Naturhistorisches Museum, Wien (Vienna); ROM – Royal Ontario Museum, Toronto, Canada; UMMP – University of Michigan Museum of Paleontology; USNM – United States Museum of Natural History (Smithsonian Institution); YPM – Peabody Museum of Natural History, Yale University.

SYSTEMATICS

The following taxonomic sections contain descriptions of two new genera and one new species. One of these genera was previously described as a new species (*P. eocaenus* Andrews, 1901) of the genus *Psephophorus* Meyer, 1846. The original diagnosis was based solely on a single humerus, but more recently discovered and previously undescribed shell material warrants the recognition of a new genus, described below.

Order Testudines
Suborder Cryptodira
Family Dermochelyidae
Egyptemys, Gen. nov.
(Figs. 1–3)

Type Species. — *Psephophorus eocaenus* Andrews, 1901.

Referred Species. — *Psephophorus oregonensis* Packard, 1940.

Distribution. — Late Eocene, northern Egypt; Eocene of Oregon, USA.

Diagnosis. — Shell with at least five weakly-developed anteroposterior carapacial ridges; area between ridges flat or nearly so, with small numbers of ossicles (usually 1–2, occasionally 3) occupying areas between adjacent ridges; shell of fairly uniform thickness. Ridges semi-circular in cross-section and of essentially equal height above surrounding surfaces, except for middle ridge, which is slightly less prominent; ridges confined only to central portions of ossicles which they traverse; intervening distances between adjacent ridges somewhat variable; visceral surface of carapace smooth with no indication of ridges. Individual ossicles of carapace highly variable in size and irregular in shape; ossicles occupying intervals between ridges generally smaller than ossicles along ridges. Neural spine of first dorsal vertebra with parallel sides except at base, where a marked constriction occurs; anterior zygapophyses extend outward from base of neural spine at a lower level than do posterior processes; nerve opening behind neural arch considerably smaller than in *Dermochelys coriacea*; facets on lateral sides of neural arch for attachment of rib heads subrounded rather than parallelogram-shaped; anterior zygapophyses closely spaced near midline; vertical flange of bone present on anterior face of lower half of neural spine. Proportionately larger processus radialis of humerus and less robust humeral shaft than in any other leatherback species for which this bone is known.

Discussion. — *Egyptemys eocaenus* was originally described as a new fossil leatherback species which was provisionally referred to *Psephophorus* on the basis of a single humerus (Andrews, 1901). The existence of "some masses of scutes" was mentioned in passing, but none of this shell material has ever been described. Andrews (1906) shortly thereafter referred another humerus from the Fayum to this species.

Since no humerus is actually associated with the type specimen of *Psephophorus* (*P. polygonus* Meyer, 1846, from the Miocene of Central Europe), presumably Andrews was simply following the general custom of assigning most fossil leatherback remains to *Psephophorus* as a matter of convenience. There was, in fact, no apparent basis for referring the type of *E. eocaenus* to *Psephophorus*.

Subsequently recovered dermochelyid shell material from the Fayum Depression, here described for the first time, can reasonably be assumed to represent the same taxon as the humeri which Andrews originally described nearly a century ago. These shell fragments are themselves quite distinctive and, together with the humeri and a reasonably well preserved neural arch and spine from the first dorsal vertebra, provide a clear basis for recognition of a new dermochelyid genus.

The Fayum shell material clearly differs from the type and only specimen of *Psephophorus polygonus* (Meyer, 1846), the type species of the genus (see below). Only a single ridge is preserved on the sole example of *P. polygonus* so far known. This ridge is broadly rounded and prominent

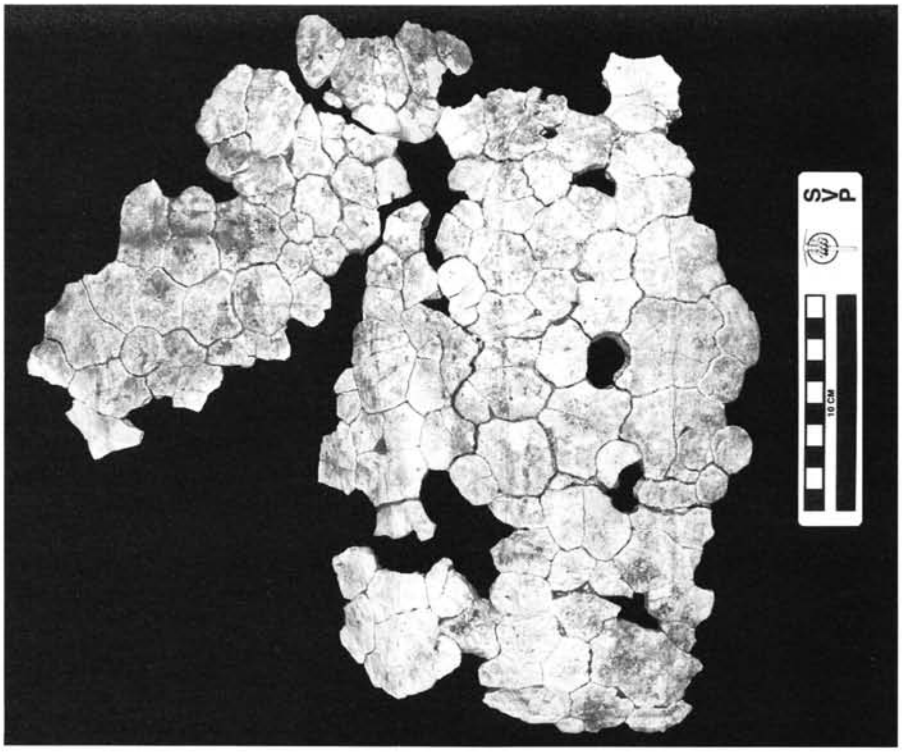

Figure 1. Dorsal view of the carapace of *Egyptemys eocaenus* (YPM 6212) with parts of five adjacent anteroposterior ridges preserved.

rather than diminutive, as are ridges in *E. eocaenus*. It gently undulates in height along its anteroposterior length rather than being of more or less uniform height, and it covers the entire width of the ossicles upon which it is situated rather than being narrowly confined to a small band along the midlines of successive ossicles. The ridge-bearing ossicles themselves are irregular in shape and are all longer than broad, which is not always true of *E. eocaenus*. Moreover, if the carapace of *P. polygonus* was characterized by more than one anteroposterior ridge, there were at least five ossicles in the spaces between ridges, not one to three ossicles as found between each of the five ridges of *E. eocaenus*.

A shell fragment from the Eocene of western USA, which is part of the type of *Psephophorus oregonensis* Packard, 1940 (along with a skull encased in a very obdurate matrix which has so far precluded its study in detail), appears to be very similar if not identical to the carapace of *E. eocaenus*. Alone among all fossil dermochelyids other than *E. eocaenus*, the shell of *P. oregonensis* is characterized by the same type of narrow, diminutive ridge, rounded in cross-section, that is one of the diagnostic features of the Egyptian fossil leatherback. Thus, we tentatively refer the Oregon material to *Egyptemys* and suggest it represents a second, more or less contemporaneous occurrence which might be conspecific with *E. eocaenus*.

Egyptemys eocaenus (Andrews, 1901)
(Figs. 1–3)

Synonymy. — *Psephophorus eocaenus* Andrews, 1901.
Type Specimen. — GMC 10028, a left humerus.

Hypodigm. — The type; BMNH R3352, the proximal half of a humerus; YPM 6212, a partial carapace with associated neural arch and spine of the first dorsal vertebra; UMMP 97538, largely disarticulated pieces of a shell with some fragmentary associated skeletal parts.

Horizon and Locality. — Qasr el-Sagha Formation, late Eocene, Fayum Depression of northeastern Egypt.

Diagnosis. — As for the genus.

Description

Shell. — The largest shell fragment yet known is represented by YPM 6212. When discovered in the early 1960s, most of the bony ossicles of the Yale shell had become disarticulated, but it has been possible to reconstruct a portion measuring approximately 33 cm anteroposteriorly and 31 cm transversely (Fig. 1). We assume that this shell fragment represents a piece of the carapace. Associated with this specimen are several much smaller pieces of shell and a number of individual ossicles that we have not been able to fit together. None of these smaller fragments exhibits characters not also seen on the reconstructed part of the shell.

There are five nearly parallel ridges on the external surface of the reconstructed segment; these serve to establish the anteroposterior axis of the shell. Whether or not additional ridges were originally present cannot be determined. The greatest transverse distance between any two of these ridges is 8.0 cm and the least is 5.9 cm. The distances between adjacent ridges seem to vary regularly; the outermost ones are about 8 cm from those medial to them, and these in turn are roughly 6 cm from the central ridge, suggesting that the middle of the five ridges may indeed coincide with the midline of the shell. The ridges do not converge toward either end but instead maintain a nearly constant distance from one another along the entire length of the specimen, which indicates that the fragment here described is from somewhere in the middle of the shell rather than at one of its ends.

The ridge spacing on the carapace of *E. eocaenus* is much closer than in modern *Dermochelys*. In a sample of four adult *D. coriacea* shells (BMNH unnumbered; MCZ 83204; ROM 2263; USNM 139891) ranging in midline carapace length from 130 to 160 cm, the distances between parallel ridges varies from 15.4 to 20.5 cm (across front third of carapace), 12.9 to 19.9 cm (midway along length of carapace), and 8.7 to 17.3 cm (across posterior third of carapace).

The reconstructed fragment exhibits moderate curvature both anteroposteriorly and transversely. The extent to which these flexures reflect the actual shape of the shell when the turtle was alive is, however, uncertain. There is clearly some distortion of the fossil, as evidenced by the separation of originally contiguous ossicles in the restoration. Part of the undersurface and some areas along the margins of the various shell fragments are in a somewhat deteriorated condition as a consequence of abrasion and erosion.

The individual ossicles of which the shell consists are of varying size and highly irregular shapes. Those forming the ridges may be broader than long or longer than broad. Those underlying the outermost ridges are generally larger than those underlying the intervening three ridges. Ossicles occupying the intervals between ridges are typically smaller than the keeled ossicles forming the ridges. The number of ossicles between adjacent ridges ranges from one to three, with two being the usual number. Faint evidence of dimpling can be discerned on the external surface of the shell and may indicate that its fresh, uneroded surface was textured with some kind of ornamentation, perhaps akin to that of *Cosmochelys* (Andrews, 1919).

Each of the five ridges is characterized by a slight dorsal thickening along the midline axis of serially arranged ossicles. None of the ridges is very pronounced and all but the middle one are of the same height, rising little more than a millimeter above the surrounding bone surface. The median ridge is even less prominent than the others. Whether this is a bona fide anatomical characteristic or whether it is instead an artifact of differential weathering of the shell's surface is unclear. All ridges are semi-circular in cross-section and all waver slightly along their lengths. Markedly depressed troughs do not occur between the ridges, as is the case in *D. coriacea*. Instead, the area between the rows of ridges is flat or even somewhat convex. The dorsoventral thickness of well-preserved ossicles ranges from 12 mm at the crest of ridges to 7 mm in the regions between ridges.

The fossil leatherback shell material in the University of Michigan collection (UMMP 97538) probably represents a single specimen. The largest of the fragments retrieved is an irregularly-shaped concretion with a maximum length of 38 cm and a maximum width of 25.5 cm. Included within this concretion are small clusters of typically dermochelyid shell mosaic plus numerous stray individual ossicles.

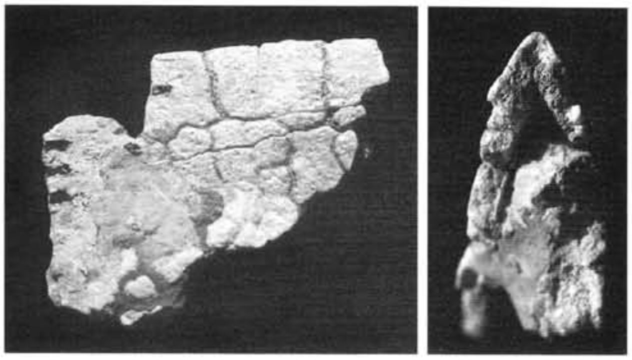

Figure 2. Fragment from the rim of the shell of *Egyptemys eocaenus* (UMMP 97538) showing the acute flexure of a series of small bony ossicles which look like miniature versions of the peripheral bones found in the bridge region of conventional turtle shells: (Left) dorsal view; (Right) transverse section through edge of shell.

The shell appears to have collapsed prior to being covered by sediment, so that miscellaneous pieces of bone occur on several different levels within the matrix. The morphology of the individual ossicles and portions of ridges which can be observed are all similar to the comparable features of YPM 6212 and clearly indicate this is still another example of *E. eocaenus*.

The specimen includes several fragments with straight edges which appear to represent parts of the shell's rim. One of these is shown in Fig. 2. The acute flexures of the small ossicles forming the rim look very much like miniature versions of the peripheral bones found in the bridge region of shells of conventional aquatic turtles. Moreover, at least with respect to the specimen shown in Fig. 2, it appears that what is presumably the underside of these folded bones terminates in a feathered edge roughly 2 cm medial to the outer border of the shell. Hence, a sheet of interlocking bony ossicles may not have continued across the ventral surface of the turtle's body. Thus, the plastron of this species may have been reduced to a bony framework as in modern *Dermochelys* and certain other fossil leatherbacks.

The type of structure at the margin of the carapace which is described here has not previously been reported in any other dermochelyid. This may eventually prove to be a feature unique to *Egyptemys* and thus a useful diagnostic character.

Axial Skeleton. — The best preserved component of the axial skeleton discovered so far is a neural arch and spine representing the first dorsal vertebra of YPM 6212 (Fig. 3). This element has not been described for any other fossil dermochelyid, so the only comparisons possible are with the living *D. coriacea*.

Several differences are readily apparent (Fig. 3). In lateral view, the anterior zygapophyses and posterior processes of *D. coriacea* are on the same horizontal plane, whereas in *E. eocaenus* the tops of the posterior processes (whose rearward-projecting tips are not preserved) extend from the neural arch at a markedly higher level than do the

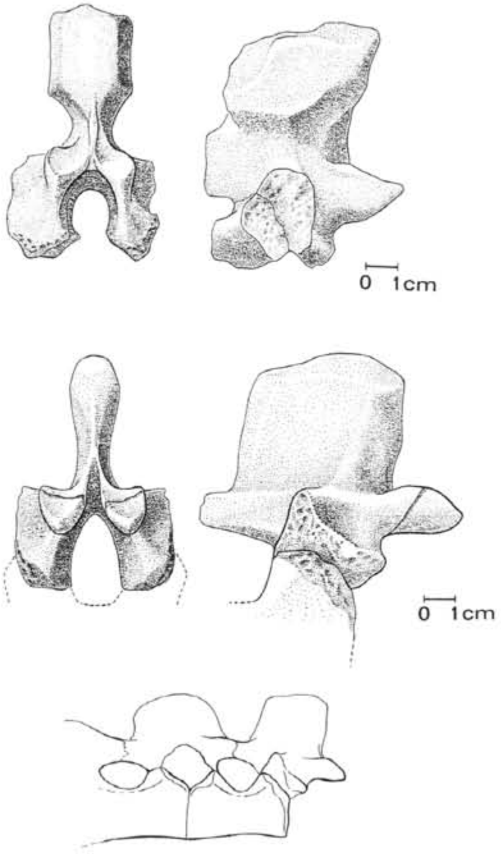

Figure 3. (Top) Anterior and right lateral views of the neural arch and spine of the first dorsal vertebra of *Egyptemys eocaenus* (YPM 6212); (Middle) comparable views of the same structures in *Dermochelys coriacea* (USNM 62754); and (Bottom) the relationship between the neural arch and spine of the first dorsal vertebra of *D. coriacea* (USNM 62754) to adjacent components of the dorsal vertebral column.

anterior zygapophyses. Also, the opening for the spinal nerve located just posterior to the first neural arch is considerably more constricted in the Egyptian fossil than in modern forms, evidently because the dorsoventral height of its posterior processes is substantially greater than in *D. coriacea*. Moreover, the lateral facets for attachment of the rib heads are subrounded in *E. eocaenus* while they are appreciably larger in area and parallelogram-shaped in *Dermochelys*.

In anterior view, the neural spine of *E. eocaenus* is massive and parallel-sided except at its base, where a marked constriction occurs. The neural spine of *D. coriacea*, in contrast, is proportionally much narrower with sides that flare out only moderately toward its top. In addition, there is a slender, vertical flange of bone present on the anterior face of the lower part of the neural spine in *E. eocaenus*. No comparable structure is found in modern leatherback turtles. Finally, the anterior zygapophyses in *D. coriacea* are more widely spaced transversely than in *E. eocaenus*.

The fact that the Fayum vertebral fragment is virtually identical in size to that of a modern adult specimen (USNM 62754) of *Dermochelys* (Fig. 3) suggests that a complete shell of *Egyptemys* would have been about the same size as that of a modern leatherback, perhaps 150 cm along its midline axis. This suggests that the number of anteroposterior ridges on the carapace of *E. eocaenus* far exceeded the five that have been preserved.

Fragments of ribs have been preserved in association with both the Yale and Michigan specimens of *Egyptemys*. These were clearly not fused to any overlying bone and exhibit the characteristic broad, flat structure which is typical of all known Cenozoic and modern dermochelyids.

Appendicular Skeleton. — The humerus is all that is so far known of the appendicular skeleton. It is sufficiently different in morphology from that of other dermochelyids that Andrews (1901) felt justified in recognizing it as representative of a new leatherback species, which he referred to *Psephophorus*. The processus radialis is proportionately much larger in *E. eocaenus* than in any other leatherback species for which this bone is known. Moreover, its shaft is considerably less robust than in other members of the family, suggesting that its anterior limbs were less hypertrophied than in the modern species.

Discussion. — The sediments of the Qasr el-Sagha Formation represent shallow lagoonal and, to a lesser extent, deltaic depositional environments (Gingerich, 1992). A rich and diverse fauna of marine mammals (cetaceans and sirenians) has been recovered from this formation. In addition, a varied assemblage of fossil turtles has also been described from these beds, including the side-necks (Pleurodira) *Shweboemys antiqua* and *Stereogenys cromeri* as well as a cheloniid, *Thalassochelys libyca*, and the leatherback *Egyptemys eocaenus* (Andrews, 1906; Wood, 1970, 1971).

Egyptemys oregonensis (Packard, 1940)

This species is assigned to *Egyptemys* on the basis of a referred shell fragment consisting of all or parts of 26 bony ossicles. A low, rounded ridge traverses 5 linearly-arranged ossicles. These are of somewhat irregular size and shape. All of the ridge-bearing ossicles are wider than long. Insofar as it has been preserved, this shell remnant is virtually indistinguishable from what is known of the carapace of *E. eoceanus*.

The original diagnosis of *E. oregonensis* was based on a skull which was compared only to *Dermochelys*, from which it clearly differs (Packard, 1940). This skull requires further preparartion and a redescription, especially with reference to other fossil dermochelyid skulls now available.

Natemys, Gen. nov.
(Figs. 4–5, 9–11)

Type Species. — *Natemys peruvianus*, sp. nov.

Distribution. — Late Oligocene, southern coast of Peru.

Etymology. — Named in honor of the senior author's younger son, Nathaniel (Nat) Wiley Wood, who has endured his prolonged struggle against brain cancer with remarkable courage, uncommon dignity, and an unfailing sense of humor.

Diagnosis. — Differs from all other known dermochelyid taxa in having both carapace and plastron comprised of a mosaic of large numbers of bony ossicles varying considerably in size and shape. Anteroposterior ridges are absent on both carapace and plastron, both of which appear to have been smooth-surfaced. Scute sulci are absent. Carapace has at least two parallel rows of irregularly spaced, greatly enlarged and elongated ossicles with deeply scalloped borders, largely ringed by clusters of smaller, more or less oval ossicles; together, this assemblage forms a distinctive "sunflower" pattern. Clusters of ossicles forming "sunflower" patterns in adjacent rows are offset from one another. A third row of moderately elongated, uniformly sized ossicles is also present on the carapace; no readily definable clusters of smaller ossicles are associated with these. All the rows of enlarged ossicles are presumably aligned with the anteroposterior axis of the shell. Three to five generally smaller ossicles intervene between the parallel rows of enlarged ossicles. Only one row of enlarged, roughly equidimensional ossicles is preserved on the plastron, oriented in the same direction as the prominent carapace rows. In this row, larger ossicles with scalloped edges alternate regularly with somewhat smaller, oblong ossicles with straight sides. A feebly developed "sunflower" pattern is associated with only some of the scallop-edged ossicles of this row. No well-defined lateral rows of enlarged ossicles are present on either side of this row. Many plastral ossicles are elongated transversely, including one isolated, enlarged, scallop-edged ossicle surrounded by smaller satellite ossicles which form a "sunflower" pattern.

Natemys peruvianus, sp. nov.
(Figs. 4–5, 9–11)

Type Specimen. — Museo de Historia Natural, Lima, Peru, uncatalogued; a partial carapace and plastron.

Hypodigm. — The type only.

Horizon and Locality. — Late Oligocene Pisco Formation, southeastern coast of Peru (Larson, 1990). The type locality (Fig. 6) is in the Pisco Basin near the west bank of the Río Ica, approximately 1.5 km southwest of Hacienda Ullujaya, due east of a terrain feature named Las Tres Pyramides, roughly 9 km southsoutheast of Cerro La Bruja, Ocucaje, Dept. Ica, Peru (14°38'S, 75°38'W; Fig. 7). Part of the type specimen was collected during February 1989 and the rest in March 1990 by Susan Hendrickson and Peter Larson.

Diagnosis. — As for the genus.

Description

Shell. — This specimen clearly represents the remains of a fossil dermochelyid turtle. It exhibits the characteristic mosaic of bony ossicles which typifies all but the most primitive members of its group. In fact, certain of its features (see discussion) unequivocally ally it closely with the best represented of all previously described fossil leatherback turtles, "*Psephophorus*" *rupeliensis* from the early Oligocene of Belgium.

When discovered, the type and only known specimen of *Natemys peruvianus* was perched atop a low pedestal of soft sediment raised perhaps 10 to 20 cm above the surrounding erosion surface (Figs. 6 and 8; S. Hendrickson, *pers. comm.*). As the base of this pedestal was gradually eaten away by erosion, irregularly shaped and sized chunks progressively spalled off from the periphery of the flat slab of collapsed turtle shell which it supported. Efforts to fit these exfoliated fragments back together have only been partly successful. What remains, therefore, of a specimen that had at one time been far more complete is an elongate sheet of bone measuring roughly 81 cm along its longest axis by 52 cm at its greatest width (Figs. 4–5).

A surprising and, we believe, diagnostic feature of this specimen is that two separate, continuous, essentially horizontal layers of bone have been preserved, separated by a thin layer of intervening, rather coarse sediment which contains abundant remains of relatively small marine fossil bivalves. In effect, the remains of this turtle's shell have formed a fossil "sandwich," with a median layer of sediment compressed between two flat slabs of bone (Fig. 9).

There are two alternative explanations for this peculiar (at least in terms of dermochelyid shell morphology) preservation. One is that this particular taxon is characterized by having fully ossified carapacial and plastral bony mosaics. The other conceivable explanation is that a large expanse of the carapace had buckled after the turtle's death and folded over on itself, resulting in two layers.

There are several reasons for believing that the carapace and plastron of *Natemys* were both completely covered by a layer of intricately interlocking bony ossicles:

1) the pattern of ossicles differs on the two exposed surfaces, as will be described below;

2) rows of enlarged ossicles on both slabs are lined up in almost the same orientation, suggesting that the dorsal mosaic simply settled down onto the ventral one;

3) both the thickness of the mosaic and also the sizes of the individual ossicles are considerably greater in *Natemys* than in *Dermochelys*. Consequently, there was probably greater structural integrity of the shell in *Natemys* than in *Dermochelys*, and hence the taphonomic processes of preservation might well have affected the former differently from the the latter. The bony mosaic of *Natemys* was probably far less susceptible to folding the way that shells of recently dead *Dermochelys* sometimes do; and

4) if the shell had folded inward on itself, especially in such a large preserved slab, there should be evidence of at least minor separations between some of the ossicles, but all are as tightly sutured as they were in life. There are no sediment-filled cracks between adjacent ossicles, as there would be if the mosaic had been sharply flexed.

Admittedly, if the foregoing interpretation is correct, one might well expect to find some evidence of the axial skeleton (such as ribs, dorsal vertebrae, and limb girdles) between the two layers of bony mosaic, but no such evidence

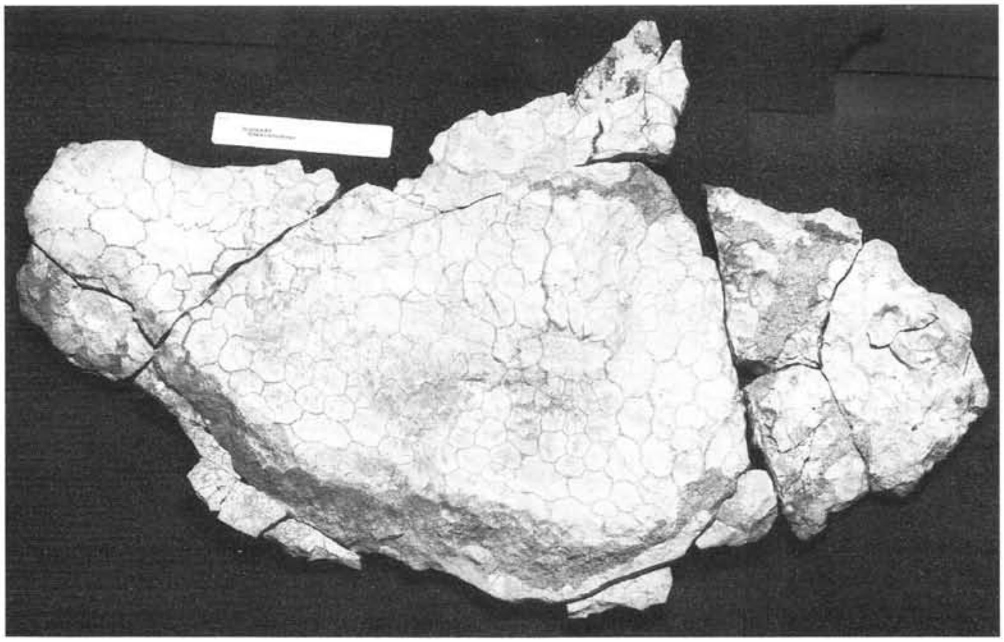

Figure 4. Type specimen of *Natemys peruvianus* (Gen. nov., sp. nov.) from the late Oligocene of coastal Peru. Presumed carapacial surface.

exists. No axial or appendicular elements of the skeleton were found, either sandwiched between the two slabs of bony ossicles or scattered around their weathered periphery.

As an alternative explanation which might account for the lack of axial skeletal remains between the two mosaic slabs, one might suppose that a large section of the carapace had collapsed, causing adjacent parts to fold inward toward each other or perhaps slide over one another. This has been observed to happen sometimes in *Dermochelys* (P. Pritchard, *pers. comm.*). If this were true, however, there are several features that are difficult to explain that one might expect to see:

1) varying degrees of fracturing on both slabs, or at least some partial separation of adjacent ossicles, neither of which is evident;

2) similar patterns and arrangements of the bony ossicles comprising the two different slabs. However, the differences in these features between the two slabs are greater than seen on any of the carapaces of *Dermochelys* that we have been able to examine in museum collections;

3) at least some axial skeleton remnants associated with the shell (though not necessarily between the two slabs) because such a large piece of it was preserved. Yet there are

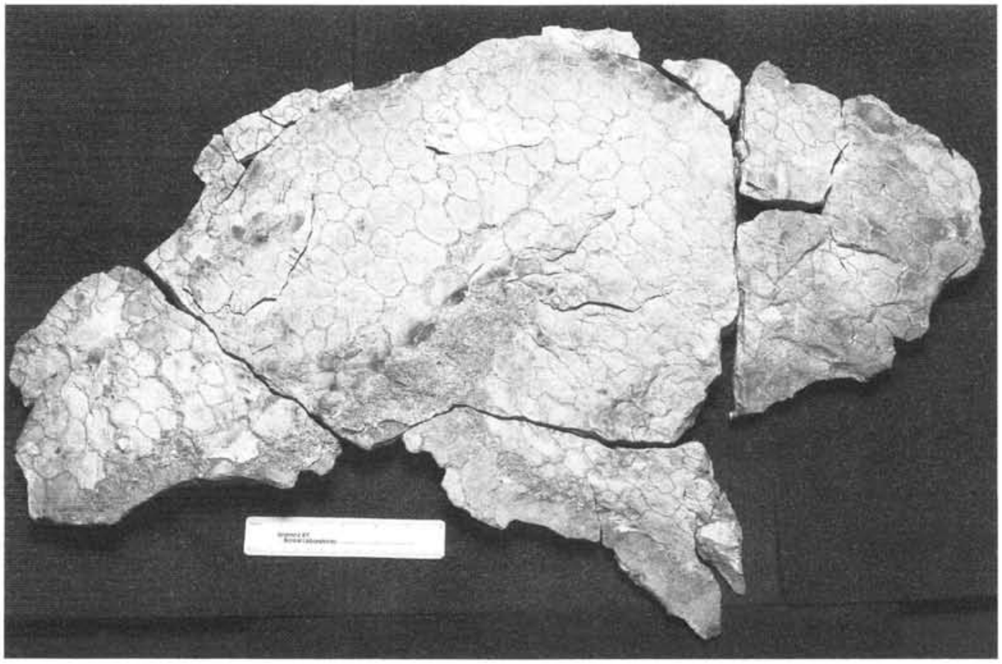

Figure 5. Type specimen of *Natemys peruvianus* (Gen. nov., sp. nov.) from the late Oligocene of coastal Peru. Presumed plastral surface.

Figure 6. Type locality for *Natemys peruvianus*, with pedestal in foreground upon which the specimen was perched.

none. Thus, the absence of axial skeleton elements is equally puzzling no matter which hypothesis is favored.

On balance, therefore, the first of the two possible scenarios – that there was a bony mosaic covering the plastral as well as the carapacial surfaces – appears to be less problematical and has been adopted as being the more likely explanation.

When viewed in low-angle light, the surface of the shell, in areas where the effects of erosion have not been too severe, reveals faint traces of irregular dimpling, suggesting that the original, undamaged surface may have been characterized by the same kind of rough texturing as has been reported for several other fossil dermochelyid taxa (most notably *Cosmochelys*).

The external surfaces of the two shell layers (interpreted as the carapace and plastron, respectively) show evidence of considerable abrasion, presumably the consequences of eolian sand-blasting after the sediments within which the fossil had been buried had eroded away. The resultant undulating surfaces sometimes make it difficult to trace the outlines of sutures between adjacent ossicles.

Figure 7. Map of Peru showing location of the discovery site of *Natemys peruvianus*.

Nevertheless, the general pattern of the shell's ossicles can be confidently described. This pattern clearly differs on the two exposed surfaces, so we will first describe what we believe to be the carapace (based on its close resemblance to "*P.*" *rupeliensis* material from Belgium, as well as the fact that this was the top surface of the specimen when it was discovered; Fig. 8).

Carapace. — The single most striking feature of the dorsal aspect of the shell is a linear row of enlarged ossicles which are aligned more or less along the anteroposterior axis of the shell as it is preserved and extend along its entire length. These ossicles vary somewhat in size. Many of them are elongated congruently with what we presume to be the anteroposterior axis of the shell. They range in midline length between 4.0 and 6.5 cm, while the maximum width does not appear to exceed 5.0 cm. Precise dimensions are difficult to provide because the lateral margins of the larger ossicles in this conspicuous row are deeply and irregularly scalloped.

In terms of relative size, there is no apparent regularity in the spacing of these enlarged ossicles. From the narrow end of the shell fragment towards its broader end, the arrangement of the 13 ossicles forming this distinctive row can be expressed as follows (with L = relatively elongate ossicles and S = comparatively shorter ones); L, S, L, L, L, S, S, S, S, L, S, S, S. Even the smaller ossicles in this row tend to be larger in size than most of the other ossicles located to either side.

Associated with the emarginated sides of each of the larger ossicles are semi-circular clusters of much smaller, generally oval ossicles arranged like the petals of a flower radiating outward from and surrounding a central disk (Fig. 10). We refer to this distinctive arrangement as the "sunflower" pattern of ossicles. A somewhat similar arrangement of ossicles can be discerned in some of the other fossil dermochelyids that have previously been described (see discussion).

Parallel to this prominent row of enlarged ossicles there appears to be another row of moderately elongated but generally narrower ossicles than those just described. These tend to be more uniform in size, measuring between 4.0 and 4.5 cm in midline length. None of the ossicles in this sequence has the strongly scalloped lateral edges character-

Figure 8. The type specimen of *Natemys peruvianus* as found *in situ* in the field.

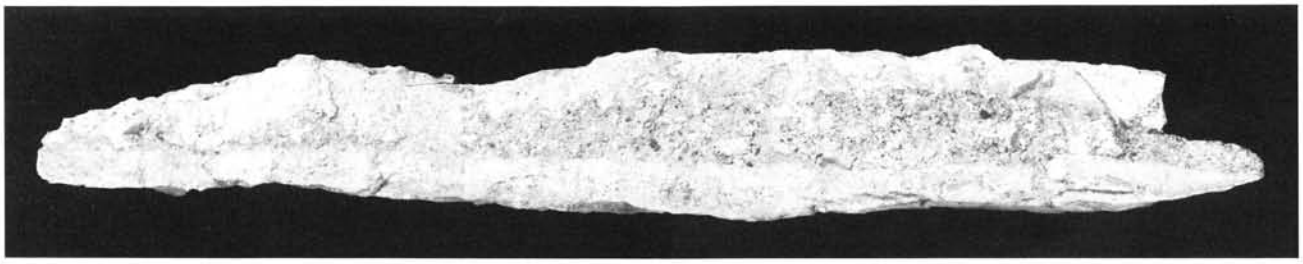

Figure 9. Cross-sectional view of a piece of the shell of the type specimen of *Natemys peruvianus*, showing a median layer of matrix sandwiched between the bones of the presumed carapacial and plastral surfaces.

istic of the larger bones in the previously described row. Moreover, less of this lateral row has been preserved, with only part or all of eight ossicles being discernible. There is no evidence of a "sunflower" pattern of smaller satellite ossicles associated with any of the individual bones in this row. The lateral distance between the two rows of elongated ossicles is roughly 13 to 14 cm.

Intervening between these two parallel rows are anywhere from three to five smaller ossicles of varying size and shape. Some are more or less triangular, oval or sub-rounded, while others may be loosely described as pentagonal or hexagonal. Standard geometric terminology is inadequate to describe the irregular shapes of some of these ossicles. Whatever their particular shapes, these ossicles typically measure 2.5 to 3 cm in length along their longest axis, which may be oriented in almost any direction. Some of the ossicles forming "petals" of the "sunflowers" may reach a length of 4 cm or even slightly more.

Partially preserved clusters of elongated ossicles, some of them reaching a length of 5 cm, can be observed on one edge of the slab. These strongly suggest the former presence of still another row of enlarged ossicles arranged along the anteroposterior axis of the carapace. Given the relatively large size of these putative "petals," our hypothesis is that the central ossicles around which they were probably arranged were at least as large as, if not larger than, the scallop-edged ones in the first of the two rows already described. Furthermore, judging from the positions of these clusters at the edge of the specimen, we suspect that the large, scallop-edged ossicles in adjacent rows were laterally offset from each other.

How many more or less parallel rows of enlarged ossicles were present in a complete carapace cannot be determined on the basis of the evidence at hand. But it seems probable that the shell remnant described here is only a relatively small portion of what had originally been a much larger carapace, easily measuring 150 cm or more in total length. Field notes recorded at the time of the specimen's discovery suggest that its diameter, prior to its partial disintegration from weathering, must originally have been been ca.100 cm across (S. Hendrickson, *pers. comm.*). Ridges do not seem to have been present. Evidently the dorsal surface of the carapace was smooth.

Plastron. — The obverse side of this specimen, which is interpreted as part of a fully ossified plastral mosaic, is less

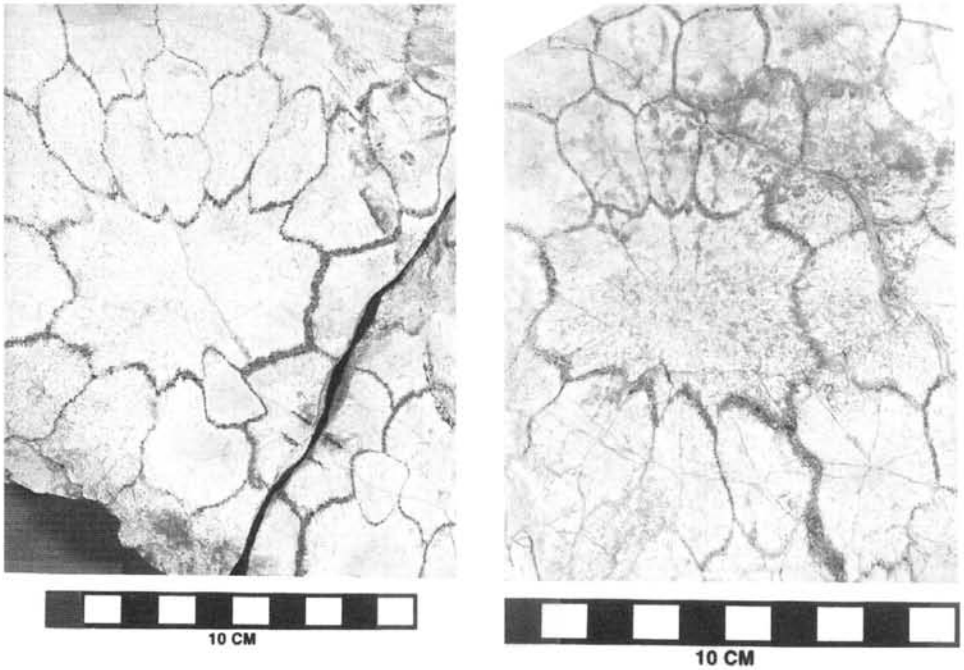

Figure 10. Two "sunflower" pattern clusters of ossicles on the carapace of *Natemys peruvianus*. The anteroposterior axis of the shell runs horizontally from left to right.

well-preserved than the carapace. Little, if any, of the original external surface has survived intact. Thin wedges of bone, never more than 5 to 6 mm thick at most, have exfoliated off the surface in many places, leaving miniature "escarpments" as evidence of their former positions. The resultant uneven, exposed surface thus represents varying levels of internal bone structure underneath the original external surface. Consequently, tracing the outlines of individual ossicles is often difficult and not always possible. As is true for the other side of the specimen, there is no indication that ridges were ever present.

In the center of this slab, and aligned with its anteroposterior axis, is a prominent row of enlarged, roughly equidimensional ossicles. Outlines of 12 consecutive ones are clearly discernible. Slightly larger ones (about 5 cm by 5 cm) with scalloped lateral margins alternate regularly with somewhat smaller (about 3 to 4 cm by 4 cm) more or less oblong ossicles with generally straighter sides. This median row corresponds fairly closely in position to the row of 13 overlying, enlarged ossicles which extends down the center of the carapace slab on the opposite side of the specimen, suggesting close alignment of these two rows (one on the carapace and the other on the plastron).

Two enlarged ossicles nearest the broad end of the specimen show a feeble "sunflower petal" pattern of clusters of smaller, elongated ossicles extending laterally from their scalloped margins. A tendency toward this kind of ossicle arrangement is not evident in any of the other enlarged bones in this row.

No well-defined lateral rows of enlarged ossicles can be discerned on either side of this median plastral row. However, there is one apparently isolated cluster of ossicles at one edge of the specimen which forms a distinctive "sunflower" pattern, albeit one differing in proportions from those on the carapace. This cluster features an enlarged central ossicle that is, in marked contrast to those of the carapace, broader than long with respect to the anteroposterior axis of the shell (6.0 cm wide by 4.5 cm along the midline). Radiating outward from its scalloped margins are smaller, mostly elongate and oval satellite ossicles (3 to 4 cm long) forming the "petals" of the "sunflower" pattern.

A preponderance of the ossicles preserved on this side of the slab, in contrast to those on the reverse side, are elongated transversely with respect to the anteroposterior axis of the shell. Thus, the shapes and arrangements of the bony ossicles on the two sides of the specimen differ markedly.

A small piece from the edge of this turtle's shell has been preserved (Fig. 11). Whether this is from the border of the carapace or plastron cannot be determined. The feathered edge of this fragment is moderately sinuous. It is partially rimmed by a discontinuous row of semicircular ossicles, although portions of more irregularly shaped ossicles also participate in formation of the edge as well.

While it is difficult to be quantitative, in view of the undoubtedly very large size of the turtle when it was alive, as well as the fact that the outer surfaces of both slabs appear to be heavily weathered, the shell bone appears to be relatively thin, although not nearly as thin as that of the equally enormous modern leatherbacks. There is no evidence of scutes covering the shell. Presumably, like the living species, the Peruvian dermochelyid's shell was covered by a thin veneer of skin.

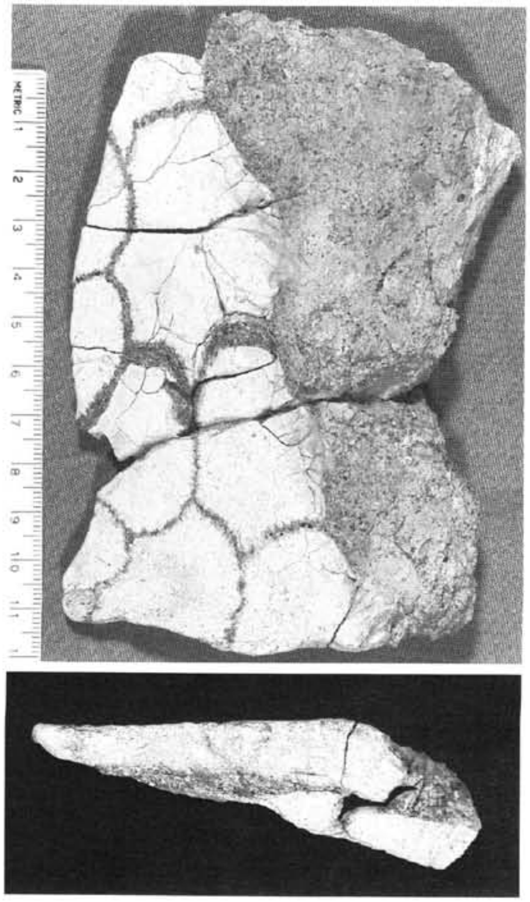

Figure 11. Fragment from the margin of the shell of *Natemys peruvianus*: (Top) view of outer surface; (Bottom) cross-sectional view, showing edges of both carapace and plastron.

Discussion. — *Natemys* is the first fossil dermochelyid known from South America. The occurrence of fossil leatherback turtles on this continent is not particularly surprising given the pan-oceanic distribution of the sole surviving modern species, as well as the fact that dermochelyid nesting beaches occur today along the northern coast of the continent (e.g., Trinidad, French Guiana, and Venezuela; Pritchard and Trebbau, 1984) as well as nearby in Panama, Costa Rica, and Mexico. The southernmost non-nesting records of the living leatherback species *D. coriacea* in South America are occurrences at Isla Chilöe, Chile (on the continent's western coast) and Mar del Plata, Argentina (on the continent's east coast; Pritchard and Trebbau, 1984).

The fact that *Natemys* had a fully ossified plastral mosaic, comparable in structure to its carapace, serves to differentiate it readily from all other known dermochelyids. While it has occasionally been suggested that other fossil leatherbacks may also have had fully ossified plastral mosaics (e.g., *Psephophorus polygonus*, Seeley, 1880; *Psephophorus rupeliensis*, Van Beneden, 1883, and Dollo, 1888, but refuted by Seago, 1979; *Psephophorus calvertensis*, Palmer, 1909), convincing evidence to support these claims has not yet been forthcoming.

Several features of *Natemys* invite comparison with the Belgian fossil dermochelyid "*Psephophorus*" *rupeliensis*. Both lack ridges or keels on their carapaces and both are characterized by greatly enlarged, scallop-edged ossicles arranged in parallel rows which presumably correspond in position to the ridges typically found in other dermochelyids. *Natemys* is clearly more similar to "*P.*" *rupeliensis* than to any other previously known dermochelyid. This relationship will be more formally documented in the phylogenetic section of this paper.

A New Specimen of "*Psephophorus*" *rupeliensis* Van Beneden, 1883

(Fig. 12)

"*Psephophorus*" *rupeliensis* is represented by far the best material of all fossil dermochelyids. Numerous specimens were recovered in the late 1800s from Oligocene sediments in Belgium. Most examples of "*P.*" *rupeliensis* are housed in the collections of the IRSNB in Brussels. Although the type consists primarily of limb material, the majority of "*P.*" *rupeliensis* specimens are represented by portions of carapaces that are unusually large (when compared to other fossil dermochelyid remains).

Studies of the "*P.*" *rupeliensis* material were undertaken by Van Beneden (1883) and Dollo (1888). Despite some striking morphological differences, both authors erroneously referred their Belgian material to the genus *Psephophorus*, and this practice has been continued ever since (e.g., Broin and Pironon, 1980).

Examination of a previously undescribed specimen from Belgium in the collections of the Carnegie Museum of Natural History (CMNH 19750; Fig. 12) indicates, however, that "*P.*" *rupeliensis* differs significantly from the type species of *Psephophorus*, *P. polygonus* (see below). Subsequent examination of the "*P.*" *rupeliensis* material housed in the collections at Brussels has confirmed this conclusion.

The Carnegie Museum specimen is part of the Bayet collection, purchased early in the museum's history from a European source. Locality data associated with this specimen simply state "from the Oligocene (Rupellian) of Boom, Belgium." It is a roughly oval slab of bone measuring approximately 110 cm along its anteroposterior axis and 50 cm across its greatest transverse width. A substantial portion of the dorsal surface is heavily pitted, presumably as the result of post-mortem damage. The pattern of bony ossicles in this damaged region is impossible to discern.

Fortunately, part of the carapace surface has survived intact, and includes two unmistakable features which readily serve to differentiate the Belgian fossil leatherbacks from all other known representatives of the family except *Natemys*. These features are:

1) the complete absence of ridges or keels of any kind on the surface of the carapace; and

2) enormously enlarged, elongate ossicles with scalloped margins, linearly arranged, and generally surrounded by clusters of smaller satellite ossicles to form a "sunflower" pattern.

The elongate, scallop-edged ossicles of "*P.*" *rupeliensis* are arranged in parallel rows, with the "sunflower" clusters in adjacent rows being laterally offset from one another. Within a particular row, the large ossicles are irregularly spaced, sometimes being adjacent to each other, but more often occurring as an isolated feature separated from others in its row by smaller intervening ossicles.

The three largest ossicles on the shell measure approximately 10.2, 9.9, and 6.2 cm along their midline axes. The first two of these are the largest individual ossicles known from any dermochelyid shells, living or fossil (although probably not exceptional with respect to other "*P.*" *rupeliensis* shells, for which measurements of the largest ossicles have not yet been recorded).

Oddly, given the abundance of relatively well preserved and highly distinctive shell material of "*P.*" *rupeliensis* that has been recovered, it is surprising that the type specimen consists only of limb material (two partial humeri), some vertebral centra, and an elongate, bent bony bar identified as part of the plastral rim – probably a hyo- or hypoplastron – such as is found in modern *Dermochelys*. If this last fragment has been correctly identified, then the plastron of "*P.*" *rupeliensis* would have consisted of only a more or less oval bony frame forming its outer rim, across which would have stretched a layer of thick fibrous skin in which, perhaps, a few ossicles might have been imbedded.

As an aside, there is some question about what exactly comprises the type of "*P.*" *rupeliensis*, since three humeri from two different localities (Terhagen and Niel) plus a few other assorted elements are all catalogued (as IRSNB EFR 13 and 14, corresponding to old catalog numbers IRSNB 1655 and 1654, respectively) as "plesiotypes." Straightening out this confused situation is beyond the scope of this paper and will be dealt with in a separate publication, at the same time that a new generic name will be proposed for "*P.*" *rupeliensis* (see below).

Clearly, "*P.*" *rupeliensis* and *Natemys* are more similar to each other than to any other known dermochelyid. They are close in terms of geological age, "*P.*" *rupeliensis* occurring in mid-Oligocene sediments (Meuter and Laga, 1976), while *Natemys* was found in late Oligocene sediments. Both lack keels or ridges on their carapaces, and both have markedly enlarged, linearly arranged, and generally irregularly spaced ossicles with scalloped margins, around which are arrayed clusters of smaller, elongate ossicles forming distinctive "sunflower" patterns. The largest ossicles on the Carnegie Museum shell are considerably larger than those of *Natemys*, but it is conceivable that this difference may be related to relative shell sizes. The Peruvian specimen of *Natemys* might simply have been a smaller turtle than is represented by the remains of CMNH 19750, or the parts of the shell that have been preserved may not be comparable. At any rate, comparisons of the maximum sizes of the scalloped

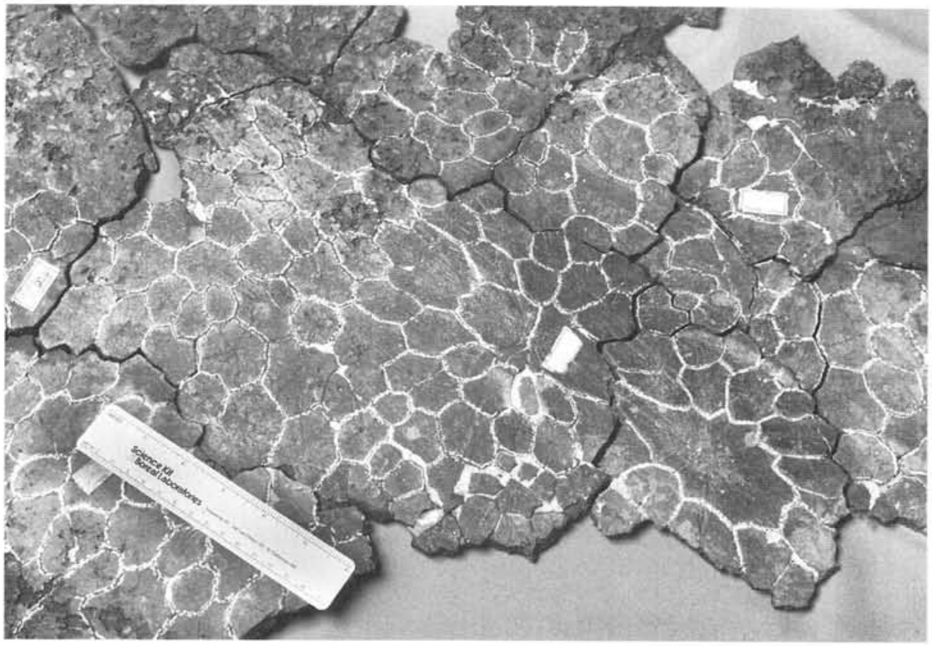

Figure 12. A large portion of the carapace of "*Psephophorus*" *rupeliensis* from the Oligocene of Belgium (CMNH 19750). Three "sunflower" pattern clusters of ossicles can be seen, two of them being contiguous.

ossicles alone is probably a relatively weak basis for differentiation between these two taxa.

The most obvious and significant difference between "*P.*" *rupeliensis* and *N. peruvianus* lies in the structure of their respective plastra. Whereas "*P.*" *rupeliensis* appears to have had a largely unossified plastron, essentially comparable to that of modern *Dermochelys*, *Natemys*, in contrast, evidently had a unique, fully ossified plastral mosaic composed of variably sized and irregularly shaped ossicles.

One other specimen should be mentioned in the context of this discussion. Müller (1849) briefly described and beautifully illustrated a small portion of a fossil dermochelyid shell (Fig. 13) from the "Zeuglodon Beds" (Eocene) of Alabama, USA. This shell fragment is flat-surfaced and consists of part or all of 13 articulated ossicles. Its most notable feature is a large (roughly 5 cm in midline length), scallop-edged ossicle surrounded, to the extent which preservation permits determination, by a cluster of somewhat smaller ossicles. This is a pattern strongly reminiscent of the shells of both "*P.*" *rupeliensis* and *Natemys*. Müller regarded this specimen as a representative of *Dermatochelys*, a synonym of the living *Dermochelys*, an attribution which is now clearly inappropriate because of the very large sizes of all the ossicles and the considerable thickness of the bone. The specimen was housed in the "Königlich Anatomisches Museum" of Berlin. We have not been successful in determining whether or not it still exists.

OVERVIEW OF THE DERMOCHELYID FOSSIL RECORD

Over the course of nearly a century and a half, a miscellaneous assortment of fossil dermochelyid remains (usually quite fragmentary) has gradually accumulated from Tertiary sediments in western Europe, northern Africa, and scattered North American localities. With relatively few exceptions, most of this material has been referred, often gratuitously, to the extinct genus *Psephophorus* (e.g., *P. calvertensis*, *P. eocaenus*, *P. oregonensis*, *P. rupeliensis*, *P. scaldii*, *P. pseudostracion*, and cf. *Psephophorus* from Italy, New Zealand, and Antarctica; see Broin and Pironon, 1980, for an excellent summary of much of this material). Even the most nondescript of fossil dermochelyid fragments have routinely been referred to *Psephophorus* (e.g., Dames, 1884; Lienau and Schleich, 1986; Dodd and Morgan, 1992). The general inference has long been that some form of *Psephophorus* eventually gave rise to the modern genus *Dermochelys*, which as yet has no unequivocal representation in the fossil record.

Within the past few years, a considerable amount of additional new fossil dermochelyid material has been discovered, for the most part, and in contrast to the earlier specimens, from the southern hemisphere. These new discoveries include fragments from Antarctica (de la Fuente et al., 1995a, 1995b), New Zealand (Köhler, 1994 and *pers. comm.*), Japan (Hirayama and Chitoku, 1992; Hirayama, 1993, 1994), and also the Peruvian *Natemys*, described herein.

In terms of its significance, the material from Antarctica (so far known only from a handful of mostly disarticulated ossicles) is interesting from a zoogeographic point of view but so incompletely preserved as to be taxonomically uninformative below the familial level. The Maastrichtian material from Japan is potentially very important for an understanding of early dermochelyid evolutionary history, but it has not yet been described in detail.

However, some of the new fossil dermochelyid material (from New Zealand and Peru) is clearly important for both taxonomic and zoogeographic reasons. A formal description

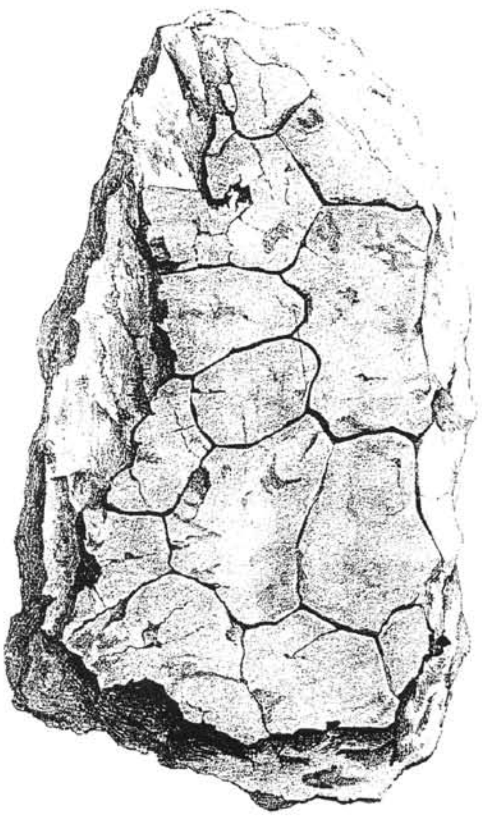

Figure 13. Fragment of a fossil dermochelyid shell from the Eocene of Alabama (figure from Müller, 1849).

of the New Zealand specimens is being prepared (R. Köhler, *pers. comm.*). This occurrence represents a relatively primitive type of dermochelyid characterized by a lack of derived characters beyond having the shell composed of a mosaic of relatively small bony ossicles. There are no keels or ridges, no linear arrangements of enlarged ossicles, no readily observable variation in the thickness of the shell bone, and no obvious differentiation in the sizes or shapes of individual ossicles. *Natemys*, as already indicated, is of particular interest because it helps to identify and define a previously unrecognized, major lineage of extinct leatherback turtles.

No summary of important new fossil dermochelyid material would be complete without mention of some extraordinarily well preserved specimens from the Eocene and Oligocene coastal plain sediments of South Carolina belonging to the collections of the Charleston Museum. Because these fossils have yet to be formally described, their significance cannot be fully assessed at present.

Another specimen of particular interest (USNM 23699) is from the Eocene of Alabama. It consists of perhaps 200 very thick, mostly disarticulated dermochelyid ossicles in a wide variety of shapes and sizes, all presumably from the shell of a single specimen. Though collected long ago (1929), this specimen has never been described. Its special significance lies in the only five bones which have been reassembled (Fig. 14). These represent part of an anteroposterior ridge which was formed by the upward flexure of the entire carapace, to produce a broadly rounded arch. This is the earliest known example of this type of keel structure, which is seen subsequently in specimens from two mid-Tertiary Atlantic coastal plain localities, one in Maryland ("*P.*" *calvertensis*) and one (not yet formally described) in South Carolina, and survives in modified form in *D. coriacea*.

The two middle bones in the articulated series of USNM 23699 have moderately (in one case) to strongly (in the other case) scalloped lateral margins. The midline length of the entire ridge fragment is 18.6 cm, while the midline lengths of the individual successive ossicles are 4.0, 4.5, 5.2, and 4.9 cm. The visceral surface of each of these serially arranged ridge bones is characterized by an elongate, roughly oval midline concavity.

In order to evaluate what this growing assemblage of fossils implies about the evolutionary history of dermochelyids, it is necessary to ascertain what anatomical characters are likely to be of greatest taxomonic and phylogenetic use. Since most fossil dermochelyids are represented only by shell fragments, the following discussion focuses exclusively on shell anatomy in the hope of making maximum use of the available sample of specimens. Some particularly well preserved and unusually informative shell material has already been discussed in the taxonomic section of this paper. For the balance of the fossil and living leatherbacks not yet considered, existing knowledge is summarized below.

Eosphargis and *Cosmochelys*

Some fossil dermochelyids (e.g., *Eosphargis gigas*, *E. breineri*, and *Cosmochelys dolloi*) have been relatively well described and clearly represent valid taxa.

Eosphargis is best represented by a remarkably complete specimen of *E. gigas* on exhibit at the IRSNB (Quintart and Plisnier-Ladame, 1968) as well as other much less complete material of both *E. gigas* and *E. breineri* from the Eocene of England, Belgium, and Denmark (Nielsen, 1959, 1963). *Eosphargis* has a shell morphology that appears to be intermediate between a typical marine turtle (Cheloniidae) and a dermochelyid. Its shell is greatly reduced. The plastron is represented only by rod-like elements forming a bony framework around what amounts to a giant median fontanelle, a condition typical of most leatherback turtles. The carapace, too, has undergone reduction. Neurals (with a modest midline ridge) and peripherals still remain, but pleurals have disappeared. No typical dermochelyid mosaic of bony ossicles is present.

Cosmochelys dolloi (Andrews, 1919), as preserved, presents the following characters:

1) parts of four adjacent, weakly developed ridges are preserved, one somewhat more prominent than the others. There is, in addition, evidence of a fifth ridge;

2) ridges are formed on the surfaces of rows of roughly hexagonal or (in one case) quadrangular ossicles. There is no upward indentation of the visceral surface beneath these carapacial ridges;

3) the ridge crests converge to a pointed apex and are of uniform height above the surrounding shell surface along their respective lengths;

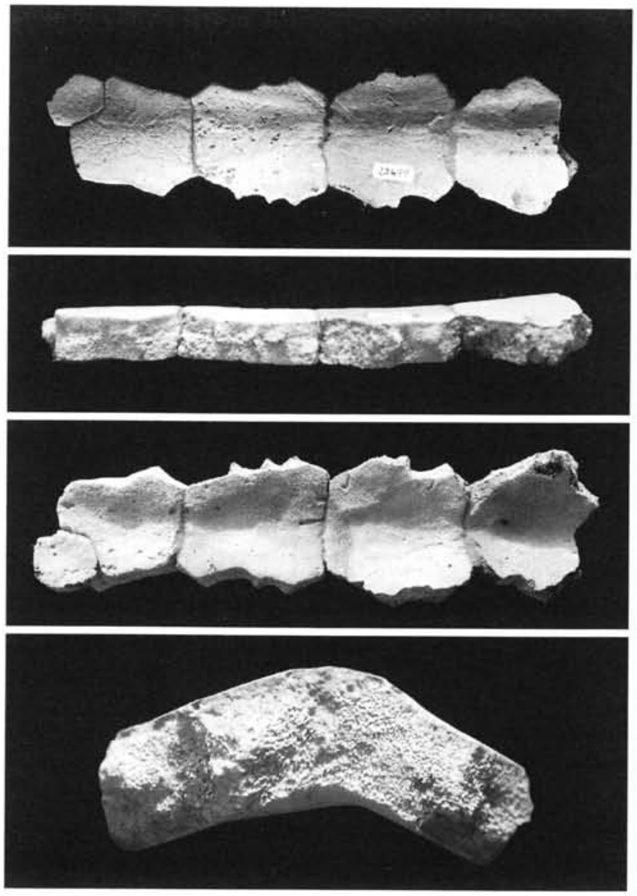

Figure 14. The only articulated ossicles of USNM 23699, a dermochelyid from the Eocene of Alabama. These reassembled ossicles form a ridge which is shown in: (Top) dorsal view; (Top Middle) lateral view; (Bottom Middle) ventral view; and (Bottom) at one end, to show the arched structure of the ridge.

4) a relatively small number of bony ossicles intervene between the adjacent ridges; and

5) the outer surface of the carapace is more deeply sculpted (with linear wrinkles radiating outward from the center of each ossicle) than in any other dermochelyid.

Oddly, in his otherwise excellent description, Andrews (1919) did not fully illustrate the dorsal surface of the carapace (part of which is shown in his Pl. 2) although the entirety of the ventral surface was depicted in his Fig. 3. Based on our examination of the type and only known specimen of *Cosmochelys* (BMNH R4338), we can supplement the original description of the outer surface of the shell with the following observations (Fig. 15):

1) the four parallel longitudinal ridges preserved on the type are unevenly spaced. The distance between the most prominent ridge and the smaller ones to either side of it is roughly 6.5 cm, while the distance between one of these smaller ridges and a neighboring one lateral to it is 9.5 cm. This appears to be the same pattern of ridge spacing as in *Egyptemys*.

2) evidence of still another ridge, situated on relatively large, isolated quadrangular ossicles, also is preserved. This must have been located laterally to any of the ridges preserved on the main slab of shell bone. Thus, portions of five different ridges have been preserved and, for reasons of symmetry, the minimum number of longitudinal rows is likely to have been at least seven, as Andrews himself noted; and finally,

3) only two or three bony ossicles intervene between the most prominent of the ridges and the smaller ones immediately to either side of it. Four to five ossicles then separate one of these lateral ridges from the next one beyond it.

Psephophorus

The genus *Psephophorus*, based on *P. polygonus* Meyer, 1846, has been until now largely a wastebasket taxon. As noted earlier, the species *Egyptemys eocaenus* and *E. oregonensis* have in the past been erroneously referred to this genus. The species *P. scaldii* and *P. ingens* cannot really be included within *Psephophorus* with confidence, since they are based only on partial or complete humeri, a bone not preserved in the type species of the genus. Knowledge of *P. polygonus* is, in fact, based solely on shell characteristics.

The type and only specimen of *Psephophorus polygonus* is housed in the collections of the Natural History Museum in Vienna. A clear understanding of its salient characteristics may help to prevent *Psephophorus* from being used as a taxonomic dumping ground for future fossil dermochelyid discoveries of uncertain affinity.

Only part of what has long been regarded as the type still exists (Fig. 16), the other half originally illustrated by Seeley (1880) having since become lost. For this reason, it is regrettable that Seeley did not fully illustrate the specimen he described in such an otherwise thorough manner; ossicles along the outer edges of the specimen were present to some unknown extent but not depicted. Moreover, this specimen technically should be considered the neotype because, ac-

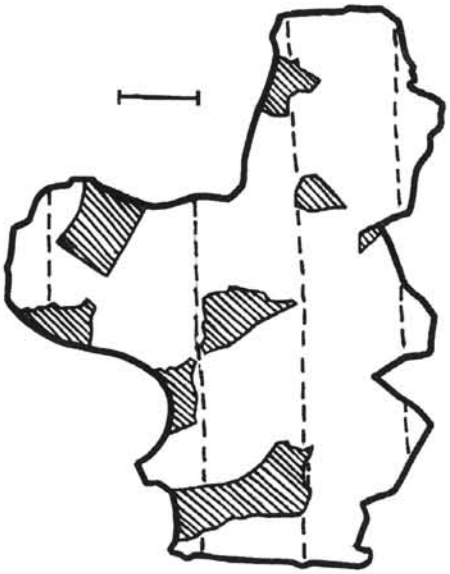

Figure 15. Outline drawing of dorsal surface of the carapace of *Cosmochelys dolloi* (BMNH R4338; the type), showing positions and spacing of the longitudinal ridges. Bar scale = 5 cm.

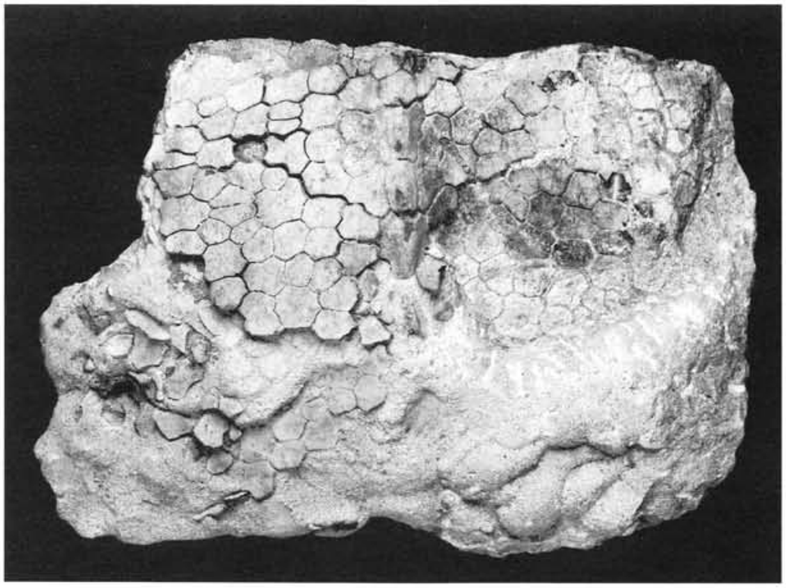

Figure 16. The surviving portion of what has generally been regarded as the type specimen of *Psephophorus polygonus* from the Miocene of the Austro-Czech border. Compare with Pl. 15 in Seeley (1880).

cording to Seeley (1880), the name *Psephophorus* was first applied to some isolated dermal ossicles by Meyer (1846). The whereabouts of this material is now unknown.

Distinctive features of *P. polygonus* include:

1) a single longitudinal ridge has been preserved. This ridge is broadly rounded at its crest and has gently sloping sides which extend to the lateral margins of the individual ossicles upon which the ridge is situated. The visceral surface of the carapace beneath the ridge is flat, not pushed up to correspond to the contour of the overlying ridge;

2) the crest of the ridge is of variable height with respect to the surrounding shell surface (Fig. 17). Peaks and valleys along this ridge seem to coincide with the transverse sutural junctions of every second ridge-forming ossicle;

3) the ossicles upon which the ridge is situated tend to be somewhat elongated anteroposteriorly and in some cases are larger than ossicles found on either side of the ridge. The shapes of the ridge-bearing ossicles are highly variable and irregular;

4) if there were additional ridges on the shell of *P. polygonus*, these were separated from the one that has been preserved by five or more intervening ossicles; and

5) the dorsal surface of most of the carapace ossicles is marked by what Seeley (1880) aptly described as "a beautiful radiating sculptured ornament."

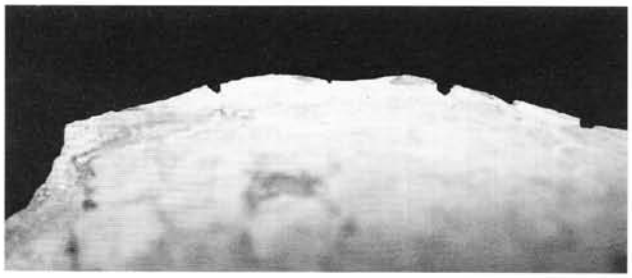

Figure 17. Lateral profile of the ridge of the type of *Psephophorus polygonus*, showing its undulating crest.

In his generally excellent account of *P. polygonus*, Seeley (1880) noted: "Von Hauer considers that there is a second shield, which lies parallel to the first, and under it, at an interval of scarcely half an inch." Seeley himself offered no opinion about the presence or absence of this supposed second layer of bone. But subsequent students of dermochelyid fossils have accepted Von Hauer's opinion as establishing the existence of a fully ossified plastron. However, examination of the type does not reveal the presence of a second layer of shell bone.

Although "*Psephophorus*" *rupeliensis* is relatively well represented in the fossil record, it has been surprisingly poorly described. Seago's unpublished Ph.D. thesis (1979) is the first thorough analysis of the exceptional sample of shell material available in the collections of the IRSNB. As already shown, "*P.*" *rupeliensis* is characterized by the absence of carapace ridges as well as parallel rows of enlarged ossicles, sometimes enormous and scallop-edged, forming "sunflower" pattern clusters of ossicles. In view of these features, "*P.*" *rupeliensis* obviously does not fit within the definition of *Psephophorus* (*sensu stricto*) as represented by the type of this genus. Similarities between the carapaces of "*P.*" *rupeliensis* and *Natemys* might indicate that they are congeneric. However, the plastra of these two taxa appear to differ markedly. Thus, the Belgian material of "*P.*" *rupeliensis* should be designated as a new genus.

Dermochelys

All fossil leatherback taxa so far formally described differ rather drastically from the sole surviving species, *D. coriacea*, whose diagnostic carapace features can be summarized as follows:

1) seven tectiform anteroposterior ridges, whose crests are capped by elongate nodules intermittently spaced along

the length of each keel. The central keel is always the most prominent one, with ridges becoming progressively smaller laterally;

2) the crest of each of the ridges is of somewhat variable height, undulating up and down along its length;

3) the carapace mosaic is thickest underneath the axes of the ridges and becomes extraordinarily thin in the troughs between adjacent keels;

4) the visceral surface of the carapace is arched upwards beneath each keel;

5) individual carapace ossicles tend to be much smaller than in any other dermochelyid; and

6) many more ossicles intervene between adjacent ridges than in any other known leatherback turtle (12–18 in an unnumbered BMNH carapace; 11–17 in MCZ 83204; 7–16 in ROM R2263; 10–15 and 15–18, respectively, in two uncatalogued shells in the Rijksmuseum, Leiden). These Dutch shells are of particular interest because they suggest that the number of ossicles between adjacent ridges on comparable parts of the shell is not necessarily correlated with size. The smaller specimen, with a length of 115 cm over its midline curvature, is the one with 15–18 ossicles, while the larger shell, with a midline length of 165 cm, has between 10–15 similarly situated ossicles. In all cases, the number of ossicles depends on what part of the shell the count was taken; lower ossicle counts occur toward the rear of the shell where the keels start to converge.

As is evident from the foregoing review of those fossil and living leatherback taxa which are known from adequate shell remains, carapace structure is sufficiently variable and diagnostic that it may readily separate one dermochelyid lineage from another. Hence, shell characters can provide an appropriate basis for phylogenetic analysis.

PHYLOGENY

Until now, no comprehensive attempt has been made to determine phylogenetic relationships within the family Dermochelyidae. Figure 18 represents the first such effort.

A data set of 22 shell characters for 13 taxa including a hypothetical outgroup based on all other chelonioids was compiled (Table 1). The analysis used PAUP 3.1.1 (Swofford, 1993) to obtain a single shortest tree of 26 steps, with a consistency index of 0.84 and a retention index of 0.89. Although this cladogram resolves nearly all the taxa, there were 25 cladograms one step longer that produced a consensus tree in which most of the resolution in Fig. 18 was lost. This indicates that only a few changes in character distributions could seriously alter the shortest cladogram.

Several named fossil dermochelyid taxa (e.g., "*P.*" *scaldii*, "*P.*" *ingens*, "*P.*" *pseudostracion*) have been omitted because they are known only from limb or skull material which is not associated with any diagnostic shell remains.

The specific shell characters used for the analysis of dermochelyid phylogeny (Table 1) are as follows:

(1) *Neural bones* (present = 0, absent = 1). These are present in the late Cretaceous Japanese dermochelyid (Hirayama, 1993, 1994) and certainly still existed in *Eosphargis*, but are lost in all subsequent leatherbacks.

(2) *Peripheral bones* (present = 0, absent = 1). Of all forms generally recognized as dermochelyids, these are present only in the Japanese fossil leatherback and *Eosphargis*.

(3) *Pleural bones* (present = 0, absent = 1). In the Japanese fossil dermochelyid there is moderate distal reduction of the pleurals comparable in extent to what is typically found in many marine turtles, both extinct and extant. Pleurals are absent in all other members of the family.

(4) *Shell scutes* (present = 0, absent = 1). Evidence of shell scutes on the Japanese fossil dermochelyid is preserved on only the central portion of the carapace (several neurals and proximal portions of adjacent pleurals). Hirayama and Chitoku (1992) remark that "the nearly complete loss of scute sulci" is a derived character exhibited by their material. Scute sulci can clearly be seen crossing the neurals of *Eosphargis* (e.g., the complete specimen on display at the IRSNB at Brussels; Quintart and Plisnier-Ladame, 1968), but all other fossil dermochelyid shells lacked scutellation, as does the modern form.

(5) *Median plastral fontanelle* (small or absent = 0, large = 1). Outgroup possibilities include Cheloniidae and Protostegidae, which have small median plastral fontanelles. These, however, are not as exaggeratedly large as in dermochelyids.

(6) *Plastral bones reduced to a rod-like peripheral framework* (absent = 0, present = 1). A moderately (but not exceptionally) large fontanelle is present in the plastron of the Japanese form. *Eosphargis* was characterized, in typical dermochelyid fashion, by a huge central fontanelle with the conventional plastron bones reduced to a bony frame around the rim. Alone among all dermochelyids, as best as can be determined from present evidence, *Natemys* had a bony plastral mosaic composed of large numbers of relatively small ossicles rather than typical plastral bones (even as in the modified form characteristic of typical dermochelyids). Since its plastral structure is not comparable to that of typical turtles, the bony plastron of *Natemys* does not represent a character reversal.

(7) *Broad, flat ribs* (absent = 0, present = 1). Ribs are still fused to the undersides of the pleural bones in the Japanese fossil dermochelyid (Hirayama, 1994). They are free-standing and broadly flattened in *Eosphargis* and all other fossil leatherbacks in which ribs have been preserved.

(8) *Shell composed of a mosaic of small bony ossicles* (absent = 0, present = 1). *Eosphargis* apparently represents an intermediate stage in the loss of dermal shell bone, somewhere between the fairly standard chelonian shell morphology of the late Cretaceous dermochelyid from Japan and the highly characteristic carapaces (as well as plastron in the case of *Natemys*) of all other leatherbacks, consisting of a mosaic of very large numbers of variably shaped, sized, and arranged ossicles.

(9) *Anteroposterior ridges (or keels) on the ossicles of the carapace* (absent = 0, present = 1). With the exception of the most primitive forms (i.e., the Japanese fossil dermochelyid and *Eosphargis*), one or more ridges, rather variable in structure from one taxon to another, are present on the carapaces of most leatherback turtles. They are, however, notably absent in specimens from the Eocene of New Zealand, *Natemys*, and the "*P.*" *rupeliensis* remains from Belgium. Despite the lack of ridges, *Natemys* and "*P.*" *rupeliensis* have linear rows of enlarged and often elongated ossicles which appear to correspond in position to the keels of the other leatherbacks.

(10) *Ridges expressed on external surface of carapace mosaic only* (absent = 0, present = 1). In some fossil dermochelyids, there is no upward flexure on the visceral surface of the carapace corresponding to a ridge on its external surface (e.g., *Egyptemys eocaenus* and *E. oregonensis*, *Cosmochelys*, and *Psephophorus polygonus*; Fig. 19). But in other cases this flexure is present. This is most notable in *Dermochelys*, but also seen in "*P.*" *calvertensis*, the South Carolina fossil dermochelyid (not included in the cladogram because it has not yet been described in detail), and USNM 23699, a specimen from the Eocene of Alabama. This fundamental difference in ridge architecture may be an important character for identifying fossils closely related to *D. coriacea*.

(11) *Ridges either arched or tectiform* (absent = 0, present = 1). The ridges of *Dermochelys* are strongly tectiform, more prominent than in any other dermochelyid. The carapace bone of this genus is markedly thicker under the ridges than between them (Fig. 20), whereas shell thickness does not appear to vary in other fossil dermochelyids with arched ridges.

(12) *Height of separate ridges* (uneven = 0, uniform = 1).

(13) *Undulating ridge crests* (absent = 0, present = 1). Weakly developed ridges (as in *Cosmochelys* and both species of *Egyptemys*) appear to be of uniform height along their lengths, while more pronounced ridges have crests that undulate up and down in lateral profile.

(14) *Ridges rounded in cross-section on dorsal carapace surface but not expressed on underlying visceral surface* (absent = 0, present = 1). This type of ridge is diminutive and weakly developed, semi-circular in cross-section and has a flat visceral surface (e.g., *Egyptemys eocaenus* and *E. oregonensis*).

(15) *Ridges rounded in cross-section of carapace with upward flexure of both dorsal and visceral surfaces* (absent = 0, present = 1). This type of ridge is much broader, more prominent, and is arched on both the inner and outer surfaces of the carapace (as in USNM 23699, as well as the shell from the Oligocene of South Carolina, and also "*P.*" *calvertensis*). *Psephophorus polygonus* is coded as a "?" in the data matrix because it does not really fit into either character states (14) or (15). It is instead intermediate in structure; the apex of its keel is rounded, but its sides slope away from the peak rather flatly. And while the ridge is moderately prominent, the visceral surface of the carapace beneath it is flat.

(16) *Ridges pointed in cross-section* (absent = 0, present = 1). This character state can be discerned in three very different types of dermochelyids – *Eosphargis*, *Cosmochelys*,

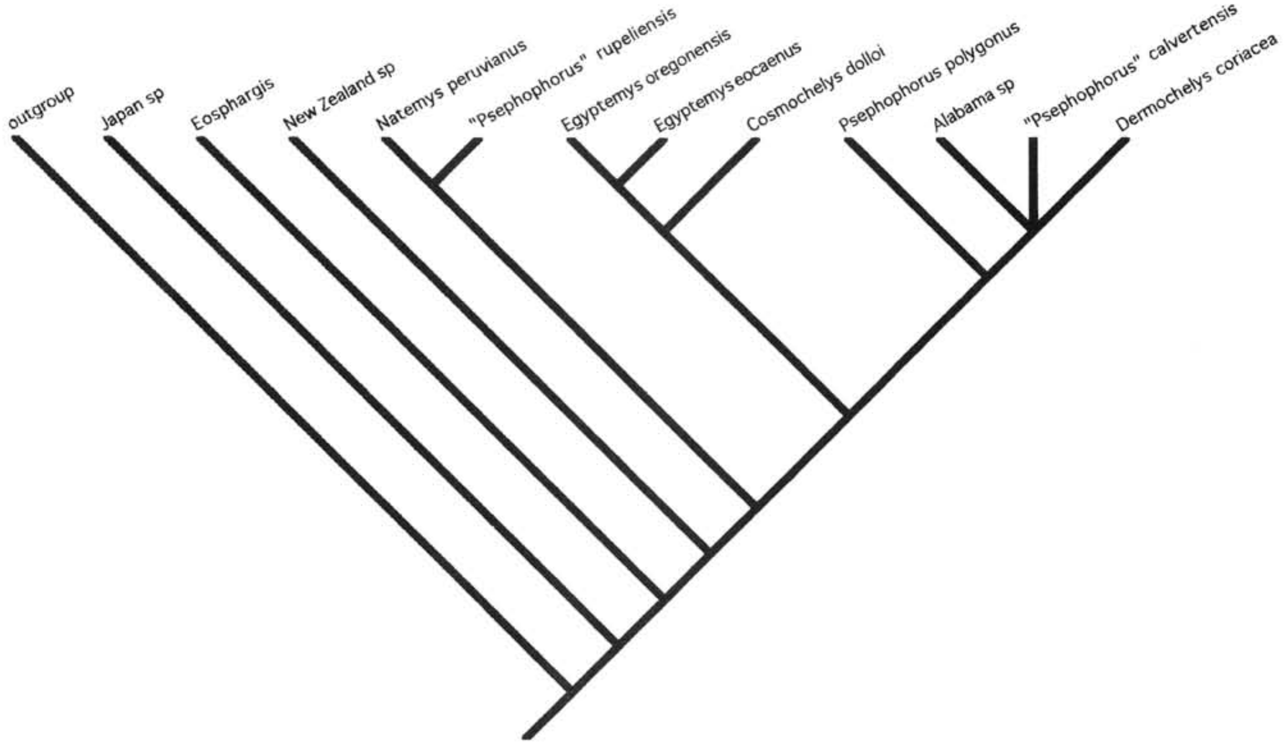

Figure 18. Hypothetical relationships within the Dermochelyidae. See text for explanation of characters used to establish successive nodes.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Japan sp	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Eosphargis	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
4	Natemys peruvianus	1	1	1	1	1	?	?	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0
5	"Psephophorus" rupeliensis	1	1	1	1	1	1	?	1	0	0	0	0	0	0	0	0	1	1	1	0	1	0
6	New Zealand sp	1	1	1	1	1	?	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	Egyptemys oregonensis	1	1	1	1	1	?	?	1	1	1	0	1	0	1	0	0	0	0	1	?	?	?
8	Egyptemys eocaenus	1	1	1	1	1	?	1	1	1	1	0	1	0	1	0	0	0	0	1	1	0	0
9	Cosmochelys dolloi	1	1	1	1	1	?	1	1	1	1	0	1	0	0	0	1	0	0	1	1	0	0
10	Psephophorus polygonus	1	1	1	1	1	?	?	1	1	1	0	0	1	?	?	0	0	0	0	0	0	1
11	Alabama sp	1	1	1	1	1	?	?	1	1	0	1	?	?	0	1	0	0	0	1	?	?	?
12	"Psephophorus" calvertensis	1	1	1	1	1	?	?	1	1	0	1	?	?	0	1	0	0	0	?	?	?	?
13	Dermochelys coriacea	1	1	1	1	1	1	1	1	1	0	1	0	1	0	1	1	0	0	1	0	0	1

Table 1. Data matrix of 22 shell characters for 13 taxa of fossil and living dermochelyid turtles. See text for explanation of characters.

and *Dermochelys*. However, the midline keel on the carapace of *Eosphargis* is not really homologous to those of *Cosmochelys* and *Dermochelys* because it is situated atop a row of neural bones, whereas in the latter two genera keels are formed on a surface of bony ossicles unique to leatherback turtles. In *Cosmochelys*, ridges are weakly developed and there is no indication of the presence of ridges on the visceral surface of the plastron. While the precise number of anteroposterior ridges is unknown in *Cosmochelys*, there appears to have been at least seven. The seven keels in *Dermochelys* are highly distinctive and truly unique. As already noted, the midline keel is the most strongly developed while lateral keels decrease somewhat in prominence towards the sides of the carapace. The position of each keel is prominently expressed on the visceral surface of the carapace by a strong upward flexure. Maximum shell thickness occurs directly under the apex of the keel. Because of the fundamental differences in the structure of the keels described here for the different genera, the value of this character for phylogenetic purposes is poor.

(17) *Clusters of ossicles forming "sunflower" patterns* (absent = 0, present = 1). This distinctive arrangement, with a relatively large, scallop-edged central ossicle surrounded by an array of smaller, more or less oval ossicles forming the "petals" of the "sunflower," occurs regularly only in *Natemys* and "*P.*" *rupeliensis* and represents one of several characters which together uniquely serve to define a ridgeless lineage of fossil dermochelyids. This appears to be a strong character.

(18) *Some shell ossicles greatly elongated along anteroposterior axis* (absent = 0, present = 1). This feature is found only in the ridgeless leatherbacks *Natemys* and "*P.*" *rupeliensis*, and comprises part of a suite of characters which makes this such a readily definable lineage.

(19) *Ossicles vary greatly in size and shape* (absent = 0, present = 1). Ossicle size and shape vary enormously in the ridgeless leatherbacks *Natemys* and "*P.*" *rupeliensis*, as well as in the modern *Dermochelys* and various fossils with moderately to strongly upwardly flexed ridges (e.g., USNM 23699, the South Carolina shell, and "*P.*" *calvertensis*). Uniformity in ossicle size and shape is widespread among Eocene dermochelyids and may therefore be considered the primitive condition. There appears to have been a reversal in this character state, *Psephophorus polygonus* having reverted to the primitive condition.

(20) *Number of ossicles between ridges* (less than 1 or 2 = 0, only 1 or 2 = 1).

(21) *Number of ossicles between ridges* (not 3 to 5 = 0, only 3 to 5 = 1).

(22) *Number of ossicles between ridges* (not 5 or more = 0, 5 or more = 1). There are always somewhat variable numbers of intervening ossicles on a given shell, so the numbers given here represent typical ranges. The number of ossicles in different leatherback taxa varies considerably and is dependent on two not necessarily related variables: (a) the sizes of the individual ossicles; and (b) the distance between adjacent ridges or rows. Three discrete categories can be recognized. In the *Natemys* – "*P.*" *rupeliensis* grouping, the number of ossicles intervening between parallel rows of linearly arranged ossicles varies from 3 to 5. In the *Cosmochelys* – *Egyptemys* grouping, there are typically only one or two (occasionally 3) ossicles between adjacent ridges. And in both *P. polygonus* and *D. coriacea* there are five or more ossicles between neighboring keels on the carapace. These character states appear to be particularly robust ones.

While the cladogram (Fig. 18) which results from the foregoing character analysis is not based on an overwhelming amount of data, it represents the first testable hypothesis for turtles of this family. Moreover, it provides a variety of insights into the evolutionary history of leatherback turtles.

The cladogram, for example, suggests that the New Zealand fossil leatherbacks are the sister group of all other dermochelyids having mosaic shells. In addition, a well-defined and previously unrecognized group, now extinct, is represented by *Natemys* and "*P.*" *rupeliensis*. This group is characterized by the lack of carapace keels plus the presence of rows of distinctive "sunflower" pattern clusters of ossicles centered around the largest individual dermochelyid ossicles yet discovered.

The cladogram further reveals that there were two, and very possibly three, different groups of mosaic-shelled dermochelyids which independently evolved non-homologous types of carapace ridges. Of these, the *Egyptemys* – *Cosmochelys* group, so far known only from the Eocene, is

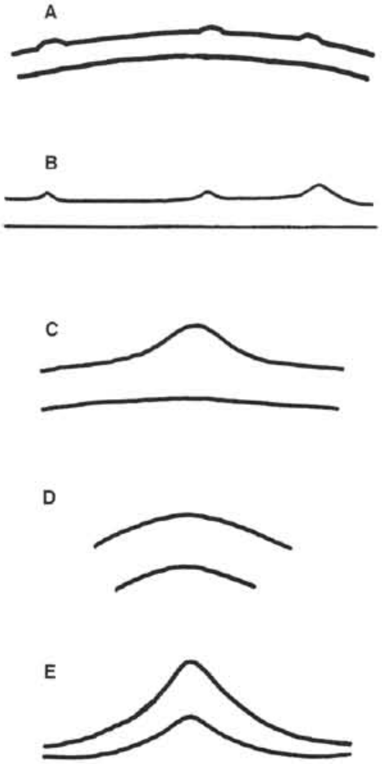

Figure 19. Variation in carapacial ridge architecture in fossil and living dermochelyid turtles: (A) small rounded ridges, all of similar height above shell surface, with varied spacing between ridges, and no evidence of ridges on visceral surface of carapacial mosaic, as seen in *Egyptemys eocaenus*; (B) small pointed ridges, one being higher above shell surface than all others, with varied spacing between ridges, and no evidence of ridges on visceral surface, as seen in *Cosmochelys dolloi*; (C) a single prominent broad ridge, rounded at apex, whose crest undulates up and down along its length, and whose presence is not indicated on the visceral surface of the bony mosaic, as seen in *Psephophorus polygonus*; (D) broadly rounded ridge whose presence is expressed on both external and visceral surfaces of the shell, with bone of uniform thickness, as seen in USNM 23699; and (E) prominent tectiform ridges, whose crests undulate up and down along their lengths, with flexure of ridges evident on both outer and inner surfaces, and bone of variable thickness, as seen in *Dermochelys coriacea*.

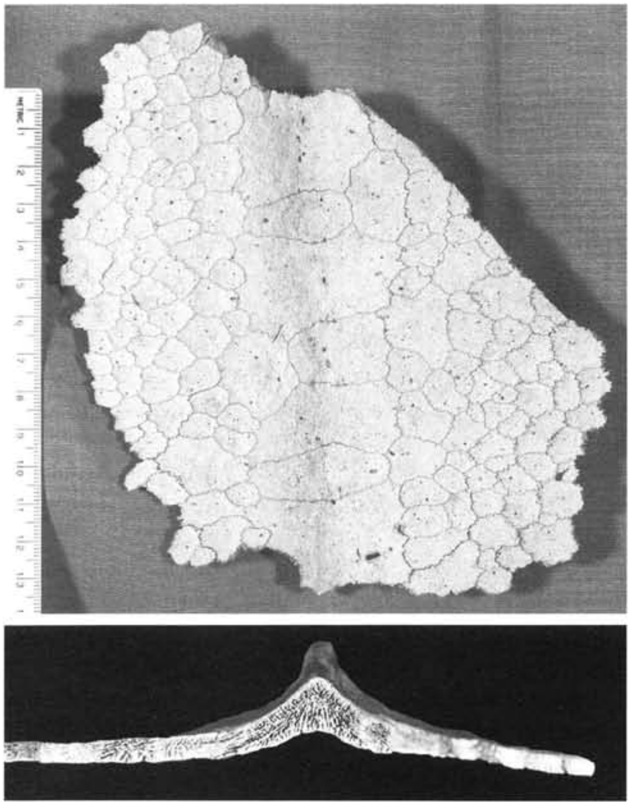

Figure 20. (Top) Fragment of the visceral surface of the carapacial mosaic of *Dermochelys coriacea* (P.C.H. Pritchard collection, unnumbered). The large ossicles underlie an anteroposterior keel which is shown in cross-section (Bottom).

the most primitive. The carapaces of these genera have weakly developed, relatively closely-spaced ridges. A second group, which includes *Dermochelys*, is characterized by much more prominent and widely spaced keels produced by flexure of the entire shell. Representatives of this group, spanning most of the Tertiary, enable tentative identification of the following evolutionary trends in shell morphology, which gave rise to the single surviving member of the family, *Dermochelys*:

1) a progressive decrease in mosaic shell thickness over time;

2) a concomitant decrease in the sizes of individual ossicles, which in turn presumably led to an increase in the overall number of ossicles forming the carapace;

3) a progressive increase in the prominence of the carapace ridges, which are formed as flexures of the entire shell instead of being expressed only on the dorsal surface of the carapace;

4) the development of undulating crests along the ridges; and

5) an increase in the number of ossicles intervening between adjacent ridges.

Finally, the somewhat problematical *Psephophorus polygonus* may represent still another separate group of distinctly ridged leatherbacks. Furthermore, it appears that *Psephophorus* was a rather minor element in the history of dermochelyids rather than being the major leatherback taxon represented in the fossil record.

Overall, the cladogram reveals a remarkable diversity of readily diagnosable taxa. There is only one unresolved trichotomy in the cladogram, a relatively minor one involving dermochelyids with well-developed keels produced by flexure of the entire shell (USNM 23699, "*P.*" *calvertensis*, and *Dermochelys*).

In the early Tertiary (Eocene), at least three different dermochelyid groups appear to have coexisted (four, if *Eosphargis* is taken into consideration as well). Representatives of one of these are known only from New Zealand (and possibly eastern North America as well, if Müller's Berlin specimen is included). Members of the second group (*Egyptemys* and *Cosmochelys*) are found only in northern and western Africa, and an example of the third (*Dermochelys*) group is known only from southeastern USA (Alabama). Because the fossil record of leatherback turtles is still very sketchy, it is unclear whether these three groups had cosmopolitan, overlapping geographic distributions, or how they might have partitioned the marine habitat if such geographic overlap did occur. Subsequent to the Eocene (see next section), there was a steady decline in dermochelyid diversity for reasons which are not yet clear.

How *Psephophorus polygonus* may fit into this general conceptual framework is unclear. Its combination of characters does not readily permit its allocation to any of the three other groups here informally recognized. Perhaps it is a peculiarly specialized or aberrant member of one of these. Or perhaps it represents still another adaptive radiation which is not yet well enough known in the fossil record to permit its adequate characterization.

While still very spotty, the fossil record of leatherback turtles is nonetheless now good enough to show that this family has had a considerably more complex evolutionary history than was previously appreciated. It does not appear that *Psephophorus* evolved into *Dermochelys*, as has been the prevailing assumption until now (Broin and Pironon, 1980). And the phylogenetic tree representing dermochelyid evolution is actually quite "bushy" rather than being essentially unbranched or, as might alternatively have been assumed, largely a wastebasket of undiagnosable scraps.

DECREASING DERMOCHELYID DIVERSITY OVER TIME

Table 2 is an attempt to sort out distinctive dermochelyid morphotypes in terms of their occurrences over the course of geological time. The recently discovered dermochelyids from the late Cretaceous of Japan are not included in this table because they have not yet been described, but they may be the most primitive known dermochelyids.

Aside from the Japanese occurrences, all other fossil dermochelyids are known from the Tertiary. No leatherback remains have yet been recovered from Paleocene sediments. But in the mid- to late Eocene there abruptly appeared a remarkable diversity of morphologically distinct dermochelyids from all over the globe: Africa (*Cosmochelys* and *Egyptemys*), Europe (*Eosphargis*), North America (with possibly two different taxa from Alabama), and New Zealand. Thus, in the Eocene, leatherback turtles were widespread and also remarkably diverse; this period marks a time of peak diversity in the history of dermochelyids.

Table 2. Summary of recognizable fossil leatherback turtle morphotypes during the Tertiary, based on shell characters only. Several named taxa (e.g., "*Psephophorus*" *scaldii* and "*P.*" *pseudostracion*) are deliberately omitted from consideration here because they are known only from limb or skull material.

Geological Age	Taxa
Recent	1. *Dermochelys coriacea*
Pliocene	1. A single indeterminate ossicle has been described
Miocene	1. *Psephophorus polygonus* 2. "*Psephophorus*" *calvertensis*
Oligocene	1. *Natemys peruvianus* 2. "*Psephophorus*" *rupeliensis* 3. South Carolina specimen (not yet described) 4. Probably also present: a tectiform-ridged taxon
Eocene	1. *Cosmochelys dolloi* 2. *Egyptemys eocaenus* and *E. oregonensis* 3. *Eosphargis gigas* and *E. breineri* 4. "*Psephophorus*" (New Zealand) 5. Shell with tectiform ridges (USNM 23699) 6. Shell from Alabama (Müller, 1849)
Paleocene	0. No fossil dermochelyids known

By the Oligocene, dermochelyid diversity had diminished somewhat. *Natemys* and "*Psephophorus*" *rupeliensis*, from Peru and Belgium respectively, appear to be closely related members of a single lineage whose ancestry might be represented in the Eocene by the Alabama fragment described by Müller (1849). Wonderfully preserved, but not yet formally described, material from South Carolina represents a second easily recognizable morphotype, characterized by well-developed carapacial ridges and, apparently, a largely unossified plastron. Until it is described in detail, however, its phylogenetic relationships cannot be assessed.

Although not yet actually found in the Oligocene fossil record, one other readily definable lineage must have existed during this time because its representatives appear in both underlying Eocene rocks and overlying Miocene sediments as well. This would have been a form having moderately flexed tectiform carapace ridges, similar to USNM 23699 (from the Eocene of Alabama) and "*P.*" *calvertensis* (from the Miocene of Maryland), the related fossils which bracket it in time. Leatherbacks such as these might well represent part of the lineage which ultimately gave rise to the modern *Dermochelys*. Therefore, it would seem that there were probably at least three distinctive types of Oligocene dermochelyids.

Two different kinds of fossil dermochelyids can be recognized in the Miocene. One is represented by the type of *Psephophorus*, *P. polygonus*. "*Psephophorus*" *calvertensis* probably represents a second type of Miocene leatherback although its taxonomic status will remain uncertain (Weems, 1974) pending its redescription based on newly collected material in the collections of the Calvert Marine Museum (B. Purdy, *pers. comm.*).

By the end of the Miocene, therefore, known dermochelyid taxonomic diversity had become reduced from an early Tertiary maximum of at least six species to just two. The only Pliocene leatherback material so far described is a lone ossicle from Florida (Dodd et al., 1992) and only a single species survives today, *D. coriacea*.

Over the span of the last 50 million years, several lineages of leatherback turtles have become extinct. Determining what factors promoted the early Tertiary diversity of dermochelyids, and those that caused the subsequent decline, is not possible at this stage in our understanding of the evolutionary history of this specialized turtle family.

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