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Taphrosphys sulcatus (Leidy)
from the Cretaceous of New Jersey

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ABSTRACT

The side-necked turtle genus *Taphrosphys* Cope has been reported from the Cretaceous of New Jersey, the Eocene of Peru, and the Paleocene of Zaire. A study of the postcranial osteology based on new material from New Jersey allows a revision of the New World species previously assigned to this genus. Two valid species are recognized: *Taphrosphys sulcatus* (Leidy) from the Late Cretaceous of New Jersey and *Taphrosphys olssoni* (Schmidt) from the Eocene of Peru. *Taphrosphys molops* Cope, *T. longinuchus* Cope, *T. leslianus* Cope, *Prochonias enodis* Cope, *Prochonias longinuchus* Cope, and *Prochonias leslianus* Cope are all synonyms of *Taphrosphys sulcatus* (Leidy). The types of *Taphrosphys dares* Hay, *Taphrosphys strenuus* Cope, and *Taphrosphys miocenica* Collins and Lynn are incomplete specimens that cannot be

diagnosed adequately and are considered to be *nomina dubia*. *Amblypeza entellus* Hay is based on a mixed type specimen. I have chosen a lectotype that is identifiable as *Taphrosphys sulcatus* and have synonymized *Amblypeza* with *Taphrosphys*. A new diagnosis of *Taphrosphys* indicates that *Taphrosphys* may be differentiated from other pelomedusids by the following combination of characters: large intergular scute and small gular scutes; semicircular xiphiplastral indentation; long, narrow pubic scar on xiphiplastron; and circular ischiac scar near edge of xiphiplastron. A review of the stratigraphic occurrence of *Taphrosphys* in New Jersey concludes that previously reported Tertiary records are incorrect, and that the known specimens from New Jersey are Late Cretaceous in age.

INTRODUCTION

The New Jersey coastal plain occupies an important place in the history of vertebrate paleontology because it was the site of some of the earliest vertebrate fossil collecting in North America. Joseph Leidy and Edward Drinker Cope, pioneers in American vertebrate pale-

ontology, both worked in Philadelphia and paid close attention to fossils from the nearby Cretaceous and Tertiary exposures in New Jersey. Unfortunately, however, the interest was not sustained; new discoveries of better preserved specimens from western North America and the grad-

[1]Department of Vertebrate Paleontology, the American Museum of Natural History; Adjunct Assistant Professor, Department of Geological Sciences, Columbia University.

ual abandonment of New Jersey marl pits (in favor of commercial fertilizer) resulted in fewer specimens collected and studied. Much New Jersey material was improperly collected and most type specimens consist of dubious fragments. The more recent discovery and careful collection of two side-necked turtle skeletons from Sewell, New Jersey, is therefore of some interest. The new material is more complete than other specimens of this genus and provides new anatomical information as well as an opportunity to revise the systematics of the genus *Taphrosphys*. In this paper I deal with taxonomy at the species level and the postcranial morphology of *Taphrosphys*; the relationships of *Taphrosphys* to other pleurodires is the subject of a later paper.

Acknowledgments

This paper would not have been possible without the cooperation and assistance of Mr. Richard Regensburg and Mr. William Dilkes, the advanced amateurs who discovered and collected the two specimens described here (see Regensburg, 1965, for a popular account). Their foresight in photographing the specimens *in situ* and their competent collecting of the material, reflects the high standards of many amateur paleontologists. I began this project in 1964 as an undergraduate under the direction of Dr. Richard K. Olsson, Rutgers University. Dr. Donald Baird, Princeton University, brought the problem to my attention. I am indebted to both of them for their patience and guidance. A number of people have aided my examination of specimens and I thank them for their courtesy and time: Dr. Horace Richards and Mr. Earl Shapiro, Academy of Natural Sciences, Philadelphia; Mr. David Parris, New Jersey State Museum; Dr. John Ostrom, Yale University; and Dr. Richard Zweifel, the American Museum of Natural History. Mr. Keith Madden and Mr. James Maddox of Woodbury, New Jersey, discovered and collected the best skull of *Taphrosphys* (to be described elsewhere) and I thank them for bringing it to my attention. Mr. Richard White, then of the Academy of Natural Sciences, Philadelphia, located a number of specimens and discussed geologic problems with me. Drs. Donald Baird, Richard Tedford, and Malcolm C. McKenna read

the manuscript and offered constructive criticism. Ms. Linda Slater very kindly typed the manuscript.

Abbreviations

AMNH, Department of Vertebrate Paleontology, the American Museum of Natural History
AMNH Herp, Department of Herpetology, the American Museum of Natural History
ANSP, Academy of Natural Sciences
FMNH, Field Museum of Natural History
NJSM, New Jersey State Museum
PU, Geology Museum, Princeton University

SYSTEMATICS

DIVISION TETRAPODA

COHORT AMNIOTA

SUPERORDER SAUROPSIDA

ORDER TESTUDINES

INFRAORDER PLEURODIRA (COPE, 1868b)

FAMILY PELOMEDUSIDAE COPE, 1868a

SUBFAMILY BOTHREMYDINAE (BAUR, 1891), NEW RANK

TAPHROSPHYS COPE, 1869a

Platemys: Leidy, 1856, p. 303.
Prochonias Cope, 1869b, p. 89.
Podocnemis: Schmidt, 1931, p. 252.
Amblypeza Hay, 1908 (in the restricted sense used in this paper, see below), p. 122.

Type Species. Platemys sulcatus Leidy, 1856.
Known Distribution. Late Cretaceous of New Jersey, Eocene of Peru.
Diagnosis. (Based on shell criteria only, cranial features will be described in a later paper.) Pleurodire known from skull and postcranium. Carapace oval, broader posteriorly, no nuchal notch; 7 neurals, costals 7 and 8 meeting at midline. Eleven pairs of peripherals, mostly with acute free edges but varying to obtuse in bridge region. No nuchal (cervical) scale, first marginal scale about equidimensional, pleural scales extending well onto peripheral bones. Anterior lobe of plastron short, broad, and rounded; posterior lobe broad in constrast to *Podocnemis expansa*

and possessing a semicircular xiphiplastral notch. Large entoplastron; mesoplastra small and extending well onto bridge; pubic scar long and narrow, ischiac scar round and near edge of xiphiplastron. Intergular scute large, separating small gulars, humerals, and part of pectorals. Scapula, humerus, femur and pelvis essentially as in *Podocnemis*; coracoid curved and flaring distally; ungual phalanges broad and flat.

Discussion. A study of the skull in *Bothremys* and *Taphrosphys* is the subject of a later paper and the cranial aspects of the diagnosis are deferred until then. The relationships of these two genera will also be discussed in this later paper, but my work up to the present suggests that *Bothremys* and *Taphrosphys* have an ancestor in common that neither has in common with other turtles. For this reason I am resurrecting Baur's family Bothremydidae to include *Bothremys* and *Taphrosphys*, but reducing it to subfamily rank and placing it in the Pelomedusidae. There is some reason to think that this latter taxon may be paraphyletic but I have no alternative at this time.

Hay (1908, p. 104) noted that Cope named two new genera, *Taphrosphys* and *Prochonias*, for the same species (*Platemys sulcatus* Leidy) in the same year, 1869. "Which of these names has precedence depends on which was issued first to the public, the April number of the American Naturalist or Cook's *Geology of New Jersey*. Investigations not wholly satisfactory seem to show that the latter was first publisht [*sic*], probably some time about the first of March, 1869" (*ibid*). I accept Hay's conclusion that *Taphrosphys* was published (Cope, 1869a) earlier than *Prochonias* (Cope, 1869b).

Taphrosphys sulcatus (Leidy)

Platemys sulcatus Leidy, 1856, p. 303.
Taphrosphys molops Cope, 1869a, p. 735.
Prochonias sulcatus (Leidy): Cope, 1869b, p. 89.
Taphrosphys molops var. *enodis* Cope, 1870, p. 158.
Prochonias longinuchus Cope, 1870, p. 159.
Taphrosphys leslianus Cope, 1870, p. 159.
Prochonias enodis Cope, 1870, p. 162.
Taphrosphys longinuchus Cope, 1870, p. 162.
Prochonias leslianus Cope, 1870, p. 165.
Amblypeza antellius Hay, 1908, p. 122.

Type Specimen. AMNH 2522, fifth, sixth, and seventh left peripherals and left xiphiplastron (Leidy, 1865, pl. 19, fig. 4). Although only the peripherals were figured by Leidy, it is the xiphiplastron that has the diagnostic features of the genus. If future workers doubt the association of these elements (which I do not) then the peripherals must be designated as the lectotype.

Locality and Horizon. "Tinton Falls, N.J." (Leidy, 1865, p. 109). No further information is available. The locality has not been relocated and the horizon of the type is not known.

Diagnosis. Plastron relatively narrower than in *T. olssoni*; xiphiplastral notch shallower and not so circular as in *T. olssoni*; anterior plastral lobe relatively longer than in *T. olssoni*; xiphiplastral points more lateral compared with *T. olssoni*.

Referred Specimens. PU 18706, partial shell (described below) collected by Regensburg and Dilkes, August, 1960, from the lowermost portion of the Hornerstown Formation, Sewell, New Jersey; PU 18707, partial shell with associated limb and skull fragments (described below), same data as in PU 18706; PU 18708, left xiphiplastron, same data as in PU 18706; NJSM 10410; a plastron, no data; NJSM 11340, skull fragments collected by Parris, 1973, from the lowest foot of the Hornerstown Formation, Inversand pit, Sewell, New Jersey; AMNH 1347, nuchal and first peripheral, "Cretaceous, New Jersey" (label), Cope Collection; AMNH 1343 (Hay, 1908, p. 118), plastral fragments, "Cretaceous, upper Marl" (label), Cope Collection; AMNH 1129 (Hay, 1908, p. 119), fragments of shell, "Birmingham, 10-21, 1868, EDC" (label), Cope Collection; AMNH 1470 (Hay, 1908, p. 119, fig. 119), neural bones, nuchal, carapace fragments, "Barnsboro, 9/8 1870" (label), Cope Collection; AMNH 1472 (type of *Taphrosphys molops* Cope, figured in Cope, 1870, pl. 7, fig. 16; text figs. 43, 44; Hay, 1908, figs. 112-116), shell fragments, West Jersey Marl Company pits, Barnsboro, New Jersey, August 25, 1868, Cope Collection; AMNH 1474 (Hay 1908, figs. 117, 118), xiphiplastron and other fragments, Birmingham, New Jersey, Cope Collection; AMNH 1477 (Hay, 1908, fig. 120), shell fragments, West Jersey Marl Company pits, Barnsboro, New Jersey, 1855, Cope Collection; AMNH 1471 (Hay, 1908, fig. 106), anterior plastral bones, mixed
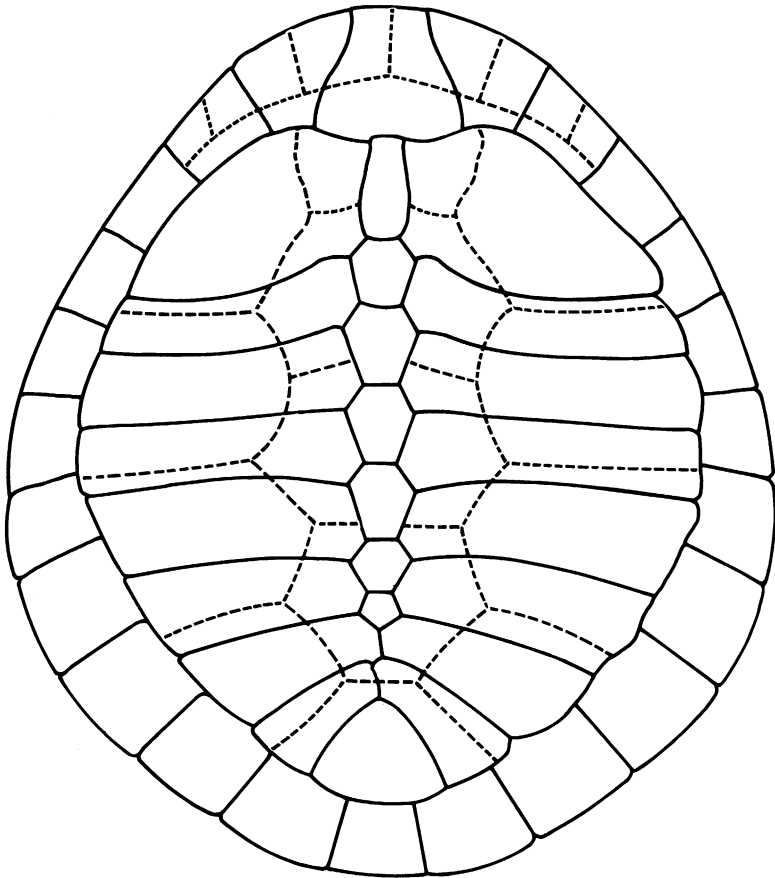
FIG. 1. *Tephrosphys sulcatus*. Dorsal view of carapace, sutures solid, sulci dashed. Restoration based primarily on PU 18706.

with AMNH 1470 (label), Cope Collection; AMNH 1467 (type of *Taphrosphys leslianus* . Cope, figured in Hay, 1908, figs. 103-105), partial shell, Hornerstown, New Jersey, collected by Dr. S. Lockwood, Cope Collection; AMNH 1124 (type of *Taphrosphys longinuchus* Cope, figured in Hay, 1908, figs. 101, 102), partial shell with limb fragments (this specimen was apparently mixed with the type of *Adocus agilis* Cope, AMNH 1135), David Haines's marl pit, Medford, New Jersey, March 15, 1870, Cope Collection; AMNH 1468 (Cope, 1870, p. 166, fig. 45;[1] Hay, 1908, figs. 99, 100), shell fragments, Barnsboro, New Jersey, Cope Collection; AMNH 1469,

shell fragments, West Jersey Marl Company pits, Barnsboro, New Jersey, 1869, Cope Collection; AMNH 2524 (Cope, 1870, p. 165, fig. 45), nuchal bone, Barnsboro, New Jersey, in the Rutgers University Cook Collection until 1970; ANSP 15544, carapace with partial skull and limb elements, collected by Keith Madden and James Maddox from the "bone bed" at the Inversand pits, Sewell, New Jersey (Richards and Gallagher, 1974; White, 1972).

Discussion. I recognize two New World species of *Taphrosphys*: *T. sulcatus* (Leidy) from the Cretaceous of New Jersey and *T. olssoni* (Schmidt) from the Eocene of Peru (Schmidt, 1931; Zangerl, 1947). Wood (1973, p. 7) suggested that *Bantuchelys congolensis* (Dollo) from the Paleocene of Zaire should be referred to *Ta-*

[1]Two consecutive figures in Cope, 1870, are both labeled figure 45 but illustrate different specimens.

phrosphys. As Wood will soon be describing this form, I am going to restrict the comparisons to *Taphrosphys olssoni.*

For the sake of clarity I include a new diagnosis of *T. olssoni* as well as of *T. sulcatus.* The only known specimen of *T. olssoni* consists of an internal mold of the shell plus a nearly complete plastron. As Zangerl noted (1947), the diagnostic characters of *Taphrosphys* are nonetheless determinable: large intergular scute and small gular scutes; semicircular xiphiplastral indentation; long, narrow pubic scar on xiphiplastron; circular ischiac scar near edge of xiphiplastron.

The Cope species placed in synonymy with *T. sulcatus* are largely based on fragmentary and incomplete material that was redescribed and figured by Hay (1908). I have re-examined this material and concluded that the differences related by Cope and Hay are either errors (intergular scute shape in *T. molops,* suprapygal shape in *T. longinuchus*) or ascribable to individual variation within a single species.

Taphrosphys nodosus Cope (1870) has been synonymized with *Peritresius ornatus* by Baird
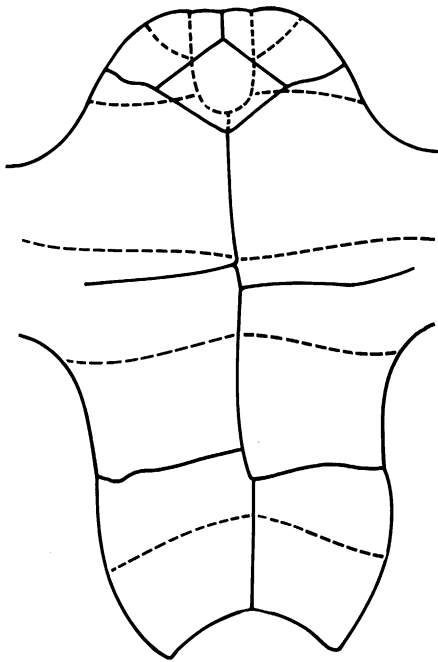

FIG. 2. *Taphrosphys sulcatus.* Ventral view of plastron, sutures solid, sulci dashed. Restoration based primarily on PU 18706.

(1964). *Taphrosphys dares* Hay (1908) is identifiable as a pleurodire but the type is so incomplete that the taxon must be considered a *nomen dubium. Taphrosphys miocenica* Collins and Lynn (1936) was referred to *Bothremys* by Gaffney and Zangerl (1968). Unfortunately, the type consists only of the anterior part of the plastron, and the intergular-gular scute pattern seen in *Bothremys barberi* and "*B.*" *miocenica,* although quite distinct from *Taphrosphys,* also occurs in the living South American species of *Podocnemis.* Therefore, at the present time, it is not possible to assign this form to a genus and it should be considered a *nomen dubium.* The type of *Taphrosphys strenuus* Cope, 1870, is a mixed specimen consisting of unidentifiable fragments of a questionable pelomedusid and a toxochelyid. This taxon should also be considered a *nomen dubium.*

Amblypeza entellus Hay (1908) is based on a mixed type specimen. The unique nature of this taxon as diagnosed by Hay was the presence of a nuchal scute in a pelomedusid pleurodire where previously such a scute had never been reported. There was no data concerning the locality or conditions of association of the plates, and the portions of the shell bearing the nuchal scute (NJSM 11342 and 11343, Hay, 1908, fig. 125) are identifiable as the toxochelyid sea turtle, *Osteopygis.* The xiphiplastron (NJSM 6614, Hay, 1908, fig. 132) is identifiable as *Taphrosphys sulcatus* on the basis of the circular ischiac scar and shape of the xiphiplastral projections. Other fragments (not the figured elements and bearing the group number NJSM 6613) include some pieces with the ornamentation seen in the dermatemydid, *Adocus.* I am here choosing the xiphiplastron fragment as the lectotype and synonymizing it with *Taphrosphys sulcatus.*

Taphrosphys olssoni (Schmidt)

Podocnemis olssoni Schmidt, 1931.

Type Specimen. FMNH P14172, an internal mold of the shell with plastron.

Locality. Mogollon, about 20 miles NE of Negritos, Piura, Peru (Schmidt, 1931).

Horizon. Salina Group, Middle Eocene (*ibid.*).

Diagnosis. Plastron relatively wider than in *T. sulcatus;* xiphiplastral notch deeper and more circular than in *T. sulcatus;* anterior plastral lobe
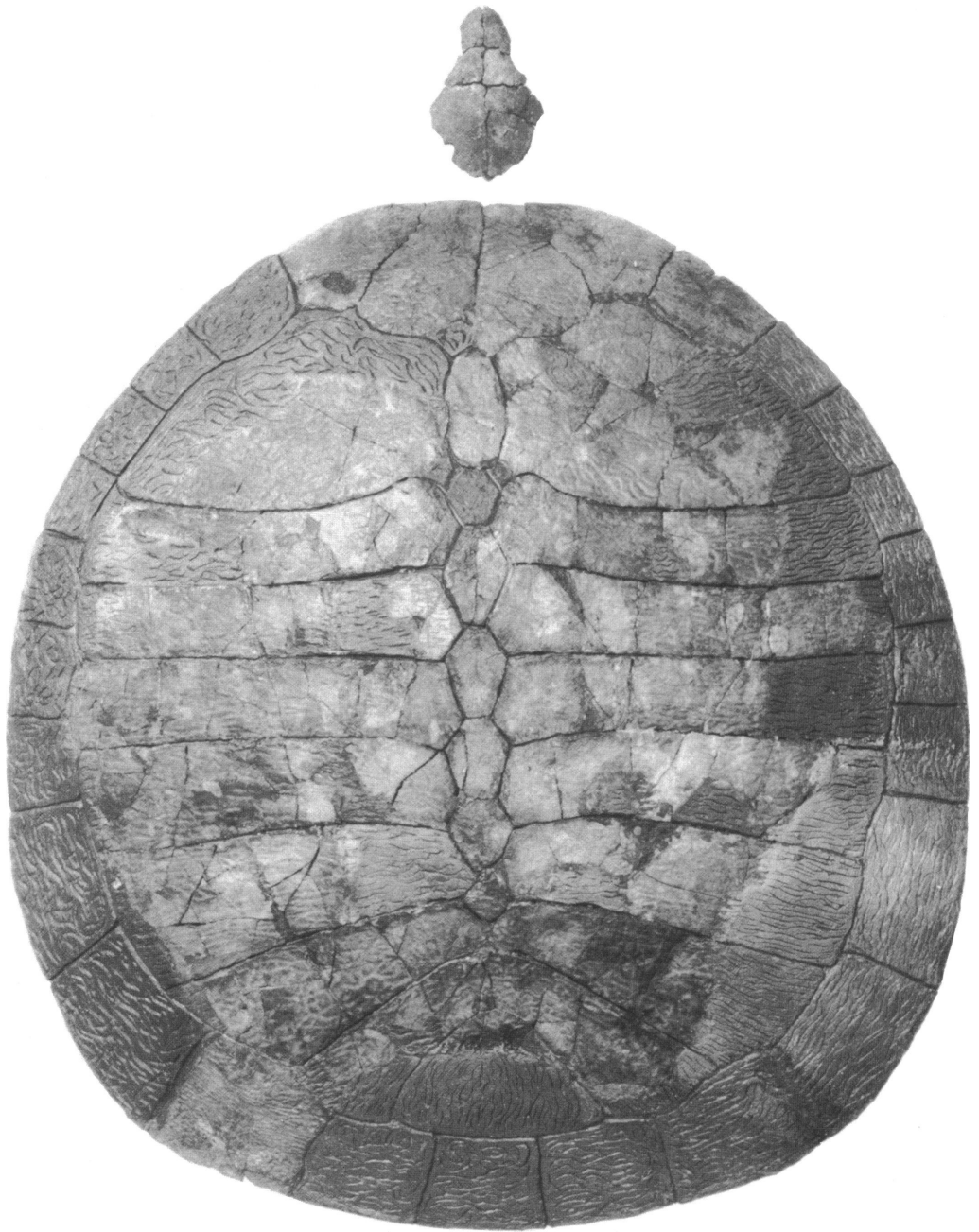
FIG. 3. *Taphrosphys sulcatus*, ANSP 15544. Dorsal view of carapace and associated skull (prefrontals, frontals, parietals only). Right and left peripherals 1 and left peripheral 10 are real, all others restored. Restoration incorrectly contains an extra pair of peripherals in the vicinity of costal 1, resulting in 12 pairs of peripherals rather than 11, which is the correct number.

relatively shorter and more rounded than in *T. sulcatus*; xiphiplastral points closer together compared with *T. sulcatus*.

Description of *Taphrosphys sulcatus*

Locality. Two unusually well-preserved skele-

tons of *Taphrosphys sulcatus* (PU 18706 and PU 18707) were found by William Dilkes and Richard Regensburg in August, 1960, at the Inversand Company pits near Sewell, New Jersey. The pit being worked at that time was roughly oval, trending north-south, the north end being the fossil site. PU 18706 was found on the west side
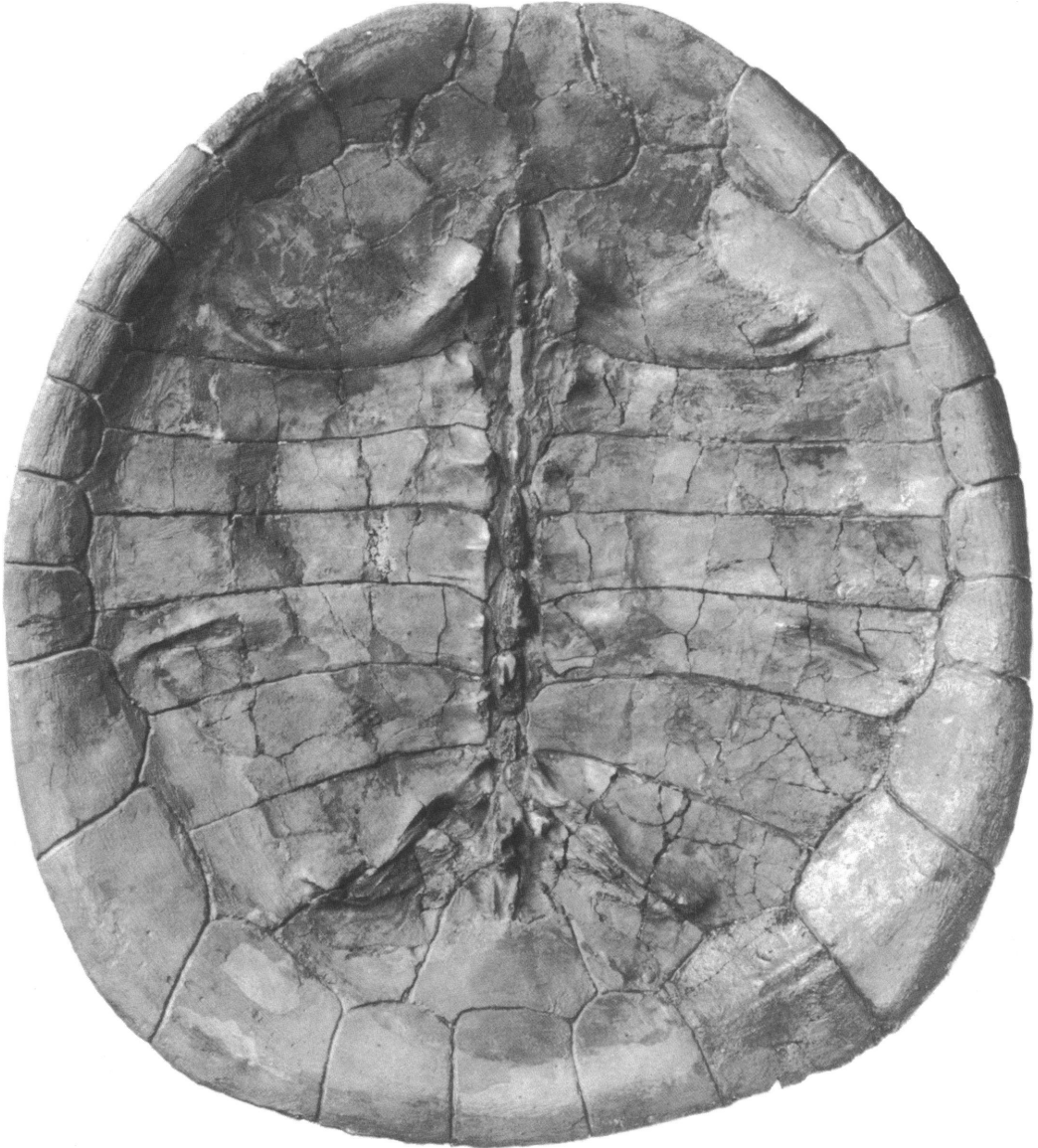

FIG. 4. *Taphrosphys sulcatus*, ANSP 15544. Ventral view of carapace. Peripherals restored incorrectly, see caption for figure 3.

of the pit and PU 18707 came from the eastern side. Two lithologic units are exposed here. The upper unit is the Hornerstown Formation (the "middle greensand" of Miller, 1956, and some earlier authors), and the lower unit has been variously termed the New Egypt Formation (of Olsson, 1963), the Navesink Formation (Minard et al., 1969, and earlier authors), the Redbank Formation (Baird, 1964), and the "chocolate marl" (many nineteenth-century authors). I am adopting Olsson's interpretations of the stratigraphy and his terminology (see section on age of the Hornerstown Formation below). These specimens of *Taphrosphys* were collected between 6 inches and 1 foot above the contact of the Hornerstown Formation and the New Egypt Formation in what is here thought to be the Cretaceous part of the Hornerstown Formation.

Portions of Specimen Preserved. PU 18706—the bones of the shell are thin but well preserved with the surface sculpturing and sulci easily discernible. The left fifth costal and neurals 1, 3, 5, and 7 are missing. All the left peripherals but 1 and 2 are missing, whereas at least portions of right peripherals 6 and 11 are preserved. The nuchal is present but the pygal is not. The plastron is complete except for the bridge processes, both mesoplastra, and the left xiphiplastron. An anterior caudal vertebra and the acetabular portions of the left pubis and ischium are also preserved.

PU 18707—the carapace and plastron of this specimen is less complete but some of the poorly known appendicular areas are present, as well as part of the skull. The bones are thicker and less

brittle than in PU 18706, but the surface patterns are obscured and the bone tends to be very powdery and weak (possibly due to a greater degree of leaching and/or surface weathering). The carapace preserves left costals 1, 3, 5, 6 (partly), 7, 8; right costals 2-4, 7 (partly), 8; neurals 2, 3, 5, 6; and the suprapygal. Right peripherals 3-9 and left peripherals 2, 3, 9, and 11, are also present. The nuchal is absent but the pygal is preserved. The plastron consists only of the posterior half (hypoplastra and xiphiplastra). The left hypoplastron has the inguinal buttress and some of the sutural contact with the mesoplastron. Three nearly complete cervical vertebrae plus fragments of four other cervicals were found associated with this shell, along with skull parts. The skull materials are well preserved and were found disarticulated with matrix in the sutured edges suggesting separation shortly before burial. The skull consists of the basioccipital, both exoccipitals, both prootics, the right opisthotic, left parietal, left quadrate (part), and a fragment of the left maxilla. The right humerus, left femur, most of both scapulae, glenoidal half of the left coracoid, right ilium, left ischium, left pubis (lacks epipubic process), and acetabular portions of the left ilium, right ischium, and right pubis make up the appendicular elements preserved. In addition three unidentified zeugopodial elements, eight phalanges, the right astragalus and calcaneum, and two unguals are present.

Preservation. Photographs taken of both specimens as they were uncovered by Regensburg and Dilkes show that although the skeletons were

TABLE 1
Measurements (in Millimeters) of *Taphrosphys sulcatus*

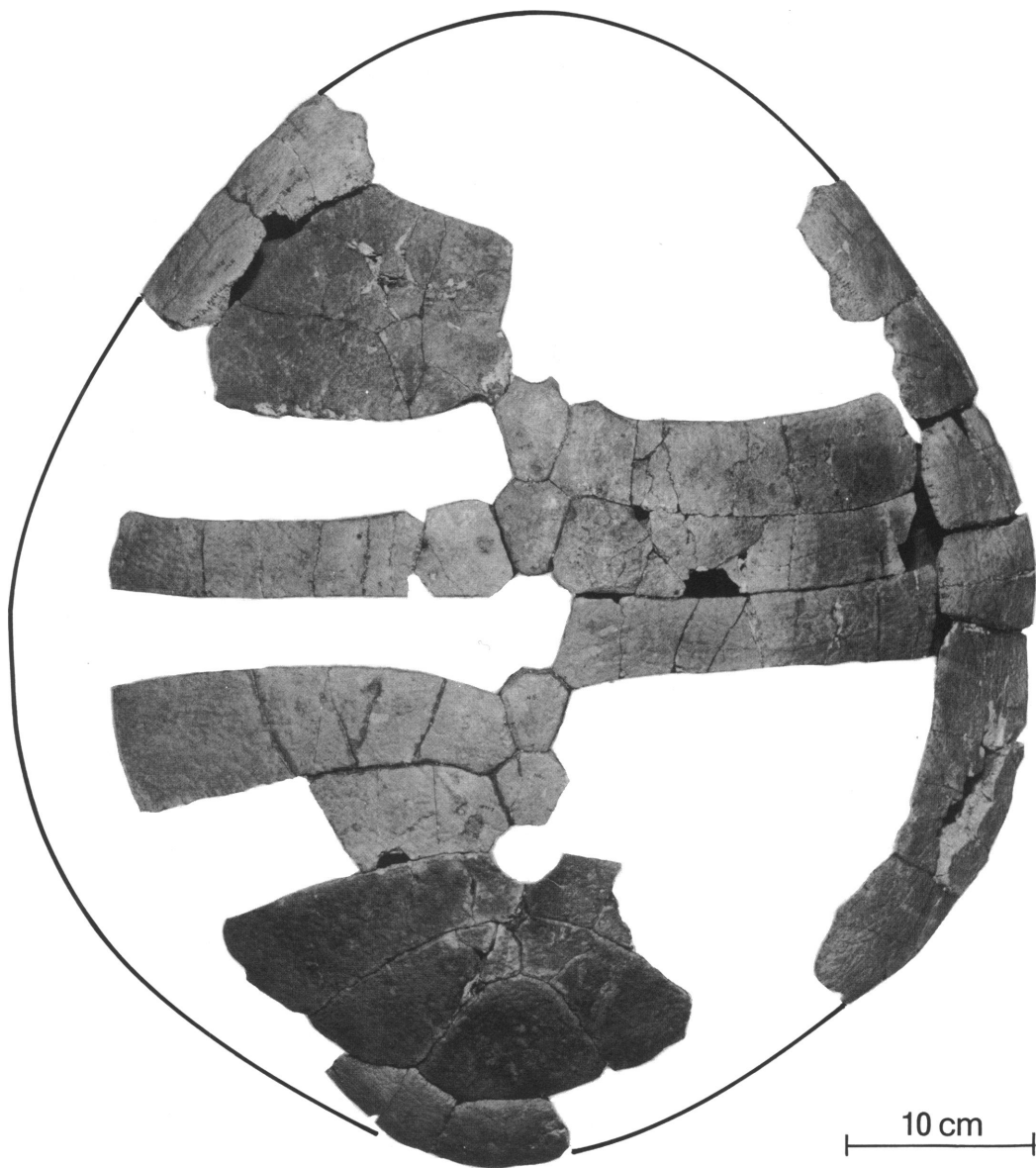|	PU 18706	PU 18707
Sagittal length of plastron	370	–
Width of plastron posterior to bridge	195 ± 10	290
Width of plastron anterior to bridge	220 ± 10	–
Length of anterior plastral lobe	85 ± 10	–
Length of posterior plastral lobe	165 ± 5	220
Length of carapace (over shell curvature)	530 (est.)	600 (est.)
Width of carapace (over shell curvature)	390 (est.)	640 (est.)

FIG. 5. *Taphrosphys sulcatus*, PU 18707. Dorsal view of preserved carapace elements. Photo courtesy of Donald Baird, Princeton University, Geological Museum.

virtually complete and not scattered far, the elements were disarticulated, overturned, and slid over one another, similar to a specimen of *Peritresius ornatus* found in the New Egypt For-

mation and described by Baird (1964, p. 22). The close association of humerus, scapula, suprapygal (ventral side up), and costals (ventral side down) seems to suggest slow bottom wave action

that would tend to disarticulate but concentrate this material.

Plastron. The plastron of *Taphrosphys sulcatus* generally agrees with the plastron of *Taphrosphys olssoni* (Zangerl, 1947). The sides of the plastron (minus bridge) are about parallel, with the anterior lobe being slightly broader than the posterior lobe. The anterior lobe is relatively short, broad, and rounded (may be slightly squared-off in some specimens), whereas the posterior lobe is also broad but about twice as long as the anterior and has the broad, semicircular xiphiplastral notch that is characteristic of this genus. The quadrilateral entoplastron is relatively large and wider than long (both externally and internally). The xiphiplastra (see fig. 118 in Hay, 1908, p. 119 for this bone in AMNH 1474) end in pointed projections, not rounded as in most other pelomedusids. The mesoplastra are not known in this species but sutural edges on other plastral elements show the size and position of the mesoplastra.

A portion of the inguinal buttress is preserved in PU 18707 and shows that the angle between the buttress and the plastral edge is about 90 degrees but not less than 90 degrees as in *Podocnemis expansa* and possibly *T. olssoni*. The visceral side of the xiphiplastra in pleurodires bears two scars for the sutural contact of the pubes and ischia. The pubic scars in *T. sulcatus* are long and narrow compared with those in *Podocnemis expansa*, whereas the ischiac scars are round and near the edge of the xiphiplastron, not triangular and well within the plate as in *P. expansa*.

The epidermal scales are also closely comparable with those of *Taphrosphys olssoni*. A large intergular completely separates the gulars
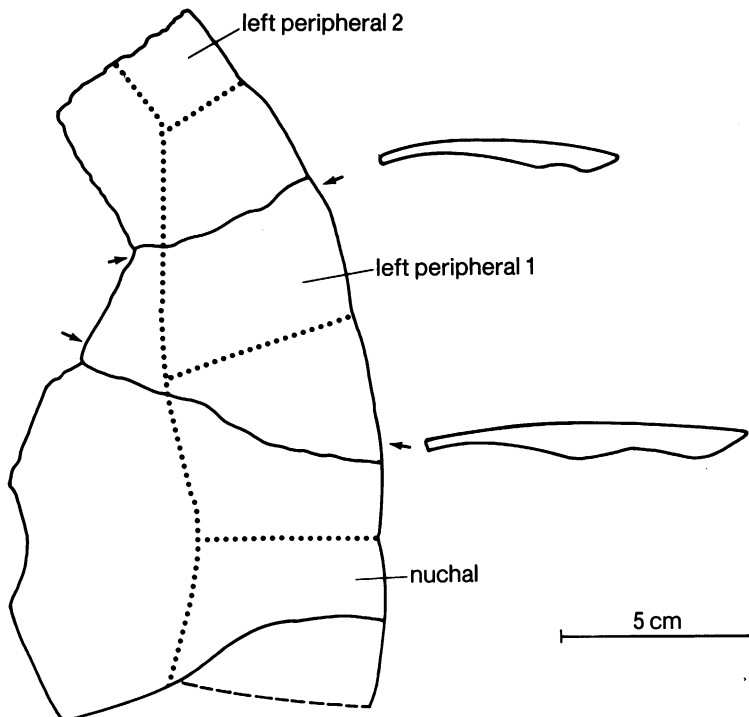

FIG. 6. *Taphrosphys sulcatus*, PU 18706. Dorsal view of nuchal and first two peripherals. Sections have dorsal surface toward top of page. Dotted lines are sulci.

and humerals as well as part of the pectorals. The gulars seem to be slightly smaller in *T. olssoni*. The intergular covers almost all the entoplastron in both species. The femoral-abdominal and pectoral-abdominal sulci in both species of *Taphrosphys* are placed closer to the hyo-hypoplastral suture than in most pelomedusids.

Carapace. Even though the taxonomically more important plastron is well preserved in *Taphrosphys olssoni*, only an internal mold of the carapace exists and, therefore, a close comparison of this area cannot be made with *T. sulcatus.*

In overall outline the carapace of *T. sulcatus* is very similar to the living *Podocnemis expansa*. It is generally oval with the posterior half flaring outward. The degree of arching is also similar, being rather moderate in both. The nuchal bone is similar to *P. expansa*, being large and expanding posteriorly. No nuchal notch (such as is found in *Bothremys*) is present and the anterior outline of the carapace is broadly rounded. The first costal has a subtriangular shape, being much longer proximally than distally. The visceral side of this costal bears a number of important structures. The axillary buttress of the hyoplastron articulates with a depression occupying about one-third of the distal length. This depression is surrounded by a ridge of bone opening on the lateral side in *T. sulcatus* but completely enclosing the buttress scar in *P. expansa*. The center of the depression is 9 mm. thick in PU 18706 and 19 mm. thick in PU 18707. The ridge curves medially until it ends in the ninth and tenth rib heads. In *Taphrosphys sulcatus* this ridge forms a well-developed crest or shelf with the acute edge pointing anteriorly. In *P. expansa* the ridge is shallow and lacks a crest. Costals 2-4 are relatively short in relation to their width compared with the same bones in *P. expansa*. Costals 5-8 flare distally and are not so wide as the more anterior ones. Costal 5 bears an elevated articulation with the inguinal process of the hypoplastron for about one-third of its length.

The visceral surface of the seventh and eighth costals has a fairly complex anatomy heightened by the variability of this area. The dorsal surface of the ilium is sutured to the undersurface of costals 7 and 8 in the region of the junction of

these two costals. Costal 8 usually bears more of the articulation than does costal 7. The sacral ribs (best seen in AMNH 1468 figured in Hay, 1908, p. 107) rise from the proximal border of the iliac scar and articulate with vertebrae 17-19. All of the eighth and part of the seventh costals meet at the midline, the rest are separated by neurals.

The peripherals are generally comparable with the same bones in *Podocnemis expansa*, but show a fairly wide degree of variation in *Taphrosphys*. Those in PU 18706 are thin, acute, and possess a wide flange (best developed on peripherals 7-9), whereas PU 18707 has thick and obtuse peripherals (only obtuse on the bridge), lacking a well-developed flange. This difference may be due to growth, sex, or individual variation. Peripherals 3-8 form the bridge attachment to the plastron and consist of two plates or faces meeting on the distal edge. The pygal is nearly square.

Neurals. The first neural is not preserved in the Princeton specimens but may be seen in the type of *Taphrosphys leslianus* (AMNH 1467). The length is half the width and constrictions are present anteriorly and posteriorly much as in *Podocnemis expansa*. As opposed to the rest of the neurals, which articulate with only one rib head, the first neural in *Taphrosphys* articulates with two, the ninth and tenth. The neurapophysis extends the length of the neural. In *P. expansa* the neurapophysis of the first neural articulates only with the tenth rib-head and, therefore, the neurapophyseal fusion extends only along the posterior half of the bone. In both genera the next five neurals (2-6) are hexagonal, longer than wide, and the greatest width is near the anterior end. The last or seventh neural is pentagonal and about equidimensional in both genera. Neurapophyses are fused to the visceral surface of each neural and articulate with one rib-head (except the first neural) extending from the lateral costal. The neurapophyses tend to become lower, thicker, and more massive posteriorly in the series.

Carapacial Sulci. Five vertebral scales seem to be the normal number in *Taphrosphys sulcatus* and all may be seen in PU 18706. They all have hexagonal shapes with the width exceeding the length. All but the last intervertebral sulcus point
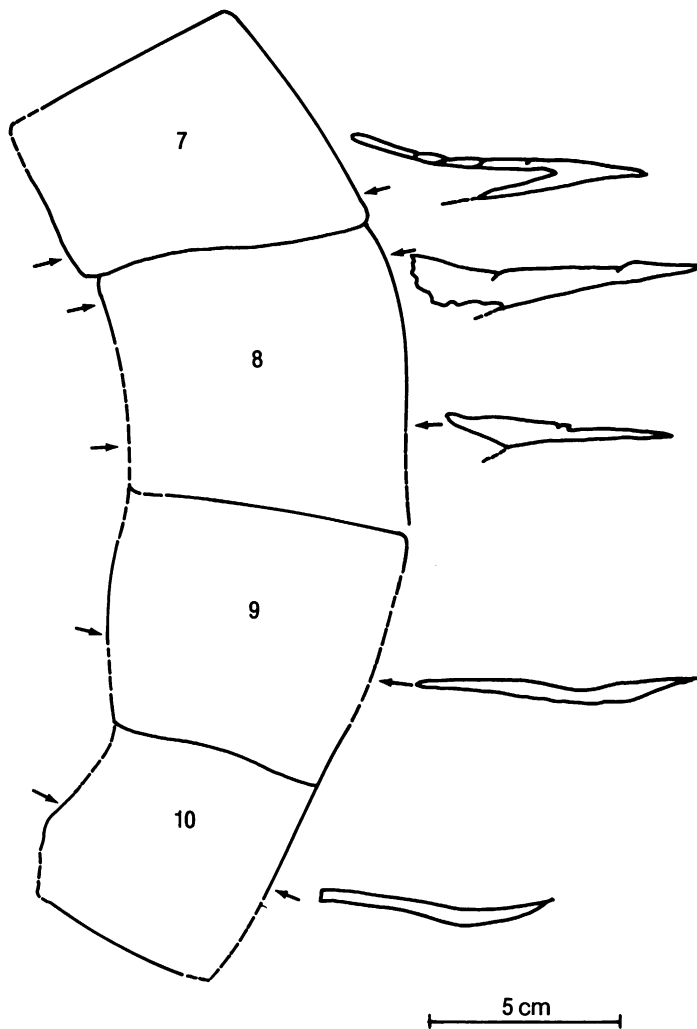
FIG. 7. *Taphrosphys sulcatus*, PU 18706. Dorsal view of right peripherals 7-10. Sections have dorsal surface toward top of page.

anteriorly. The vertebrals of *Podocnemis expansa* have similar shapes but the lengths and widths of scales 2, 3, and 4 are about equal, whereas in *Taphrosphys* the width exceeds the length. The last (fifth) vertebral is more triangular in *P. expansa* due to the narrower intervertebral sulcus, but otherwise the shapes are similar.

There are eight pleural scales and, except for the first, all have a semirectangular shape, the width being greater than the length. The first pleural scale has a nearly triangular shape with the width and length being about the same. The pleural scales cover about three-quarters of the lateral portions of the costal bones. In *T. sulcatus* they extend about halfway onto the peripheral bones but in *P. expansa* they end at the costal-peripheral suture or slightly onto the peripherals (particularly the posterior ones).

The 24 (twelve on each side) marginal scales cover relatively less of the peripheral bones in *T. sulcatus* than in *Podocnemis expansa*. No nuchal (cervical) scale has been observed in the genus.

Humerus. Only two other humeri of North American pleurodires have been described. Hay (1908, p. 115) briefly discussed a humerus found with the type of *Taphrosphys strenuus* Cope.
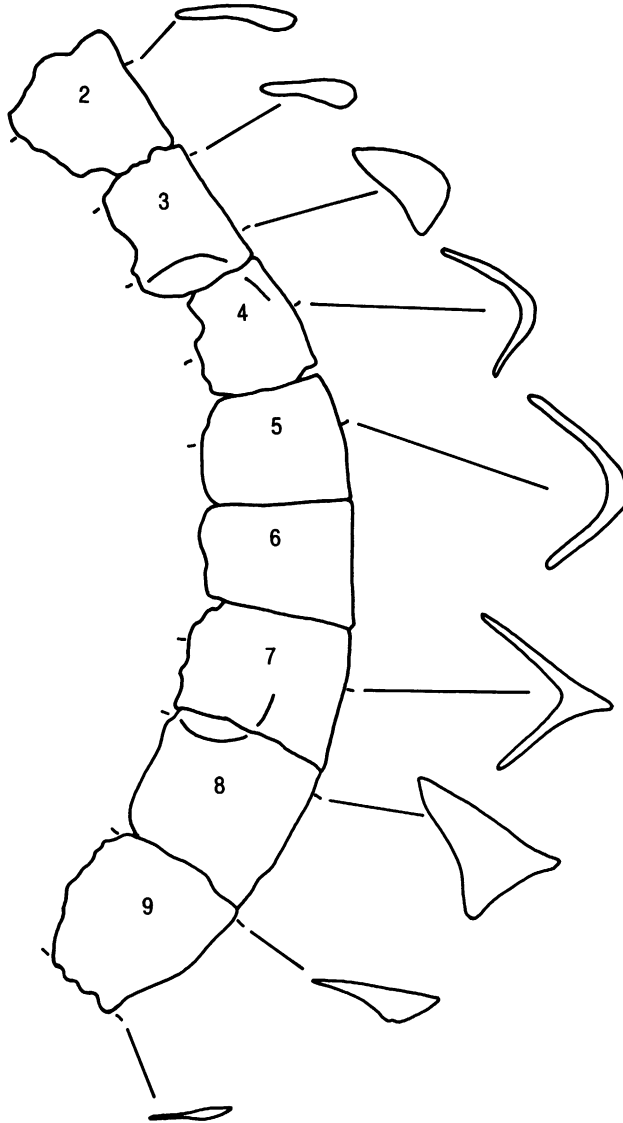

FIG. 8. *Taphrosphys sulcatus*, PU 18707. Dorsal view of right peripherals 2-9 (peripheral 2 is reversed from left side). Sections have dorsal surface toward top of page and lateral surface is on right. Bridge cavity indicated by lines on peripherals 3, 4, 7, and 8.
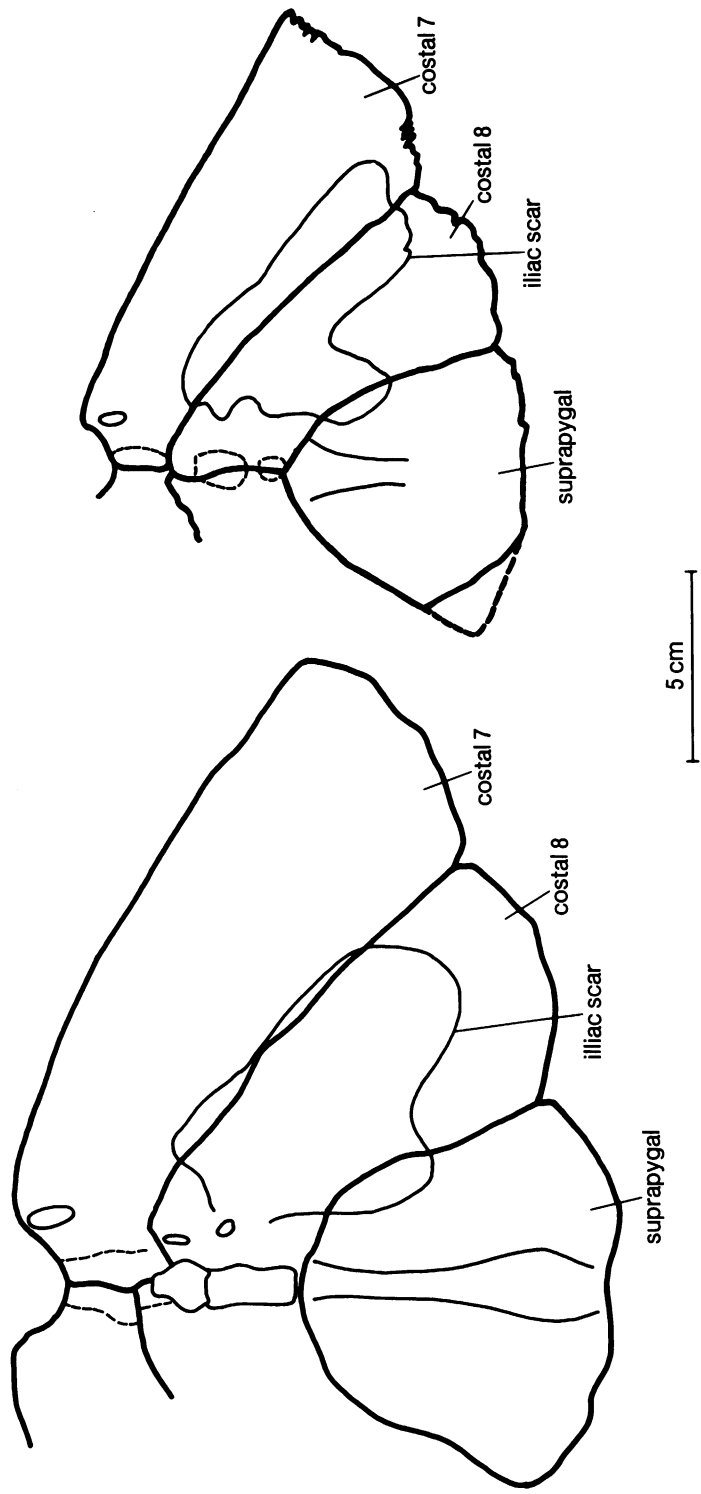
FIG. 9. *Taphrosphys sulcatus.* Ventral view of left costals 7, 8, and suprapygal to show extent of iliac sutural area. *Left:* PU 18707. *Right:* PU 18706 (reversed).
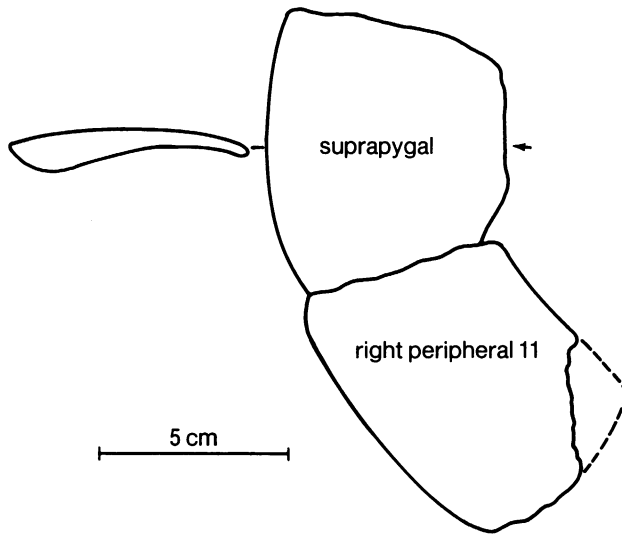
FIG. 10. *Taphrosphys sulcatus*, PU 18707. Dorsal view of suprapygal and right peripheral 11. Section has dorsal surface toward top of page.
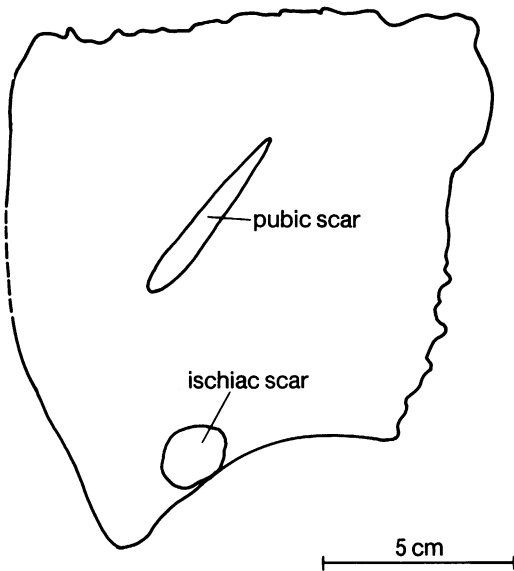

FIG. 11. *Taphrosphys sulcatus*, PU 18708. Dorsal view of left xiphiplastron showing pelvic attachment areas. See also Hay, 1908, figure 118, for similar view of another specimen.

However, after examining this specimen (AMNH 1126) I believe that it does not belong to a pelomedusid. Zangerl (1948, p. 34) described and figured the humerus of "*Podocnemis alabamae*" (=*Bothremys barberi*; see Gaffney and Zangerl, 1968) which, therefore, seems to be the only previously described pelomedusid humerus from North America.

The right humerus found associated with the shell of PU 18707 is fractured but complete and has a length of 111 mm. The bone has a much more massive appearance as compared with *Podocnemis expansa* and *Bothremys*. The hemispherical head extends at right angles from the shaft to a greater degree and is more rounded in appearance than in *P. expansa* and *Bothremys*. As in *Bothremys* an entepicondylar groove is present instead of a foramen. The degree of curvature is similar in all three genera. The radial and ulnar processes also compare closely, but the greater separation of the head from the shaft has caused a prominent "valley," not present in either *P. expansa* or *Bothremys*, to appear between the two processes. A long ridge, not observed in the other two forms, curves from the

ulnar process on the ventral side down the shaft to the anterior surface of the distal end. This ridge seems to be indicated in Zangerl's figures (1948, p. 49) but is not discernible in the specimen of *P. expansa*. Also the distal end is relatively wider in *P. expansa* or *Bothremys* as it expands to nearly the width of the radial and ulnar processes.

$$\frac{\text{distal width}}{\text{total length}} = 0.47 \text{ in } \textit{Taphrosphys} \text{ (PU 18707)}$$
and 0.30 in *Podocnemis expansa*
(AMNH Herp 62947)

Femur. Hay (1908, p. 111) briefly described two femora associated with the type of *Taphrosphys longinuchus* (AMNH 1125). The femur of *T. molops* described in detail by Cope (1870, p. 161) has since been lost (Hay, 1908, p. 119) and therefore is not available for comparative studies.

The left femur found with PU 18707 corresponds closely to the same bone in *P. expansa*. The head is large and slightly displaced from the line of curvature of the shaft. The shaft curves more than in the humerus and its proportions are not so massive. The distal end seems slightly wider than in the recent form.

Scapulae. Both right and left scapulae are preserved in PU 18707. The dorsal or longer process lacks its tip in the left scapula and the ventral process is broken in the right, but together they furnish complete knowledge of the entire bone. The dorsal process (155 mm. from glenoid to tip) is cylindrical and has a slight curve medially, more so than in *P. expansa*, which is virtually straight. The ventral process (90 mm. from glenoid to tip) has a broader proximal end than *P. expansa* and tapers somewhat distally, whereas *P. expansa* has parallel sides. The angle between the two processes in *P. expansa* has a value of 77 degrees, whereas in PU 18707 it is about 98 degrees. The process supporting the scapular contribution to the glenoid cavity extends away from the rest of the bone more in PU 18707 than in *P. expansa*.

Coracoid. The proximal portion of the left coracoid is preserved. Although the other limb elements resemble *Podocnemis expansa* rather closely, the coracoid differs in a number of characteristics. The glenoid cavity is quite similar in relative size and shape but the scapular articulating face is larger in PU 18707. In *P. expansa* the shaft is straight, flares slightly distally, and has a C-shaped cross section. In *Taphrosphys* the
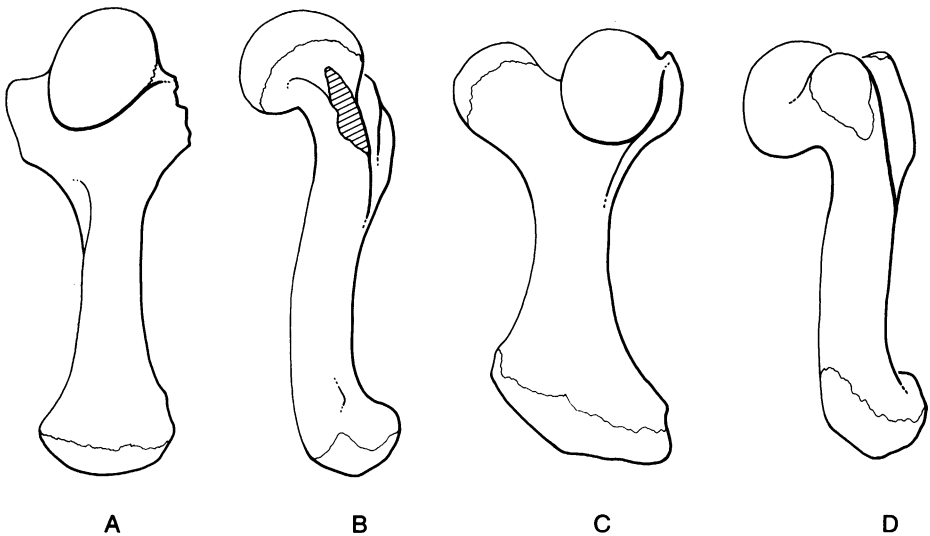

FIG. 12. *Taphrosphys sulcatus*, PU 18707. A, B. Left femur. C, D. Right humerus.

shaft is curved, flares about three times as much as in *Podocnemis expansa*, and has a wider but still C-shaped cross section. The widening occurs near the glenoid, increases rapidly, and remains relatively constant proximally. Its total length is not known.

Unguals. The two ungual phalanges found with PU 18707 cannot definitely be determined as to digit or limb. The hind limb unguals of *Podocnemis expansa* differ from the forelimb unguals by being slightly longer and by having the fifth ungual reduced; these characters cannot be determined from the Princeton specimen. The unguals in *Taphrosphys sulcatus* are unique among pleurodires in being paddle-shaped, broad, and thin. The flat, broad shape of these bones seems to support the suggestion that *Taphrosphys* was a more aquatic form than *P. expansa*.

Caudal Vertebrae. One nearly complete anterior caudal vertebra was associated with the shells of PU 18706. The procoelus centrum has proportions similar to *P. expansa* but bears a slight hypophysis. The transverse processes are reduced in both forms. The prezygapophyses curve dorsally more than in *P. expansa* but otherwise they are similar. The postzygapophyses, however, have little resemblance to the living form. In *P. expansa* the neural spine is low and the postzygapophyses extend straight posteriorly and participate in part of the neural arch. The spine of PU 18706 extends dorsally, then curves sharply posteriorly. The facets of all the zygapophyses are broken off.
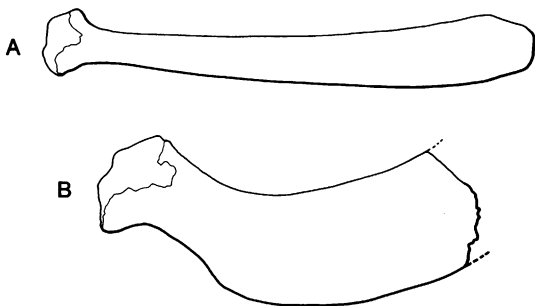

FIG. 13. Comparative views of left coracoids. A. *Podocnemis expansa.* AMNH Herp. 62947. B. *Taphrosphys sulcatus*, PU 18707.
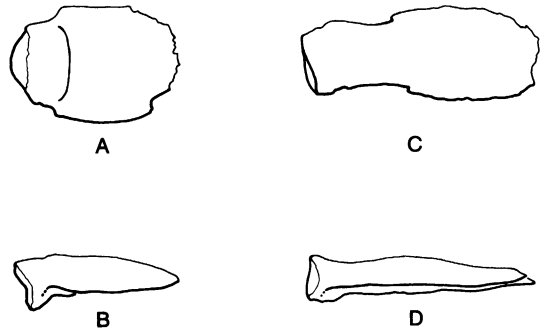

FIG. 14. *Taphrosphys sulcatus*, PU 18707. Distal phalanges not identified as to digit or limb position. Ventral (A) and side (B) views of same phalange. Ventral (?) (C) and side (D) views of same phalange.

AGE OF THE HORNERSTOWN FORMATION

There has been some controversy and discussion concerning the age of the sediments containing *Taphrosphys* and other vertebrates from the New Jersey coastal plain. That controversy exists is hardly surprising if one considers the difficulties in doing stratigraphic work in New Jersey:

1. Lithostratigraphic units are relatively thin and seem to be compressed sections in the sense that deposition was continuous but extremely slow. For example, the Hornerstown Formation is usually about 20–30 feet thick yet fossils characteristic of late Maastrichtian, early and late Paleocene and early Eocene occur in it.

2. Calcareous fossils are usually leached from surface exposures.

3. Bedding planes are almost completely imperceptible, and lithologic contacts may or may not be time parallel.

4. Glauconite forms a very fertile soil (it was mined in the past for a fertilizer), and exposures are rare and usually small.

5. Lateral variation in lithology appears to be considerable when biostratigraphic units are assumed to be time parallel.

In particular, the position and nature of the Cretaceous-Tertiary boundary in this area has been disputed and a brief review of this topic will

be necessary (see Olsson, 1963, and Minard et al., 1969, for more thorough historical summaries). The early records of *Taphrosphys* and other New Jersey coastal plain vertebrates usually state a town or county (in some cases a farm or marl company) as the locality and "upper," "middle," or "lower" marl or "the greensand" as the horizon (see Baird, 1967, for further discussion of nineteenth-century stratigraphic terminology in New Jersey). At the time of their original discovery and description the Cretaceous age of these specimens was widely accepted, although diagnostic associated fossils were not reported. Knapp (1907) formalized the stratigraphic nomenclature currently used but, most important, he placed some of the more informally named greensand units (in particular, the "middle greensand") in the Hornerstown Formation. At that time the Hornerstown, and its relatively rich vertebrate fauna, were considered to be Cretaceous in age. Later, geologic work (see Cooke and Stephenson, 1928, and references) resulted in the identification of early Tertiary macroinvertebrate fossils from the upper parts of the Hornerstown Formation and a change in age assignment of the whole lithologic unit from the Cretaceous to the Eocene (the Paleocene was not recognized by these workers at that time). The vertebrates considered by their original describers to be Cretaceous were transferred to the Eocene by paleontologists, such as Romer (1945, 1956), involved in compilations, and these age assignments have become entrenched in the literature.

Miller (1955, 1956) appears to have been the first to suggest that at least some of these age assignments were incorrect and he developed the notion that a unit lithologically indistinguishable from and underlying the Hornerstown Formation contained Cretaceous fossils and was Cretaceous in age. He called this unit the "middle greensand" because he believed that it was the same as the "middle greensand" of earlier workers, such as Leidy and Cope. The presence of undoubted Cretaceous macroinvertebrates had been noted by others (Dorf and Fox, 1957) but they were explained as being reworked from underlying Cretaceous sediments.
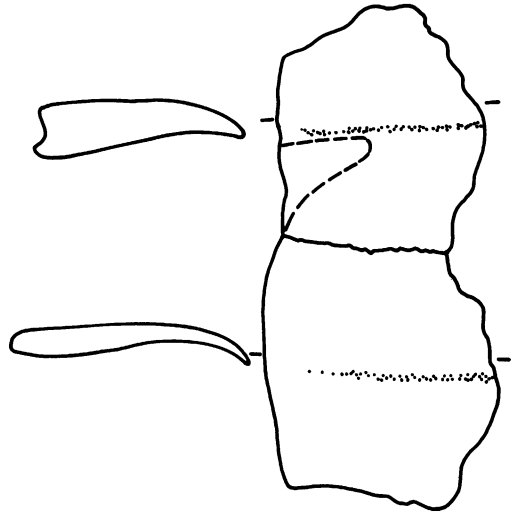
Olsson (1963) developed a biostratigraphic

FIG. 15. Peripheral bones of a toxochelyid turtle, PU 18709, found associated with a specimen of *Taphrosphys sulcatus*, PU 18707, at the Sewell pit (Baird, 1964, p. 22).

hypothesis based on planktonic foraminifera in which he recognized a series of assemblage zones in the Hornerstown Formation and the underlying (and downdip partial equivalent) New Egypt Formation. Olsson correlated his zones with the Danian, Thanetian, and Sparnacian ages of Europe. He also noted in an appendix (Olsson, 1963, p. 662) the presence of Cretaceous foraminifera in an augerhole sample from the lower portion of the formation. During 1963-1964 my own work on *Taphrosphys* took place under the direction of Olsson and Baird (see acknowledgments) and a *Sphenodiscus-Taphrosphys* association in the Inversand pit, Sewell, New Jersey, came to Olsson's attention. In a personal communication in Baird (1964, p. 23), Olsson concluded that the lower beds of the Hornerstown were probably Late Maastrichtian in age and that there was no evidence for reworking of fossils. Gaffney (MS) reassigned *Taphrosphys* to the Cretaceous and Baird (1967) reassigned some birds to the Cretaceous, whence they were originally placed nearly a century ago.

Over the past 15 years United States Geological Survey (USGS) geologists have mapped

the Upper Cretaceous-Lower Tertiary outcrop area in New Jersey and developed a hypothesis concerning the position and nature of the Cretaceous-Tertiary boundary in New Jersey (Minard et al., 1969; Owens and Sohl, 1969). Briefly, they have concluded that the Hornerstown Formation is entirely Tertiary in age and that it overlies an angular unconformity. Olsson (1963) has argued for continuous deposition across the boundary, at least in New Jersey. The question of an unconformity is of importance to a discussion of the Hornerstown vertebrate assemblage because it involves the reworking of Cretaceous fossils into Tertiary sediments. The USGS argument (Minard et al., 1969) is essentially as follows:

1. Regional thinning and pinchout of lithostratigraphic units below the Hornerstown and overlap of the Hornerstown onto progressively older beds from northeast to southwest are evidence of an angular unconformity.

2. Local evidence of an unconformity and erosional interval can be seen in "worn phosphatic and sideritic fossils and pieces of rock reworked from the underlying Cretaceous formations into the base of the overlying Tertiary formations."

Olsson and Gaffney (1970) suggested arguments against this hypothesis and concluded that the lowermost portion of the Hornerstown Formation is Late Cretaceous in age and that an unconformity is not present. I will amplify our arguments and discuss the USGS points in the order listed above:

1. The regional thinning and pinchout can be interpreted as a series of facies changes as there is no biostratigraphic evidence for missing time intervals either in the subsurface or to the southwest along the outcrop in New Jersey (Olsson, 1963). The base of the Hornerstown Formation appears to become older to the southwest; the southwest basal portion being time equivalent to some or all of the Tinton Formation in the northeast.

2. Local evidence for an uncomformity is wanting. Fossil macroinvertebrates from the basal Hornerstown Formation are characteristically represented by internal clay molds and pyritized replacements. They are very susceptible

to destruction by weathering and casual collecting but when collected with care they are usually intact and show no water-worn features. In addition, the bivalves almost always are represented by internal molds having both valves. Reworking would have disarticulated the valves or destroyed the internal clay mold. Extensive bioturbation by burrowing organisms (presumably molluscs) do cause local sediment mixing at lithologic contacts resulting in a mottled, irregular appearance of the base of the Hornerstown. Subsurface weathering and periglacial structures also tend to cause irregularities in contacts between unconsolidated sediments.

The above discussion shows that alternative explanations are possible for the features advanced by Minard et al. (1969) but the most important point is that the known biostratigraphy is inconsistent with their unconformity hypothesis. The basal Hornerstown in the southwest portion of New Jersey contains a late Maastrichtian fauna without any evidence of mixing with species restricted to the Tertiary. Furthermore, the underlying beds give no evidence of missing biostratigraphic zones. The basic difference between these interpretations seems to be the direct acceptance of lithostratigraphic information versus the direct acceptance of biostratigraphic information. The Minard et al. (1969) hypothesis involves time parallel rock units and reworked fossils, whereas Olsson and his adherents require fossils as accurate time indicators and the rejection of lithology as necessarily time parallel. At the present time the latter hypothesis seems most parsimonious.

Although earlier workers noted ammonites, dinosaurs, mosasaurs, and plesiosaurs (see Miller, 1955, 1956, for summary and references) as occurring in the "middle greensand" or Hornerstown Formation, none of the published locality information really allows a definitive assignment to the basal Hornerstown Formation as opposed to the underlying New Egypt Formation (="chocolate marl," Navesink Formation). The sections are compressed, the lithologies are similar, and the terms "upper," "middle," and "lower" were often used somewhat arbitrarily (Baird, 1967). Miller (1956, p. 729) remarked that no ammonites had been collected from the

FIG. 16. Field photograph of a specimen of *Taphrosphys sulcatus*, PU 18707, *in situ* showing disarticulated and "shingled" arrangement of plates. Photo taken by Mr. R. Regensburg, August, 1960, at the Inversand Company pit, Sewell, New Jersey. See figure 17.

"middle greensand" since the period of extensive marl digging but since Miller's paper a number of well-documented instances are known.

1. PU 87231, *Sphenodiscus lenticularis* (=*lo-batus*) identified by Karl Waage (personal commun., 1964) was found 6 inches to 1 foot above the New Egypt-Hornerstown contact in association with PU 18706, a skeleton of *Taphrosphys sulcatus* described in this paper. Col-
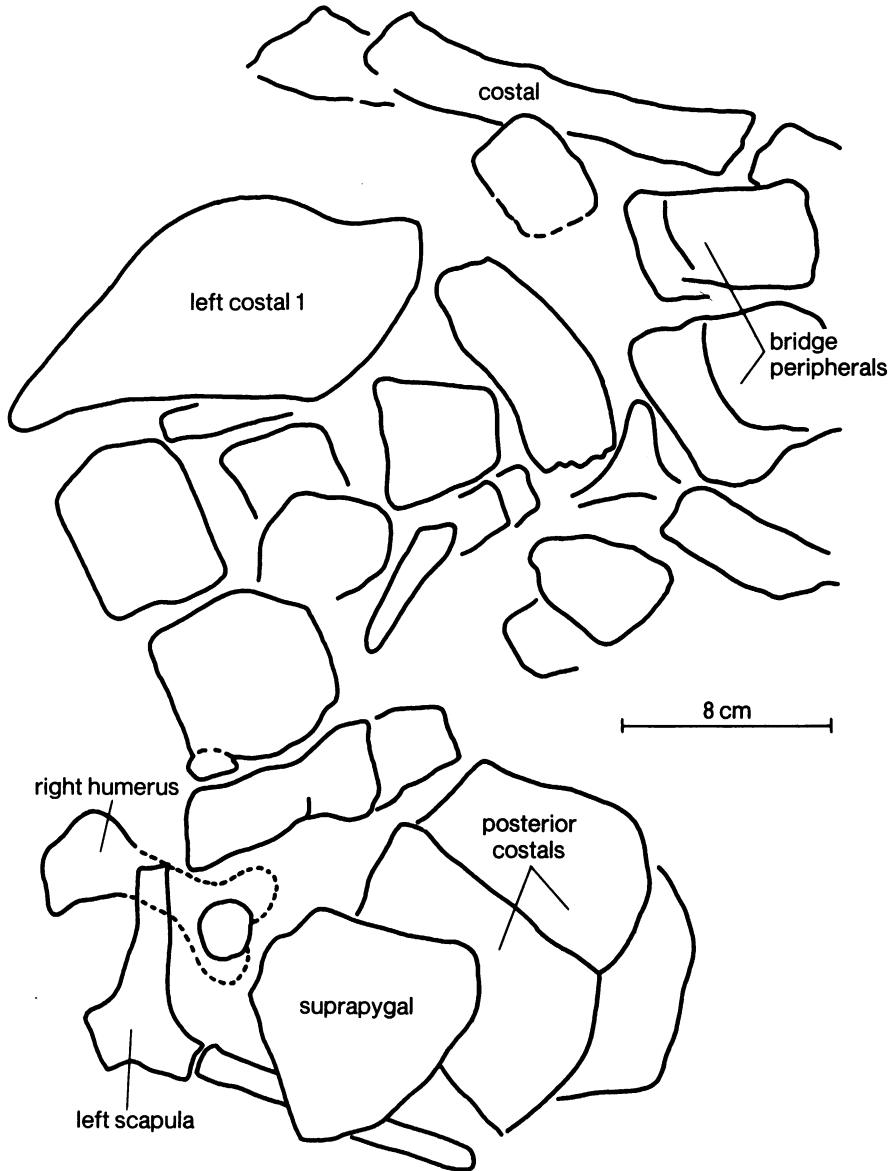

FIG. 17. Key to figure 16.

lected by Richard Regensburg and William Dilkes in August, 1960, at the Inversand Company pits, Sewell, New Jersey.

2. A specimen of *Sphenodiscus* cf. *lenticularis* found in the "bone bed" at Sewell was associated with ANSP 15544, a partial skeleton of *Taphrosphys sulcatus* (figs. 3, 4).

3. White (1972, p. 7) reported that *Sphenodiscus lenticularis, Placenticeras placenta,* and *Baculites ovatus* were collected in the "bone bed" within 5 feet of the Hornerstown-New Egypt contact.

4. David C. Parris (New Jersey State Museum) has collected the following specimens from the basal portion of the Hornerstown Formation at the Inversand pit: NJSM 11321 *Baculites ovatus* (six specimens), NJSM 11328 *Sphenodiscus lobatus* (10 specimens), and NJSM 11284 an unidentified ammonite (two specimens).

One of the difficulties in biostratigraphic correlation of the greensand units is the usual leaching of calcareous fossils (particularly aragonitic shells) in surface exposures. Recently, however, significant evidence concerning the position of the Cretaceous-Tertiary boundary has resulted from the discovery of organic-walled dinoflagellates. Koch and Olsson (1974, p. 46) reported that: "A distinctive dinoflagellate assemblage . . . is present in the Tinton Formation and in the beds below the Hornerstown in central and southern New Jersey. Furthermore this flora is present in the basal foot or so of the Hornerstown. This flora differs from that of the older Navesink and Redbank formations and in the subsurface is associated with the planktonic foraminiferal *Abathomphalus mayaroensis* zone and the coccolith *Nephrolithus frequens* Zone, both of which are recognized as the topmost zones of the Cretaceous in widely separated parts of the world."

In conclusion, despite statements to the contrary, it seems most likely that the basal portion of the Hornerstown Formation in central and

FIG. 18. *Left*: Field photograph of shell of *Taphrosphys sulcatus*, PU 18706, *in situ* showing disarticulated and "shingled" arrangement of the plates. Photo taken by R. Regensburg, August 1960, at the Inversand Company pit, Sewell, New Jersey. *Right*: Northeast area of Inversand Company pit, Sewell, New Jersey, taken by R. Regensburg, August, 1960. Position of PU 18707 indicated by circle. Contact of Hornerstown Formation and New Egypt Formation indicated by arrow. Lowest ledge is formed by New Egypt Formation.
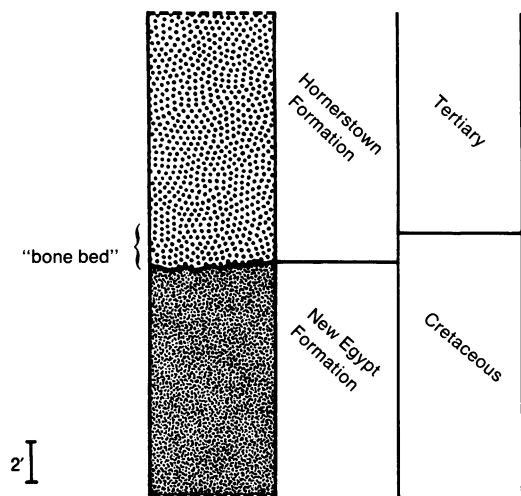
FIG. 19. Stratigraphic section at the Inversand Company pit, Sewell, New Jersey.

southern New Jersey is late Maastrichtian in age.

Taphonomy. Characteristically, vertebrate fossils in museum collections from the New Jersey coastal plain are broken fragments, representing a very small part of an individual, and usually rather uninformative. At least two authors (Cooke and Stephenson, 1928; Minard et al., 1969) have used this fact as evidence that the bones were reworked from Cretaceous deposits into Tertiary units. Zangerl (1953), Baird (1964), Gaffney and Zangerl (1968), and White (1972) have argued that vertebrates are more often found partially complete and in semiarticulation and that casual collection (an understatement for nineteenth-century specimens) of fragile, water soaked remains in unconsolidated matrix resulted in the atrocious condition of most specimens. After collection, exposure of the fossils to air and humidity usually caused pyrite in the bone to decompose thus further damaging or destroying the material.

The *Taphrosphys* specimens described here were carefully collected and the figures show that the specimens were disarticulated to some extent and the plates "shingled" over each other (see Baird, 1964, p. 22 for a similar occurrence of *Peritresius* from the New Egypt Formation at

Sewell). This is consistent with disturbance by benthonic scavengers and infaunal burrowers. In any case, it is clearly impossible for these skeletons to have been reworked.

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