MIDDLE MIOCENE SEA TURTLES (SYLLOMUS, PROCOLPOCHELYS, PSEPHOPHORUS). FROM THE CALVERT FORMATION

ROBERT E. WEEMS

Reprinted from Journal of Paleontology
Vol. 48, No. 2, March 1974
pp. 278–303
Made in United States of America
Copyright © 1974, The Society of Economic Paleontologists and Mineralogists
MIDDLE MIOCENE SEA TURTLES (SYLLOMUS, PROCOLPOCHELYS, PSEPHOPHORUS) FROM THE CALVERT FORMATION

ROBERT E. WEEMS
9209 Terrapin Court, Richmond, Virginia, 23228

Abstract—All known sea turtles from the Calvert Formation are referable to only three species: Psephophorus calvertensis, Procolopchelys grandaeva, and Syllomus aegyptiacus. The genus Chelonia, previously reported from the Calvert, cannot be demonstrated to have been present. P. calvertensis, a dermochelyid, is the rarest of the Calvert sea turtles and is very poorly known. P. grandaeva, a cheloniod not previously reported from the Calvert is now known from four occurrences. These occurrences are sufficiently complete to show that Carolinopchelys wilsoni and “Euclastes” melii are not generically distinct from Procolopchelys and should be included in that genus as distinct species. The most common Calvert turtle is the cheloniod S. aegyptiacus. This turtle exhibits considerable but gradational variation among the specimens available. A number of names have been incorrectly assigned to variants within this population (Syllomus crispatus, Petreusia virginiana, Chelonia marylus) In addition two other synonyms (Kurobechelys tricarinata from Japan. Trachyspis aegyptica from Egypt) are known which serve to indicate the worldwide distribution of S. aegyptiacus in the Miocene.

Acknowledgments

The research for this paper was conducted during the summers of 1966 and 1967 when I was a participant in the Smithsonian Summer Intern program. During this time facilities and specimens were made available by the Department of Paleobiology and the Department of Biology. Special thanks go to Nicholas Hotto III, who donated half his office and innumerable hours of his time toward guidance of the research. Without his personal interest and effort this study would never have materialized as a formal paper. Other individuals who kindly offered assistance in preparing this paper are as follows: Donald Baird of Princeton University made the type material of Procolopchelys grandaeva available to the author for comparisons. Eugene S. Gaffney of the American Museum, Frank C. Whitmore of the United States National Museum, and Rainer Zangerl of the University of Chicago critically reviewed the manuscript and offered suggestions for improvement and consolidation. Zangerl pointed out the close similarity between Syllomus aegyptiacus and Kurobechelys tricarinata. Lawrence B. Isham pre-

Explanation of Plate 1

Fig. 1—Dorsal view of anterior carapace of "Trachyspis" aegypticaa Lydekker (type). Photograph courtesy of the British Museum of Natural History.
2—Lateral view of sixth cervical (USNM 13859) of Syllomus aegyptiacus Lydekker, showing concave anterior face (left) and planar posterior face (right), ×0.8.
3—Ventral view of sixth cervical (AMNH 1661) of Syllomus aegyptiacus Lydekker, showing prominent facets on anterior (upper) edge of centrum, ×0.8.
4—First digit (metacarpal, two phalanges) of Procolopchelys grandaeva Leidy (USNM 24888), ×1.0.
5—Lateral view of eighth cervical (USNM 13859) of Syllomus aegyptiacus Lydekker, showing anterior face (left) and convex posterior face (right), ×0.8.
6—Lateral view of eighth cervical (USNM 24872) of Syllomus aegyptiacus Lydekker, showing ventral process engulfed in an arthritic growth, ×0.8.
7—Lateral view of caudal (USNM 24870) of Syllomus aegyptiacus Lydekker, ×0.8.
8—Detailed view of carapace sculpture on the type specimen of Syllomus aegyptiacus Lydekker; photograph courtesy of the British Museum of Natural History.
9—Lateral view of seventh cervical (AMNH 1661) of Syllomus aegyptiacus Lydekker, showing planar anterior face (left) and convex posterior face (right), ×0.8.
pared the posterior view reconstruction of the skull of *Procolpochelys grandaevia* shown in Text-figure 14. Photographs for the plates were prepared by the United States National Museum except for Pl. 1, fig. 1 and 8, which were supplied by the British Museum of Natural History through the courtesy of A. J. Charig. Faye C. Weems typed the manuscript and assisted in proofing the text throughout the long and tedious interval of rewriting and reassessment between inception and completion of this paper. Finally, thanks go to Robert A. Graham and John S. Moses for the days and weeks they spent with the author collecting

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Shell length (mm)</th>
<th>Peripherals sutured</th>
<th>total¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>USNM 13859</td>
<td>360 (est.)</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td>USNM 13825</td>
<td>480</td>
<td>2.5 ± 0.5</td>
<td>0</td>
</tr>
<tr>
<td>AMNH 1661</td>
<td>520</td>
<td>6.0</td>
<td>1.5</td>
</tr>
<tr>
<td>USNM 24871</td>
<td>540</td>
<td>4.5 ± 0.5</td>
<td>1.25</td>
</tr>
<tr>
<td>USNM 24873</td>
<td>580</td>
<td>8.5</td>
<td>2.5</td>
</tr>
<tr>
<td>USNM 24872</td>
<td>590</td>
<td>8.0</td>
<td>—</td>
</tr>
<tr>
<td>USNM 24874</td>
<td>590</td>
<td>7.0 ± 0.5</td>
<td>—</td>
</tr>
<tr>
<td>USNM 24870</td>
<td>618 (complete)</td>
<td>8.0 ± 0.5</td>
<td>2.0</td>
</tr>
</tbody>
</table>

¹ For convenience of counting, the pygal is considered to be a twelfth peripheral.
under often trying circumstances along the Nomini Cliffs of Virginia.

THE ESTABLISHMENT OF SYLLOMUS AEGYPTIACUS LYEDEKKER IN THE CALVERT FORMATION

The sea turtles with carapace sculpture from the Calvert Formation (Miocene, Atlantic Coastal Plain) have been assigned to three taxa, Syllomus crisatus Cope, Peritresius virginianus Berry & Lynn, and Chelonia marylandica Collins & Lynn. The type specimen of P. virginianus is poorly preserved and represents a very immature individual, while the other two types consist mostly of a few fragmentary bones of the carapace and limbs. Eight additional carapace specimens, representing more complete material, have been collected in the past few years from the same horizons that yielded P. virginianus and C. marylandica. These specimens share characters which have been used to distinguish the three putative Calvert taxa and indicate that a single very variable population is present.

It has been demonstrated repeatedly that the scutes of a turtle shell vary considerably among the individuals of a single species (Parker, 1901; Newman, 1906; Lynn, 1937; Lynn & Ullrich, 1950; Zangerl & Johnson, 1957). Variation of bony elements is not as extensively documented, but it also seems to be high in marine forms as well as in better studied terrestrial forms (Parker, 1901; Newman, 1906; Lynn, 1937; Zangerl & Turnbull, 1955). Growth contributes heavily to individual variation in sea turtles. For example, in modern forms suturing between peripherals and costals often takes place progressively from front to back with advancing age until the posterior costoperipheral fontanelles are completely closed; Chelonia mydas is the only living species in which the costoperipheral fontanelles persist throughout life (Boulenger, 1889; Deraniyagala, 1939). In the Syllomus specimens at hand sutures between peripherals and costals are formed continuously as far back as the seventh costal in the larger shells; behind this point small fontanelles persist. The correlation between costoperipheral suturing and carapace size can be seen in Text-fig. 1 and Table 1. Although two slopes are suggested, these probably represent sexual dimorphism rather than the presence of two species. No other morphologic characters are known to correlate with the observed differences in size (Table 2).

Three other types of variation which are common but which apparently are not correlated with each other or with growth patterns include (1) splitting of the first neural, (2) development of an extra postneural and costal, and (3) formation of longitudinal dorsal keels. In four specimens in the present sample the space between the first pair of costals is occupied by two elements. This condition is termed here a "split neural" because the two elements partly overlie the same neural arch and are therefore probably derived from an originally single neural. The split neural may be restricted to the space ordinarily occupied by the first neural, as in USNM 24872 (Pl. 2, fig. 1), or it may encroach variably upon its posterior neighbor, as in USNM 13859, USNM 24873, and USNM 13825. The range of variation is shown in Text-figure 2. At the posterior end of the neural series an extra postneural is variably developed. In USNM
In USNM 24874 no keels are present; in USNM 24870, USNM 24871, and USNM 24873 there is only a medial keel; in AMNH 1661, USNM 13859, USNM 13858, USNM 13825, and USNM 24872 there are three parallel keels, one on each side of the medial keel about one-fourth of the distance from the midline to the periphery. These variations are summarized in Table 2. Duplication of the postneural appears to be related to duplication of the eighth costal; otherwise correlation is low among the features considered above. The lack of correlation suggests random mixing of genic or developmental characters within a single population and indicates that they are not significant for taxonomic distinctions.

The distribution within this fossil population of eight costals, nine costals, or double headed eighth costals suggests that these conditions possibly were controlled by the presence of two alleles in the population, neither dominant over the other. The lack of irregularly or only partially developed double headed eighth costals argues against this being simply a common congenital variation. Unfortunately the sample is not large enough yet to test this hypothesis by statistical analysis to see if the assumed "p" and "q" allelic frequency is close to Hardy-Weinberg equilibrium. Such a check should eventually prove feasible as more shells are collected, however. Assignment of the other variant features to either a genetic or congenital origin is not feasible yet, even tentatively. Certainly they represent gradational conditions in the geometry of the shells and not discretely different conditions as does the eight or nine costal condition.

TAXONOMIC REVIEW

The generic assignment of Peritresius virginianus Berry & Lynn (1936) was based upon trionychid-like sculpture and the presence of fontanelles roughly similar to those of the then fragmentary type of Peritresius, P. ornatus Leidy. Recently, however, Baird (1964) has demonstrated from more complete material that P. ornatus is a lophochelid toxochelid on the basis of its cordiform outline, serrated margin, and steep mid-dorsal keel with epithelial elevations. The specimens at hand show none of these features. Instead, the low-arched shell, planar joint between the sixth and seventh cervicals, nuchal with ventral attachment surface for the neural arch of the eighth cervical, and prococious caudal vertebrae demonstrate clearly that they are cheloniiids (Romier, 1956) and therefore cannot be assigned to Peritresius.
Table 2—Carapace variations in *Syllomus aegyptiacus*.

<table>
<thead>
<tr>
<th>Individual</th>
<th>Sex</th>
<th>Lateral keel</th>
<th>1st neural</th>
<th>3rd postneural</th>
<th>8th costal</th>
<th>Median keel</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH 1661</td>
<td>F</td>
<td>+</td>
<td>$\frac{1}{2}/\frac{1}{2}$</td>
<td>+</td>
<td>1/1</td>
<td>+</td>
</tr>
<tr>
<td>USNM 13859</td>
<td>F</td>
<td>+</td>
<td>$\frac{1}{2}/\frac{1}{2}$</td>
<td>-</td>
<td>1</td>
<td>+</td>
</tr>
<tr>
<td>USNM 13858</td>
<td></td>
<td>+</td>
<td>$\frac{1}{2}/\frac{1}{2}$</td>
<td>-</td>
<td>1</td>
<td>+</td>
</tr>
<tr>
<td>USNM 13825</td>
<td>M</td>
<td>+</td>
<td>$\frac{1}{2}/\frac{1}{2}$</td>
<td>-</td>
<td>2</td>
<td>+</td>
</tr>
<tr>
<td>USNM 24870</td>
<td>M</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>1/1</td>
<td>+</td>
</tr>
<tr>
<td>USNM 24871</td>
<td>M</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>1</td>
<td>+</td>
</tr>
<tr>
<td>USNM 24872</td>
<td>F</td>
<td>+</td>
<td>$\frac{1}{2}/\frac{1}{2}$</td>
<td>+</td>
<td>2</td>
<td>+</td>
</tr>
<tr>
<td>USNM 24873</td>
<td>F</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>+</td>
</tr>
<tr>
<td>USNM 24874</td>
<td>M</td>
<td>-</td>
<td>$\frac{1}{2}/\frac{1}{2}$</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>USNM 16742</td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

1 F—female, M—male.
2 + signifies present, - signifies absent.
3 1 signifies a simple united neural, $\frac{1}{2}/\frac{1}{2}$ signifies a "split" neural.
4 1 signifies bearing one rib head, 2 signifies bearing two rib heads, and 1/1 signifies a division into two distinct costals.

Collins & Lynn (1936) based *Chelonia marylandica* on a fragmentary specimen and assigned it to *Chelonia* because of its "vascular grooves," although in other respects it closely resembles *P. virginianus*. Because of the poor quality of their material this assignment was tentative; it was expected that a new genus would be established when better material was found. It is now evident that the "vascular grooves" are only worn sculpture and do not contain foramina larger than foramina in *P. virginianus*. This eliminates the essential reason for distinguishing *C. marylandica* from *P. virginianus*.

The third taxon, *Syllomus crispatus* Cope (1896), was erected to accommodate two costal fragments and a humerus (illustrated in Hay, 1908). Berry's (1937) referred specimen of *S. crispatus* obviously is correctly assigned to this taxon, and some of the more recently acquired material in this study is also indistinguishable from Cope's type in all comparable features. Since *Syllomus crispatus* was erected specifically for this material, *Syllomus* is the only name which has been validly applied to any of the Calvert material. Since it also is the oldest name applied to this material, *crispatus* also has priority over *virginianus* and *marylandica* as a species name.

Berry had separated *P. virginianus* from *S. crispatus* largely on the basis that *S. crispatus* had no costoperipheral fontanelles. Separation of these two genera by this character is no longer valid, however, because the lack of costoperipheral fontanelles is apparently only a function of growth as discussed above and both specimens fall on the presumed female growth slope. Several other characters which appear on some of the shells and not on others, considered valid differences between these species in the past, have also been shown to be most consistent with the interpretation that a single population seems to be represented. Since only a single population seems to be represented, *S. crispatus* may be considered the only American name validly applied to all of these specimens. This conclusion is not new, for Berry (1937) suspected that "*P. virginianus*" was the same as *S. crispatus*, while Zangerl (1958) and Baird (1964) believed that all three taxa were conspecific.

Species of sea turtles today are cosmopolitan in warmer latitudes, so there is no reason *a priori* why similar distributions could not have existed in the past. The turtles referable to *Syllomus* in the Calvert are morphologically indistinguishable from two other forms previously described—*Trachyaspis aegyptiaca* Lydekker (1889) and *Kurobechelys tricarinata* Shikama (1956). Both of these forms readily fall within the range of variations seen in the Calvert population and, although the geologic age of the former is only known to be Tertiary, the latter is clearly from the Miocene. Thus neither geologic age nor morphology indicates any compelling reason for believing more than a single species is represented by all of these specimens.

Although *Kurobechelys tricarinata* clearly is a junior synonym, *Trachyaspis aegyptiaca* is the oldest name applied to remains of the turtle under consideration. This makes the species name *aegyptiaca* the proper name to be applied. However, the genus *Trachyaspis* (type species *T. lardy von Meyer*) probably should be referred to the Dermotemydidae (Rainer Zangerl, personal communication, 1973). Thus the generic name *Trachyaspis* has been applied invalidly in this case, leaving...
only _Syllomus_ as a generic name which has been applied uniquely to the species under consideration. Thus:

\[
\begin{align*}
\text{Trachyaspis aegyptiaca} & \quad \text{Syllomus crispatus} \\
\text{Peritrixius virginianus} & \quad \text{Chelonia mayslandica} \\
\text{Kurobechelys tricornata} & \quad = \text{Syllomus aegyptiicetus}
\end{align*}
\]

**SYSTEMATIC DESCRIPTIONS**

Order _Chelonia_
Suborder _Cryptodira_
Superfamily _Chelonioidae_
Family _Chelonidae_
Genus _Syllomus_

*Type species._—_Syllomus crispatus_ Cope (1896).*

*Known distribution._—_Calvert Formation (middle Miocene) of Maryland and Virginia, U.S.A.; Suez, Egypt (Tertiary); Japan (Miocene).*

*Diagnosis._—_Carapace shield-shaped and flat with a definite sculptured pattern on the dorsal surface not attributable to nutrient foramina as in _Lepidochelys_. Sculpture composed of ridges and valleys; ridges irregular in middle of costals, trending anteroposteriorly at costal margins. Nutrient foramina are very fine and do not affect the course of the sculpture. All dorsal vertebral arches fused to their overlying neu rals in adults, except the first, which is sutured against the ribs in younger individuals.*

*Diagnosis._—_Carapace shield-shaped and flat with a definite sculptured pattern on the dorsal surface not attributable to nutrient foramina as in _Lepidochelys_. Sculpture composed of ridges and valleys; ridges irregular in middle of costals, trending anteroposteriorly at costal margins. Nutrient foramina are very fine and do not affect the course of the sculpture. All dorsal vertebral arches fused to their overlying neu rals in adults, except the first, which is sutured against the ribs in younger individuals.*

*Plastron moderately reduced. Xiphiplastrum wide, separated by only a narrow fontanelle. The hypoplastra rectangular and sharply angled, meeting the hypoplastra along nearly the entire anterior border. Plastron sparingly sculptured, sculpture obscure anteriorly. Plas tral sulci are seen only in juveniles.*

*Pelvic girdle has a large ischial spine and the femur has large and elevated trochanters. The humerus has the deltopectoral crest located far down the shaft.*

**SYLLOMUS AEGYPTIACUS** Lydekker, 1889

*Trachyaspis aegyptiaca* Lydekker, 1889, p. 131–133.

*Syllomus crispatus_ Cope, 1896, p. 139.

*Peritrixius virginianus_ Berry & Lynn, 1936, p. 175–190.

*Chelonia mayslandica_ Collins & Lynn, 1936, p. 151–173.

*Kurobechelys tricornata_ Shikama, 1956, p. 35–62.

*Diagnosis._—_Same as for genus.*

*Type specimen._—_BMNH R229, deposited in the British Museum of Natural History. Fairly complete carapace consisting of parts or all of left costals 1–7, all of right costal 1–7, nuchal, neural 1–7, left peripherals 1–6, right peripherals 1–8.*

*Type locality._—_Suez, Egypt, from Tertiary strata.*

*Referred specimens._—_Eighteen, as follows: (1) AMNH 6134 ("Syllomus crispatus" Cope [type]); humerus and two costal fragments; coll. E. D. Cope; marl pits near Hanover, Virginia; Calvert Formation (middle Miocene). (2) AMNH 1661 (paratype of "Syllomus crispatus" Cope); carapace including nuchal, neura ls 1–7, postneural 3, suprapygal 1–2, pygal, portions of all costals, right peripherals 1–2, 11, left peripherals 1–6, 11, plastron including both xiphiplastrum and both hypoplastra, right and left scapulae, right and left coracoid, parts of right and left pubes and right and left ischia, one dorsal vertebral centrum, cervicals 6–7, fragmentary (?) parietal; coll. Charles T. Berry; Horsehead Cliffs, King George County, Virginia; Calvert Formation (middle Miocene). (3) USNM 13859 ("Peritrixius virginianus" Berry & Lynn [type]); carapace including neural 1, 5–6, suprapygal 1, right costals 1–5, 8, plastron including part of left hypoplastra, both hypoplastra, right xiphiplastrum, three peripherals, two dorsal vertebral centra, cervicals 6, 8; coll. W. G. Lynn; Horsehead Cliffs, King George County, Virginia; Calvert Formation (middle Miocene). (4) USNM 13858 (paratype of "Peritrixius virginianus" Berry & Lynn); carapace with neu-
Text-fig. 4—Reconstruction of the carapace of *Syllomus acaptaeus*, based on AMNH 1661. Three keels are present on the anterior portion of the carapace.

Text-fig. 5—Dorsal view of carapace of *Syllomus acaptaeus*, showing the most typical of several patterns of scute distribution during life. Anterior three medial scutes cover a low medial keel. Outline based on USNM 24870.

rals 2-7, right costals 2-8, left costals 3-7; coll. W. G. Lynn; Horsehead Cliffs, King George County, Virginia; Calvert Formation (middle Miocene). (5) USNM 13825 (*Chelonidae marylandica* Collins & Lynn [type]); carapace with neurals 2-4, left and right costals 2-4, right peripherals 4-5, left peripherals 4-6; coll. W. G. Lynn; Calvert Cliffs, Calvert County, Maryland; Calvert Formation (middle Miocene). (6) USNM 24870; carapace including nuchal, neurals 1-2, 4, 7, postneurals 1-3, suprapygs 1-2, pygal, parts of all right costals, parts of left costals 1-3, 7-8, right peripherals 4-7, 10-11, left peripheral 2, plastron includes parts of both hypoplastra and xiphiplastra, 3 dorsal vertebral centra, 3 caudal vertebrae, left ischium, both ilia, right femur; coll. Robert A. Graham and Robert E. Weems; about middle of the Stratford Cliffs, Westmoreland County, Virginia, in Zone 11 about 2 feet below Zone 12, one foot above the beach; Calvert Formation (middle Miocene). (7) USNM 24871; posterior portion of carapace with neurals 6-7, postneurals 1-3, suprapygs 1-2, pygal, right costals 4-9, left costals 4, 6-9, left and right peripherals 11, left xiphiplastron, left coracoid; coll. Robert E. Weems; eastern Stratford Cliffs, Westmoreland County, Virginia, in Zone 11 about 1 foot below Zone 12, three feet above the beach; Calvert Formation (middle Miocene). (8) USNM 24872; carapace with part of nuchal, all neurals and postneurals, portions of all costals, right peripherals 1-2, plastron including a hypoplastron, one dorsal vertebral centrum, cervical 8, portions of both ilia, both ischia, a fragment of the left pubis, proximal end of right femur; coll. T. B. Ruhoff; one-half mile below Parkers Creek, Calvert County, Maryland, in a shelf of marl exposed at low tide; Calvert Formation (middle Miocene). (9) USNM 24873; carapace with neurals 4-6, left costals 2-8, left peripherals 4-11; coll. Robert E. Weems; eastern Stratford Cliffs, Westmoreland County, Virginia, from Zone 12 about 4 feet above the beach; Calvert Formation (middle Miocene). (10) USNM 24874; anterior portion of carapace with part of nuchal, neurals 1a-1b, left costals 1-3, peripherals 2-6; coll. Robert E. Weems; eastern Stratford Cliffs, Westmoreland County, Virginia, in Zone 12 about 4 feet above the beach; Calvert Formation (middle Miocene). (11) USNM 16742; posterior carapace with neural 7, postneurals 1-3, suprapl...
pygal 1, right and left costals 6–8; coll. Col. Richard Lemke; one-half mile south of Scientists Cliffs, Calvert County, Maryland; Calvert Formation (middle Miocene). (12) USNM 24876; carapace with neurals 2, 7, postneural 1, parts of right costals 1–6; coll. Robert E. Weems; eastern Stratford Cliffs, Westmoreland County, Virginia, in Zone 12 about 4 feet above the beach; Calvert Formation (middle Miocene). (13) USNM 20375; right xiphiplastron and most of right hypoplastron; coll. R. Lee Collins; Horsehead Cliffs, King George County, Virginia; Calvert Formation (middle Miocene). (14) USNM 24878; right humerus; coll. R. Lee Collins; in Zone 12 of the Calvert Cliffs, one-half mile south of Parkers Creek, Calvert County, Maryland; Calvert Formation (middle Miocene). (15) USNM 24879; distal portion of humerus, nuchal; coll. Albert C. Myrick, Jr.; 250 yards south of Parkers Creek, Calvert County, Maryland; Calvert Formation (middle Miocene). (16) USNM 24880; left and right humeri, left radius, left ulna, three carpals; coll. Robert E. Weems; from a fallen block (probably from Zone 13) found along the western Horsehead Cliffs, King George County, Virginia; Calvert Formation (middle Miocene). (17) USNM 24881; left femur; coll. Robert E. Weems; in Zone 12 of the eastern Stratford Cliffs, Westmoreland County, Virginia; Calvert Formation (middle Miocene). (18) USNM 24882; right humerus; coll. Albert C. Myrick, Jr.; from the Stratford Cliffs about 15 feet above the beach (Zone 13?), Westmoreland County, Virginia; Calvert Formation (middle Miocene).

DESCRIPTION

The anatomy of *Syllomus aegyptiacus* has been poorly known because the high degree of morphological variation has hindered taxonomic assignment of available specimens.

---

EXPLANATION OF PLATE 2

Fig. 1—USNM 24872, dorsal view of carapace of *Syllomus aegyptiacus* Lydekker, with sulci darkened for contrast. Fourth right costal bears a tumorous bony growth, ×0.33.

2—USNM 24876, cross section of a tumorous bony growth similar to that shown in figure 1, ×1.33.

3—Left ischium of USNM 24870 (*Syllomus aegyptiacus* Lydekker) showing prominent chelydrid-like posterior process, ×1.0.

4—Right ischium of AMNH 1661 (*Syllomus aegyptiacus* Lydekker), ×1.0.

5—Right hypoplastron and xiphiplastron of *Syllomus aegyptiacus* Lydekker (USNM 13859), ventral view, ×0.5.

6—Proximal view of femur of *Syllomus aegyptiacus* Lydekker, showing arthritic spur (knob) on ridge between caput (right) and trochanter minor (lower), USNM 24872, ×1.0.

7—Left femur (USNM 24881) of a young individual of *Syllomus aegyptiacus* Lydekker, ventral view, showing trochanter major (left) and trochanter minor (right), ×0.66.

8—Right femur of a mature individual (USNM 24870) of *Syllomus aegyptiacus* Lydekker, anterior view, caput to left, trochanter minor to right, and trochanter major to rear. Note the relatively higher trochanter major in the younger individual shown in figure 7, ×0.66.
**Table 3—Measurements (mm) of plastral elements of Syllomus aegyptiacus.**

<table>
<thead>
<tr>
<th>Individual</th>
<th>Shell length</th>
<th>Xiphaplastra right</th>
<th>left</th>
<th>Hypoplastra right</th>
<th>left</th>
</tr>
</thead>
<tbody>
<tr>
<td>USNM 13859</td>
<td>360</td>
<td>94</td>
<td>36</td>
<td></td>
<td></td>
</tr>
<tr>
<td>USNM 24870</td>
<td>618</td>
<td>-?</td>
<td>-?</td>
<td>121</td>
<td>54</td>
</tr>
<tr>
<td>USNM 24871</td>
<td>540</td>
<td>111</td>
<td>53</td>
<td></td>
<td></td>
</tr>
<tr>
<td>USNM 20375</td>
<td>—</td>
<td>128</td>
<td>48</td>
<td></td>
<td></td>
</tr>
<tr>
<td>USNM 24870</td>
<td>618</td>
<td>98</td>
<td>137</td>
<td>-?</td>
<td>-?</td>
</tr>
<tr>
<td>USNM 24871</td>
<td>540</td>
<td>109</td>
<td>157</td>
<td>-?</td>
<td>-?</td>
</tr>
<tr>
<td>USNM 20375</td>
<td>—</td>
<td>111</td>
<td>147+</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

*Carapace.*—The carapace has been fully described above. Typical patterns of dermal elements and scutes are shown in Text-figures 4-6.

*Plastron.*—The hypoplastra and xiphaplastra are the best known elements (Pl. 2, fig. 5). Hypoplastra are known only poorly, and the epiplastra and entoplastron not at all. The length and width of the best preserved hypoplastra and xiphaplastra, with estimated length of the associated carapaces shown for comparison, are presented in Table 3. The plastron shows three distinctive features: (1) it is sharply arched in adults, (2) the hypoplastra are rectangular, and (3) the xiphaplastra are much wider than those of modern cheloniids. Proportions of the bones vary slightly and the angle of the hypoplastron becomes greater with age, but there is not a wide variety of distinct differences as in the carapace. The fontanelle between the left and right elements is small for a cheloniid. Only a portion of the hypoplastron is known, but apparently it is sutured with the hypoplastron along nearly its entire width. The posterior half of the plastron is reconstructed in Text-figure 7.

*Vertebrae.*—The sixth, seventh, and eighth cervical vertebrae are known. The centrum of the sixth cervical (Pl. 1, fig. 2) is concave anteriorly and planar posteriorly. The transverse processes are short; neurapophyses and ventral processes are not preserved. There are two prominent facets on the anterior ventral surface of each centrum. The centrum of the seventh cervical (Pl. 1, fig. 9) is planar anteriorly and convex posteriorly, although it is divided posteriorly into right and left heads. The ventral process is not preserved. The neurapophysis is high, with the prezygapophyses level with the top of the arch and the postzygapophyses slightly lower. There is no neural spine, although each postzygapophysis has a ridge over it. The eighth cervical is prococelous, with a trough on the dorsal surface running the length of the neural canal and giving the centrum a slightly bilobed appear-

---

**Explanation of Plate 3**

1—Humerus of *Syllomus aegyptiacus* Lydekker (USNM 24878). Internal (ventral) view of right humerus of a young individual, ×0.88.

2—External (dorsal) view of same humerus as in figure 1, ×1.2

3—Internal (ventral) view of humerus of a mature individual of *Syllomus aegyptiacus* Lydekker (USNM 24882). Note the relatively wider distal end and the more elongate lateral tubercle (upper right) than in the younger individual. ×0.88.

4—Posterior view of posterior cranium of *Procolochelys grandaeva* Leidy (NMNH 186969). This is the specimen from which the reconstruction shown in Text-figure 14 was made. ×1.33.

5—Dorsal view of same cranial fragment as in figure 4, showing posterior portion of left and right parietals and posterior process of supraoccipital, ×1.33.
Table 4—Measurements (mm) of cervical vertebrae of *Syllomus aegyptiacus*.

<table>
<thead>
<tr>
<th>Cervical number</th>
<th>Centrum width</th>
<th>Centrum height</th>
<th>Centrum length</th>
<th>Height of zygapophyses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ant.</td>
<td>post.</td>
<td>ant.</td>
<td>post.</td>
</tr>
<tr>
<td>6¹</td>
<td>12+</td>
<td>14</td>
<td>11</td>
<td>10</td>
</tr>
<tr>
<td>6²</td>
<td>11</td>
<td>17</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>7¹</td>
<td>11</td>
<td>18</td>
<td>18</td>
<td>8</td>
</tr>
<tr>
<td>8²</td>
<td>18</td>
<td>14</td>
<td>10</td>
<td>8</td>
</tr>
</tbody>
</table>

¹ AMNH 1661
² USNM 13859
³ USNM 24872

ance. The ventral process seems to have been normally developed; the one preserved, however, is engulfed in an arthritic growth (Pl. 1, fig. 6). The zygapophyses are level with the top of the arch of the neurapophysis. A transverse process extends laterally from just behind each prezygapophysis. The neural spine is low and projects backwards, but not as far as in *C. mydas*. The spine is distally grooved anteroposteriorly; this groove is medial and widens posteriorly. The measurements of the known cervicals are given in Table 4.

The dorsal vertebrae are poorly known and detailed information is not available. The neural arches all fuse to the neurals in adults (except for the first neural arch) but never seem to fuse to the centra.

The sacral vertebrae are preserved in AMNH 1661 and USNM 24870 (Pl. 4, figs. 4,5). The centra and expanded ribs of the two sacrals are fused in each. The anterior central articulation is concave and the posterior is convex. In both specimens the first sacral ribs are of nearly equal size, but in AMNH 1661 the second sacral ribs are much smaller than those of USNM 24870. In specimens of *Caretta* in the USNM collections such a difference is related to a secondary sexual difference in the size of the tails; in the males the tails are larger. In USNM 24870 the first caudal is easily identifiable because it is fused by its centrum to the sacrum; the ribs of this vertebra are expanded to about the same extent as in male *Caretta* and the centrum is nearly equal in size to the sacral centra. This strongly indicates that USNM 24870 was a male turtle and AMNH 1661 was female. The suggestion that the two apparent growth trends seen in Text-figure 1 represent a secondary sexual character of *Syllomus aegyptiacus* is largely based on the ability to sex specimens USNM 24870 and AMNH 1661.

Caudal vertebrae are associated with USNM 24870. All preserved caudal vertebrae are morphologically alike. Their centra are proc- eolus; width across the transverse processes tends to be greater than the length of the centrum, 20 mm and 14 mm respectively (as preserved), in the specimen shown in (Pl. 1, fig. 7). A caudal neural arch is preserved with USNM 13859. The zygapophyses are prominent; the neural spine is low, wide, thick, and notched posteriorly by a medial indentation. The relatively large size and robust development of the caudal vertebrae of USNM 24870 tend to confirm that they were from a male turtle.

Pectoral girdle.—Reconstruction of the pectoral girdle (Text-fig. 8) is based upon scapulae associated with AMNH 1661, and a left coracoid associated with USNM 24871. The posterior limb and dorsal limb of the scapula are fluted. The dorsal limb is slightly longer than the posterior limb, while the angle between these two limbs is about 120° (125° in the right scapula, 115° in the left). The coracoid is quite long, slender, and modestly expanded distally; its inner face resembles that of the coracoid of *C. mydas*. A longitudinal ridge passes diagonally across the outer face of the coracoid from dorsal to ventral border, instead of lying near the dorsal edge or middle of the bone as in *C. mydas*.

Front limb.—Six of seven humeri known from the Calvert Formation are morphologically identical. Because *Syllomus* greatly outnumbers other chelonians in these beds and the only other known cheloniid species has a different type of humerus associated with it, it is reasonable to assign the most frequently occurring cheloniid humerus to *Syllomus*. The association of one of the humeri (USNM 24879) with a nuchal of *Syllomus* in a fallen block of marl found along the Calvert Cliffs tends to confirm this assignment.

The most complete specimen (USNM 24878) is 94 mm long (Pl. 3, figs. 1,2) and is apparently from a young individual. USNM
24879, about 109 mm without the lateral tubercle, and USNM 24882, 143 mm (Pl. 3, fig. 3), seem to be from adults. Distally the humerus is typically cheloniid, with the ectepicondylar groove becoming surrounded by bone in older individuals. Proximally the deltopectoral crest has moved distally to the middle of the shaft as in the strongly pelagic protostegids and dermochelyids. The crest has an unusually wide space between its distal ends resembling the arrangement found in Chelonia and Dermochelys. One side of the inverted “V” of the deltopectoral crest is on the anterior edge of the shaft; the other side is in the middle of the internal (ventral) surface (Pl. 3, fig. 1). The internal ridge is high. In Cope’s type this latter ridge is broken off proximally and illustrated as if the proximal portion did not exist, hence its very unusual appearance which impressed Cope. The anterior ridge is proximally depressed, leaving the distal portion an isolated protuberance much more pronounced than in other known cheloniid genera. There is also a small secondary ridge which runs between the top of the deltopectoral crest and the lateral tubercle. The lateral tubercle lengthens faster than the rest of the humerus during growth, becoming quite long in the adult (Pl. 3, fig. 3); there is a prominent foramen on its external surface. The angles of the caput to the humerus and the humerus to the plane of movement are cheloniid, not toxochelid or chelydrid (Zangerl, 1953), so the angle at which the forelimb was presented to the water while swimming seems to have been much like that found in modern cheloniids. The total complex of characters in the humerus collectively suggests that Syllomus was more strongly pelagic than any other comparably known cheloniid.

Parts of two humeri, a radius, ulna, and three carpals, all apparently from the same individual (USNM 24880), were used to construct the forelimb illustrated in Text-figure 9. The radius is less expanded distally than in C. mydas, while the rugose surface for ligamentous attachment to the ulna is located more distally and the ulna is slightly thicker through the shaft; in other respects radius and ulna are similar in the two genera. The intermedium is the only positively identifiable carpal; the other two are probably from just behind the second and fifth digits.

Pelvic girdle.—The pelvic girdle is reconstructed from elements associated with specimens AMNH 1661, USNM 13859, USNM 24870, and USNM 24872 (Text-fig. 10). Overall, the pelvis resembles that of a primi-
tive cheloniod or even a chelydrid. The ilium is cheloniod, but the ischium (Pl. 2, fig. 3) is not as reduced and has a pronounced posterior process as in Desmatochelys or Chelydra. The pubes are morphologically intermediate between cheloniod and chelydrid configurations. The anterolateral process of the pubis is long, and the anterior notch of the pubis is broad.

**Hind limbs.**—The only bone of the hind limb that can be studied profitably so far is the femur, represented by three specimens. One, from USNM 24872, shows signs of being arthritic (Pl. 2, fig. 6); the other two, one from USNM 24870 and the other from USNM 24881, seem normal. The femur shows a number of seemingly primitive characters (Pl. 2, figs. 7,8). That these characters were not adaptations for making the femur a second paddle is indicated by the roundness of the caput, comparable in roundness to Dermatemys, which indicates a wide range of directions of rotation unlike that in the humerus. The presence of a large muscle scar on the side of the trochanter major indicates the importance of the trochanters as a point of muscle attachment in this cheloniod; the scar on the trochanter major of *C. mydas*, in which the hind limb functions only as a rudder, is proportionately much smaller. The primitive nature of the femur and the ischial spurs suggest Syllomus normally used its hind limbs in movement, probably for kicking to change direction, as modern aquatic turtles do; modern cheloniids use the hind flippers only as rudders.

A few fragments of the rest of the hind limb are preserved with USNM 13859. Only the distal end of the right tibia bears comment. It appears to be typically cheloniod except that the muscle scar on its internal surface is a depression instead of a raised rugose surface as in *C. mydas*. The supposed tarsal or carpal described by Berry (1937) is actually a nonosseous concretion, possibly a coprolite.

**Skull.**—Except for the fragment from AMNH 1661 described by Berry as part of a parietal, none of the skull of Syllomus is known. The fragment is poorly preserved and does not warrant further consideration. The bone described by Berry (1941) as the dentary of Syllomus instead seems more properly referable to an ocean sunfish, cf. *Mola* (D. H. Dunkle, oral communication, 1966).

**PATHOLOGY**

Three distinct pathological conditions were noted in the remains of *Syllomus aegyptiacus*. The most common disorder is the presence of pits in the shell, apparently bored out by a parasite or epizoan. These holes usually are shallow and well-rounded inside and often are placed randomly on the outer shell surface. Two features indicate that they were acquired entirely or in large part while the animal was alive: (1) the lack of such holes inside the shell or on the plastron, and (2) the concentration of such holes under the pygial in AMNH 1661, indicating a preference for a protected location on the living animal. Epizoan pits such as these have not been seen on any other vertebrate remains from the Calvert Formation, so the creature responsible may have lived only on *Syllomus*.

The second condition noted is an arthritic condition in USNM 24872 in which the femur shows bony growths on its surface between the trochanters and on the caput (Pl. 2, fig. 6). The eighth cervical also has the neural spine encased in a bony growth (Pl. 1, fig. 6).

The third condition is the presence in USNM 24872 and USNM 24876 of bony growths on the carapace. These appear as large amorphous lumps (Pl. 2, fig. 1) with an irregular spongy texture internally (Pl. 2, fig. 2). In both specimens they are located where two lateral scutes and a vertebral scute meet, which suggests that they were initiated by some external irritant. The growth of the lump has obliterated any indication of the nature of the original irritant, but it at least serves to show that the animals survived for an extended period after being affected by the irritant.

**RECOGNITION OF PROCOLOPOCHELYS GRANDAeva IN THE CALVERT FORMATION**

*Procolopchelys grandaeva* was described originally by Leidy (1851), and the currently accepted name was applied by Hay (1908). Recent preparation of material from the Princeton University collection, reviewed and described by Zangerl & Turnbull (1955), has given the first adequate information about the carapace. The following pages demonstrate the extension of the geographical range of this genus, formerly known only from the Mioecene marl (Kirkwood) of New Jersey, southward to central Virginia and South Carolina, and across the Atlantic to Italy. The ages of the formations in which the New Jersey and Virginia specimens were found are currently considered to be the same (middle Miocene), while the age of the South Carolina material is Upper Eocene. The Italian material is Mio-
cene in age. The genus *Procolochelys* thus is probably Eocene to Miocene in occurrence. The genus *Procolochelys* as defined herein consists of three species: (1) *P. grandaeva*, (2) *P. wilsoni*, and (3) *P. melii*.

Order *Chelonia*
Suborder *Cryptodira*
Superfamily *Chelonioidae*
Family *Cheloniidae*
Genus *Procolochelys*

*Type species.*—*Procolochelys grandaeva* Leidy (1851).

*Known distribution.*—Kirkwood Marl (middle Miocene) of New Jersey, Calvert Formation (middle Miocene) of Maryland and Virginia. Cooper Marl (upper Eocene) of South Carolina, “Calcareous” Miocene near Lecce, Italy.

*Diagnosis.*—Carapace shield shaped, elongated anteroposteriorly, moderately flattened, dorsal surface unsulptured. Nutrient foramina are small and exit without prominent channels on the dorsal carapace surface. Most of the neurals are split in two by laterally trending sutures, and some are split by longitudinally (anteroposteriorly) trending sutures as well. Each costal abuts three neural elements because of neural splitting. Neurals and costals are thick to moderately thick, as are peripherals; fontanelles between costals and peripherals apparently persistent throughout life. Vertebral scutes wide so far as known.

*Procolochelys grandaeva* Leidy, 1851

*Procolochelys grandaeva* Leidy, 1851, p. 329.

*Diagnosis.*—Characterized by costals which are quite short and broad, especially toward the posterior end of the shell. Costoperipheral fontanelles are large, even in adults. Plastron strongly reduced, becoming increasingly so with age. Skull more caretine than cheloniine, with the configuration of the basisphenoid-basioccipital suture, cross sectional shape of the posterior projection of the supraoccipital, the close relationship between the exoccipital and opisthotic, and the broad contact between the quadrate and pterygoid all confirming this affinity. Humerus most similar to *Caretta*, with tubercle short and wide, dorsomedial muscle scar round and shallow, and the deltopectoral crest quite prominent and coalesced.

*Type specimen.*—Three isolated neurals in the collections of the Philadelphia Academy of Natural Science.

*Type locality.*—Salem County, New Jersey, from the “Miocene Marl” (Kirkwood).

*Refereed specimens.*—In addition to Princeton material described by Zangerl & Turnbull (1955), five specimens as follows: (1) USNM 24889; carapace including nuchal, neurals 1b, 2a, 2b, 3a, 3b, 4a, 5a, parts of left costals 1–6, right costals 1–6, 8, fragment of suprapygal, first right peripheral; coll. Robert A. Graham and Robert E. Weems; from the western end of the Horsehead Cliffs about five feet above the beach and about one foot below Zone 12; Calvert Formation (middle Miocene). (2) USNM 24888; carapace fragment consisting of neurals 6b, 7a, 7b, 8a, 8b, suprapygal, pygal, left costals 1–8, portions of right costals 5–8, left peripherals 1, 3–9, 11; left hyoplastron, left hypoplastron, left xiphiostracal, left quadrate, basioccipital, right opisthotic, part of left parietal, left humerus, four metacarpals, two phalanges, right ilium, left femur; coll. Albert C. Myrick, Jr., John S. Moses, and Robert E. Weems; eastern portion of Stratford Cliffs, one-half foot above the beach and one foot below Zone 12, Westmoreland County, Virginia; Calvert Formation (middle Miocene). (3) USNM 1184; neural element; coll. R. Lee Collins; found near the Pamunkey River, Virginia; Calvert Formation (middle Miocene). (4) Basicranium consisting of right quadrate, right opisthotic, parts of right and left parietales, supraoccipital, basioccipital, and left exoccipital; coll. D. B. Mackie; from Governors Run, Calvert County, Maryland; Calvert Formation (middle Miocene). (5) PU 19450; fragmentary humerus; coll. Rev. J. E. Peters; from the “marls of New Jersey,” apparently the Kirkwood Formation (middle Miocene).

*Description.*

*Carapace.*—Since the type of this genus and supplementary specimens described previously in all cases consist of portions of the shell, identity for now must be established entirely from the shell and not at all from the skull. The Calvert specimens, fortunately, are sufficiently complete to allow detailed comparison. In USNM 24889 the costals have the same relative proportions as New Jersey specimens of *Procolochelys grandaeva*, the foraminial pattern is similar, and the costoperipheral fontanelles are apparently persistent throughout life (Text–fig. 11). The neurals show a strong tendency to split laterally. Although this specimen does not show any antero-posterior splitting as in two out of three specimens Zangerl & Turnbull described, the lateral splitting causes the costals to abut three neural elements apiece, a very typical feature in *Procolochelys.*
Finally the scute patterning on the carapace is nearly identical in both the New Jersey and Virginia specimens. Since the New Jersey and Virginia deposits probably are equivalent in age, no pronounced differences between the two populations are apparent, and modern cheloniids tend to be monospecific throughout an ocean basin, presumably the Virginia specimens of *Procolpohelys* belong to the same species as the New Jersey specimens. The chief difference between USNM 24889 and the New Jersey specimens is that the Calvert individual only has a total length of about 600 mm (restored), as compared with a length of at least 1100 mm for the New Jersey specimens. This was almost surely because the Calvert individual was immature at death. In the Calvert specimen the nuchal has not fully fused to the first costal, while in contrast costoperipheral fusion in the larger New Jersey specimens reaches to at least the second costal. Thus immaturity is indicated in the Calvert specimen both by its size and its complete lack of costoperipheral suturing.

A second Calvert individual is represented by USNM 24888 (Text-fig. 12). Although parts of the specimen are badly weathered, the portions recovered offer the most complete information about *P. grandaeva* to date. Although only the left portion of the carapace is well preserved, it is sufficient to show that it too is identical in every major respect with the New Jersey specimens.

Only one other Virginia specimen (USNM 1184) can be assigned to the carapace of *Procolpohelys grandaeva*, a neural fragment approximately of adult size found near the Pamunkey River. Although its provenance is given as Eocene, specimens of the Calvert porpoises *Eurhinodelphis* and *Zarhachis* are recorded from the same locality and horizon. Since the color and appearance of the neural fragment also would seem to place it in the Calvert rather than in the Eocene, it is almost surely from the Calvert and is *Procolpohelys*. The ridge along which the neural arch was attached to the neural element is slightly more accentuated than in the one neural preserved in the New Jersey specimens, but seems to be well within the range of variability expectable in *Procolpohelys*. The thickness of the bone is far too great for a water-worn *Sylomus* element, and it is far too regular to belong to *Psophophorus*. 

**Text-fig. 11**—Dorsal view of carapace of *Procolpohelys grandaeva* from the Calvert Formation. Sulci shown as hollow lines. Note anterior half of first neural indents nuchal.

**Text-fig. 12**—Dorsal view of posterior carapace of *Procolpohelys grandaeva* (USNM 24888) from the Calvert Formation.
text-fig. 13—Ventral view of plastron of Procolochelys grandaeva (USNM 24888), an immature individual. Epiplastra and entoplastron inferred from comparable elements in the New Jersey specimens. Xi—xiphiplastra, hypo—hyoplastron, hypo—hyoplastron, epi—epiplastron, ent—entoplastron.

Plastron.—Part of the plastron is preserved with USNM 24888, and allows a reconstruction of the hyoplastra, hypoplastra, and xiphiplastron. This reconstruction (Text-fig. 13) differs from Zangerl & Turnbull's only in the degree to which the inguinal notch is developed. This is surely due to age, since very young specimens of Chelonia mydas have a similarly wide notch which in adult specimens becomes largely obliterated.

Skull.—Part of the left quadrate, the basioccipital, the right opisthotic, and part of the left parietal were found with USNM 24888. By the use of these elements from USNM 24888, an isolated, previously unidentifiable and incorrectly assembled juvenile turtle basi-cranium in the USNM collections (NMNH 186969) can now be assigned to Procolochelys. Skulls of Chelonia, Caretta, Lepidochelys, and Eretmochelys were compared with each other and with the preserved portions of the two Calvert skulls. Careful comparison showed that the opisthotic and quadrate varied considerably among the four living genera, and that the opisthotic and quadrate of the Calvert specimens differed from each other less than the corresponding bones do between any two of the living genera.

The total complex of characters seen in the skull of P. grandaeva suggests affinities with all living genera of cheloniids, though more features seem to be held in common with living carettales than with living cheloniines. In the Procolochelys skulls the basioccipital is largely non-diagnostic in the condylar region, but the nature of attachment to the basisphenoid most resembles that in Chelonia and Lepidochelys. The parietals are poorly preserved. The right parietal does have a nearly straight posterior edge (Pl. 3, fig. 5) which is a juvenile feature in C. mydas but is present in the adult in Eretmochelys. The posterior projection of the supraoccipital is long; it is much thinner dorsally, being teardrop-shaped instead of oval in cross section (Text-fig. 14), thus closely resembling Lepidochelys. The supraoccipital is not dorsally expanded to contribute to the roof of the skull, as it is in all living cheloniids (Deraniyagala, 1939). The supraoccipital border of the foramen magnum is dorsally well rounded, with no ridges or grooves present. The exoccipital has only limited contact with the supraoccipital, being mostly sutured to, and sharply indenting, the opisthotic to even a greater extent than in Lepidochelys, the only living cheloniid to show this condition. The opisthotic is relatively long and attaches broadly to the quadrate. It terminates laterally in a sharp angle such as is found in Lepidochelys and Caretta but not Chelonia and Eretmochelys; the latter two have a distally rounded contact instead. The exoccipital spreads well along the side of the condylar edge of the basioccipital, but even so it is apparently a minor contributor to the condylar element. The quadrate shows a rugose area which marks the area of attachment of the pterygoid. This area extends well up the side of the quadrate, nearly to the articular surface. This condition is reminiscent of Caretta and Lepidochelys, but not of Chelonia or Eretmochelys.

Forelimb.—The humerus of Procolochelys is most similar to the humerus of Caretta in the length of the tubercle and the shape of the dorso-medial muscle scar, and least resembles the humerus of Chelonia among the four modern genera of cheloniids. The tubercle is short and rather wide, the dorso-medial muscle scar is round and shallow. The deltopectoral crest is quite prominent and coalesced. Distally the bone is sharply angled and exhibits a large area for ligamentous attachment to the radius and ulna. In overall appearance it is a very normal cheloniid humerus (Pl. 5, fig. 4,6).

The entire first digit and parts of three
metacarpals are also preserved. Only the first digit bears comment (Pl. 1, fig. 4). The metacarpal is large and quite normal except for a prominent spur on its proximal external border. The two phalanges are large and typical. A comparable development of this digit is seen in modern cheloniiids, where this digit, along with the second, has a claw. It is therefore probable that at least the first digit of *P. grandaeva* also had a prominent claw, and possibly the second digit as well.

*Pelvic girdle.*—Only the right ilium is well

**Explanation of Plate 4**

1—Posterior portion of carapace of *Syllomus aegyptiacus* Lydekker (USNM 24871), showing a separate ninth costal and a sixth vertebral scute outlined by sulci (darkened for contrast), ×0.33.
2—Right humerus of *Procolpochelys grandaeva* Leidy (PU 19450), internal (ventral) view. Note relatively longer lateral tubercle and greater width of distal end than in the humerus shown in Plate 5, figure 6, indicating the greater age of this individual, ×0.66.
3—Proximal portion of scapula (glenoid cavity facing down) of *Psophorus calvertensis* Palmer (USNM 9349), ×0.66.
4—Male sacrum of *Syllomus aegyptiacus* Lydekker (USNM 24870), with first caudal fused to sacrum (bottom). Note the relatively robust proportions compared to the specimen shown in figure 5, ×1.0.
5—Female sacrum of *Syllomus aegyptiacus* Lydekker (AMNH 1661), showing slightly different and less robust proportions than seen in the specimen of figure 4, ×1.0.
preserved. It is very similar to the corresponding ilium of modern chelonians, being rather short and robust (Pl. 5, fig. 5).

Hind limb.—The femur is less generalized than the femur of *Syllomus*. The trochanter major and caput are nearly of equal height, with the trochanter minor much lower than either of these (Pl. 5, fig. 7). Distally the femur is not well preserved, but appears nevertheless to be rather rounded and diminutive. Probably *Procolochelys* made only limited use of its hind limbs except as flippers.

**PATHOLOGY**

Since the two most complete Calvert specimens of *P. grandaeua* are immature, pathological conditions should not be expected to be as well developed as in adults which have been exposed to the hazards of life longer. Nevertheless, the lack of any epizoan pits as seen in *Syllomus* is probably significant. Only one abnormal condition in the specimens of *P. grandaeua* could be discerned, a shallow elliptical or nearly circular depression on the carapace of USNM 24889, located on the third and fourth right costals, about 2.5 cm in diameter. The shape and size is remarkably similar to the basal configuration of small specimens of *Balanus concaucus*. Possibly a barnacle of this species attached tightly to a scute of USNM 24889 and caused a slight constraint in the normal development of the turtle's carapace. Modern chelonians often are found with attached barnacles, so similar encrustations should be expected to have occurred in the past as well.

**Procolochelys Wilsoni** Hay, 1923
*Carinolochelys wilsoni* Hay, 1923, p. 119.

**Diagnosis.**—According to Hay (1923): Skull moderately prolonged in front; choanae opening on a line joining the fronts of the orbits; palatal plate of vomer with a ridge on each side; palate with two parallel sharp masticatory ridges on each side, one on the maxilla, the other on the palate, and continued forward on the vomer. Pterygoids narrow and without lateral processes. Interparietal shield prolonged backward, as in the genus *Argillochelys*. The upper surface of the skull is minutely sculptured. Frontal shield is short and broad, the interparietal shield is prolonged backward to, or nearly to, the supraoccipital spine. Over the orbits and meeting at the middle of its border are two large supra-orbital shields. Nostrils were narrow and high; the prefrontals meet along the mid-line a distance of 19 mm. The outer border of each frontal forms a part of the edge of the orbit. The squamosal appears to have joined the parietal a distance of about 20 mm.

Humerus has a shallow groove on each face of the great median process, while the process for the supracoracoide muscle (the radial process) is a rough irregular tuberosity. The shaft of the humerus of *P. wilsoni* is bent downward more than in *Chelonia* and much like that seen in *Caretta*.

**Type specimen.**—MCZ 1005 A + B (Museum of Comparative Zoology at Harvard), an essentially complete skull and a humerus.

**Type locality.**—Hay was unclear about the provenance of the type specimen of this species. Fortunately, however, Donald Baird has located the original label with the type specimen. According to him (personal communication to R. Zangerl, 1964), the specimen came from the commercial marl pits at Ingleside, Berkeley County, 14 miles northwest of Charleston, South Carolina. This marl, called locally "Ingleside Marv," is part of the Cooper Marl of late Eocene (latest Jackson) age.

**Discussion.**—The isolated basicranium (NMNH 186969) and the skull fragments and humerus of USNM 24889 are very similar to
the corresponding elements of *Carolinochelys wilsoni* Hay (1923). The skulls, where comparison can be made, are completely comparable except for the degree of encroachment of the pterygoid upon the anterior border of the quadrate. This difference, while possibly valid, also may be due to a slight acceleration of growth along the anterior border of the quadrate toward maturity or to postmortem wear in the Calvert skulls. Either possibility could easily account for the difference.

An adult chelonid humerus from the Miocene of New Jersey (PU 19450), because of its similarity to the humerus of USNM 24889, seems clearly referable to *P. grandaecva* (Pl. 4, fig. 2). It differs from USNM 24889 only in a greater length of the lateral tubercle and a larger proportionate width at its distal end (comparable to the growth changes noticeable in the humerus of *Syllosaurus*). PU 19450 also resembles closely the humerus assigned to *C. wilsoni* (Pl. 5, fig. 3) in coalescence of the deltopectoral crest, length of the lateral tubercle, distal angularity, and large distal area for ligamentous attachment. The rounded dorso-medial muscle scar in *C. wilsoni* is nearly the same shape as that in the juvenile *P. grandaecva* humerus. Thus there seems to be no significant difference between *P. grandaecva* and *C. wilsoni* insofar as they are comparable.

More complete remains of *C. wilsoni* may show discrete specific differences which will distinguish it from *P. grandaecva*, and the difference in age of the two putative species makes this likely. Even so it is extremely unlikely that any such differences will prove to be of generic significance. Therefore the name *Carolinochelys* seems to be synonymous with *Procolopoclythus*. The latter name is the older and therefore the correct generic name to be applied to both species.

**Procolopoclythus melii** Misuri, 1910


**Diagnosis.**—Characterized by neurals which are narrower than in *P. grandaecva*, costals which are relatively much longer and narrower than the costals of *P. grandaecva*, and costoperalpheral fontanelles which are considerably smaller than those in *P. grandaecva*.

**Type specimen.**—Essentially complete carapace.

**Type locality.**—Near Lecce, southern Italy, from the “calcareous” Miocene.

**Discussion.**—Zangerl & Turnbull (1955) noted a similarity and close relationship between “*Euclastes* melii” Misuri and *P. grand-
aeva. The chief features which separated the two seemed to be the presence in "E" melii of a supernumerary neural element indenting the nuchal (a feature unknown in their New Jersey specimens), narrower neural elements, and longer and narrower costals. However, the first Calvert specimen (USNM 24889) has the first neural element indenting the nuchal (Text-fig. 11). Slight expansion and splitting of this element easily would produce the condition in "E". melii. This leaves the narrower neurals and wider costals as the chief distinguishing features of "E." melii (Text-fig. 15). While a valid specific difference, this seems less important than the difference between any other well known cheloniid genera. Therefore, it is proposed that "E." melii be placed in the genus Procolopchelys as Procolopchelys melii. This avoids an improper use of "Euclastes" and emphasizes the fact that melii and grandaeva seem more closely related than any other post-Oligocene cheloniids currently known.

Order Chelonia
Suborder Cryptodira
Superfamily Dermocheloidea
Family Dermochelyidae
Genus Psephophorus

Type species.—Psephophorus polygonus von Meyer (1847).

Known distribution.—Probably cosmopolitan in Tertiary marine strata except in polar regions.

Diagnosis.—Shell composed of irregularly arranged circular to polygonal bony platelets forming a continuous mosaic over the dorsal and ventral portions of the body. Bone material is dense. Dorsal shell has one or more keels made of rows of thickened platelets. Platelet rows may be one platelet wide to several platelets wide.

Psephophorus calvertensis Palmer, 1908

Psephophorus calvertensis PALMER, 1908, p. 369–373.

Diagnosis.—Carapace composed of numerous, thick bony platelets, mostly large; slightly, or not at all, sculptured on the dorsal surface and generally longer than broad. One strong and prominent median, straight, longitudinal ridge, and several, perhaps six, minor parallel ridges, or thickenings of the plates. Minor ridges but slightly raised above the adjoining plates and seemingly decreasing in height according to their distance from the more pronounced median ridge. Plates of the ridges about twice as long as wide, the ridge slopes covering the whole surface of the plates and extending over adjoining ones; not confined to the central portions of the ridge-plates as in P. polygonus and Dermochelys coriacea. Transverse sutures generally narrower than the longitudinal sutures, and sometimes ankylosed. Plates usually very close fitting below, almost or quite ankylosed. Under surface quite uneven, having somewhat the appearance of wet clay which has been touched by the fingers; usually with a small pit near the center. Plates of the outer and posterior edges much smaller and thinner than the others, and very similar to those of D. coriacea. Plates of the plastron quite thick and smooth, with well-rounded outlines, those of the edge forming an undulating line.

Type specimen.—USNM 6059 in the collection of the United States National Museum (Smithsonian Institution). Polygonal platelets from the carapace and a neural arch from a dorsal vertebra; coll. William Palmer and David B. Mackie.

Type locality.—Probably Zone 10 of the Calvert Formation, middle Miocene, Calvert Cliffs, Calvert County, Maryland.

Referred specimen.—USNM 9349; fragmentary scapula with both scapular rods broken off; Miocene of Maryland.

Since the type specimen of Psephophorus calvertensis Palmer (USNM 6059) was discovered and described, no significant new material has been collected. Isolated polygonal platelets occasionally are found along the Calvert Cliffs where Zone 10 is exposed, the zone from which the type seems to have come (Collins & Lynn, 1936), but no intact specimen has been reported. The only addition which can be made to the currently scant knowledge of this turtle is a proximal fragment of a scapula, described as belonging to Chelone, species uncertain (Case, 1902). The fact, however, that the scapular rods diverge almost directly above the glenoid cavity (Pl. 4, fig. 3), while in cheloniids the scapular rods diverge well above the glenoid cavity (Text-fig. 8), indicates that this bone is from a dermochelyid. Until evidence is found that more than one dermochelyid is present in the Maryland Miocene, this specimen should be assigned to P. calvertensis.

Although P. calvertensis is clearly a dermochelyid (Pl. 5, figs. 1,2), its taxonomic position within that family is obscure. With very few exceptions (e.g., Packard, 1940), species of Psephophorus have been based almost ex-
clusively on patches of carapace and plastron platelets, none extensive enough to indicate the shape of the shell. As a result, this single genus includes most dermochelyid material ranging from Eocene to Pliocene in age. Skull and limb material appear to be the most valid means for distinguishing genera in this family, so a thorough review of the taxonomy of P. calvertensis must await more complete material. Therefore the name Psophophorus calvertensis is retained unchanged as a matter of convenience until meaningful re-evaluation is possible.

At present all that can be said about P. calvertensis is that probably it was strongly or completely pelagic and that it was probably the largest marine turtle in the Calvert fauna. A rough size estimate can be made based upon (1) Palmer's statement that the type of P. calvertensis was four feet wide when seen in cross section in the cliff before collection and (2) upon the size of the one neural arch preserved with the type. Judging from these, a full shell may well have been six feet long (1.8 meters). This would easily surpass the length of an adult Procolochelys shell (about four feet or 1.2 meters), and greatly surpass the length of a Syllomus shell (about 2.5 feet or 0.8 meters).

THE STATUS OF CHELONIA (CHELONE) IN THE CALVERT FORMATION

Since a number of authors have applied the generic name Chelonia (Chelone) to a wide variety of Calvert chelonian material, it seems best to review the status of this genus in the Calvert Formation. Chelonia marylandica, shown in this paper to be a synonym for Syllomus aegyptiacus, is clearly not a valid addition to the genus Chelonia. The scapula described by Case (1902) as Chelone sp. was shown in this paper to belong to a dermochelyid. Besides these previously discussed cases, there are two specimens Cope (1867) assigned to Chelone sp. Cope placed these specimens in the Philadelphia Academy of Natural Science collections, but apparently they were misplaced (Hay, 1908). Since direct observations are precluded, conclusions can only be based on Cope's descriptions. According to him, both sets of material came from near the Patuxent River in Charles County, Maryland. One was described as "a proximal portion of the costal plate which has a thickness of three lines, but rapidly thins out. Its surface exhibits transverse rugae at its proximal extremity, elsewhere the rugae are longi-tudinal, and more distinct on one side than on the other." The second consisted of "two fragments of the carapace of a large and convex species, each with a strongly marked groove for the margin of the dermal shields. The surface is without sculpture." In view of these descriptions, plus the fact that Cope did not describe and name "Syllomus crispatus" until almost twenty years later, it seems probable that the first fragment pertains to Syllomus aegyptiacus. The latter description is indeterminate, but in the absence of any other material which can be assigned even questionably to Chelonia, assignment to Procolochelys seems more reasonable. Thus there currently seems to be no solid evidence to suggest the presence of Chelonia in the Calvert Formation.

SUMMARY

Recent collecting has brought to light enough new specimens of Calvert sea turtles to allow a thorough review of the previously established taxa and to allow recognition of one previously unrecognized taxon. As a result of this review, three taxa are now recognized: Syllomus aegyptiacus, Procolochelys grandaeva, and Psophophorus calvertensis. Most specimens are referable to Syllomus aegyptiacus (including the types of Syllomus crispatus, Peritresius virginianus, and Chelonia marylandica). S. aegyptiacus apparently was cosmopolitan in distribution, since the type specimens of Trachyaspis aegyptiaca and Kurobeckelys tricarinata are also referable to this species. Procolochelys grandaeva, known previously from the Kirkwood of New Jersey, has not been recognized previously from the Calvert. The skull and limb material of the Calvert P. grandaeva specimens suggests Carolinocelys wilsonei is at least generically identical with Procolochelys, while the diversity in carapaces of P. grandaeva suggests "Euclastes" melii is also a generic equivalent of Procolochelys. Thus the genus Procolochelys is here considered to contain three species: P. grandaeva, P. wilsonei, and P. melii. No new material has been added to the sparse collection of Psophophorus calvertensis, though a scapula in the United States National Museum collections previously labelled "Chelone" has been assigned to P. calvertensis. Chelonia (Chelone), a name applied in the last century to a number of Calvert turtle remains, has in no case proved to be validly applied. This genus does not seem to have been present during Calvert deposition.
REFERENCES


Manuscript received January 17, 1973