Chapter 26

Phosphatochelys, a New Side-Necked Turtle (Pelomedusoides: Bothremydidae) from the Paleocene of Morocco

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ABSTRACT

The late Paleocene phosphates of the Ouled Abdoun Basin in Morocco have yielded the skull of a new genus and species of side-necked turtle, *Phosphatochelys tedfordi*. *Phosphatochelys* is a pelomedusoid pleurodire belonging to the Family Bothremydidae Baur, 1891, based on these characters: (1) precolumellar fossa absent, (2) condylus occipitalis consisting only of exoccipitals, (3) foramen stapedio-temporale not visible in dorsal view and very close to foramen nervi trigemini, (4) eustachian tube and stapes separated by bone, (5) incisura columellae auris closed, and (6) exoccipital contacts quadrate. Within the Bothremydidae, *Phosphatochelys* is a member of the group containing *Azabbaremys*, *Taphrosphys*, *Nigeremys*, and *Arenila*, because it has a dorsally arched palate and an open postorbital wall.

INTRODUCTION

First recognized as a group of extinct side-necked turtles in 1891 by George Baur on the basis of the skull of *Bothremys cooki* Leidy, 1865, the Bothremydidae is now thought to consist of more than a dozen skull-based genera, over half still undescribed. The purpose of this paper is to name and describe a new bothremydid that is represented by a nearly complete skull.

The Bothremydidae extend from the Early Cretaceous to the Miocene and are found on all the continents except Antarctica and Australia. Bothremydids ranged in size from less than 1 ft to more than 5 ft in length. Throughout their record, bothremydids occur as fossils in nearshore marine sediments as well as terrestrial, fresh water units. Bothremydid cranial diversity also supports the developing reinterpretation of pleurodire history as a widespread, relatively diverse group adapted to many ecologies rather than a conservative group occupying a few restricted niches. The original misconception arose from the fact that the more commonly preserved shells are unusually conservative in pelomedusoids when compared with the skull.

Although Bothremydidae was named as early as 1891 by George Baur, the term fell into disuse for most of the 20th century and the few included taxa, particularly *Bothremys* and *Taphrosphys*, were simply included in the Pelomedusidae. Broin in Antunes and Broin (1988) and Broin (1988) revived Bothremydidae, provided a new diagnosis and added taxa, such as *Rosasia*, based on skulls. Recent papers on fossil pleurodires such as Meylan (1996), Lapparent de Broin and Werner (1998), and Tong et al. (1998) use the Antunes and Broin (1988) terminology in which Bothremydidae, Podocnemididae, and Pelomedusidae (restricted to *Pelusios* and *Pelomedusa*) are contained in the Pelomedusoides (which equals Pelomedusidae in the classic sense). Bothremydids are now rec-

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ognized as a more distinctive, widespread, and diverse group than previously considered.

Useful reviews of the literature on bothremydids can be found in Broin (1988) and Antunes and Broin (1988). Information in varying degrees of completeness on previously described bothremydid skulls are as follows: *Bothremys* (Gaffney and Zangerl, 1968; Gaffney, 1977), *Taphrosphys* (Gaffney, 1975), *Rosasia* (Antunes and Broin, 1988), *Foxemys* (Tong et al., 1998), *Zolhafah* (Lapparent de Broin and Werner, 1998), *Arenila* (Lapparent de Broin and Werner, 1998), *Nigeremys* (Bergounioux and Crouzel, 1968; Lapparent de Broin and Werner, 1998), *Kurmademys* (Gaffney et al., 2001b), *Azabbaremys* (Gaffney et al., 2001c), and *Cearachelys* (Gaffney et al., 2001a). Other pelomedusoid skulls are *Araripemys* (Meylan, 1996), *Hamadachelys* (Tong and Buffetaut, 1996), and an unnamed Santana genus (represented by FR 4922; Gaffney and Meylan, 1991). A general treatment and description of pleurodire skulls, turtle skull morphology and terminology, and a literature review is in Gaffney (1979).

We use Lapparent de Broin and Werner's (1998) reference to a *Bothremys* Group and a *Nigeremys* Group (which includes *Taphrosphys* in our usage), as these continue to form monophyletic taxa in most of our current analyses. Our contents of these groups are as follows: *Bothremys* Group—*Bothremys*, *Rosasia*, *Zolhafah*, *Foxemys*; *Nigeremys* Group—*Nigeremys*, *Arenila*, *Taphrosphys*. In our current phylogenetic analyses, *Phosphatochelys* consistently is in the *Nigeremys* Group; therefore we compare it with taxa in this group, particularly its best-known member, *Azabbaremys* (Gaffney et al., 2001c).

Phosphatochelys was found in the Moroccan phosphate deposits in the Ouled Abdoun Basin. The Ouled Abdoun phosphate is located about 100 km southeast of Casablanca, Morocco. The fossiliferous deposits range in age from the Maastrichtian to the Ypresian (Late Cretaceous to Early Eocene; Arambourg, 1952; Noubhani and Cappetta, 1997). The rich turtle fauna collected recently from the Ouled Abdoun phosphate basin include pleurodires (bothremydids) and cryptodires (chelonioids; Karl et al., 1998). Other vertebrate remains include selachians (Arambourg, 1952; Noubhani and Cappetta, 1997), fishes (Cavin et al., 2000), crocodiles (Buffetaut and Wouters, 1979), plesiosaurs and mosasaurs (Arambourg, 1952), and mammals (Gheerbrant et al., 1996, 1998).

Institutional Abbreviations

AMNH	American Museum of Natural History
BMNH	British Museum of Natural History
FR	Forschungsinstitut Senckenburg, Frankfurt, Germany

Anatomical Abbreviations

bo	basioccipital
bs	basisphenoid
epi	epipterygoid
ex	exoccipital
fr	frontal
ju	jugal
mx	maxilla
na	nasal
op	opisthotic
pa	parietal
pal	palatine
pf	prefrontal
pm	premaxilla
po	postorbital
pr	prootic
pt	pterygoid
qj	quadratojugal
qu	quadrate
so	supraoccipital
sq	squamosal
vo	vomer

SYSTEMATICS

Order Testudines Linnaeus, 1758

Megaorder Pleurodira Cope, 1864

Hyperfamily Pelomedusoides Cope, 1868

Family Bothremydidae Baur, 1891

***Phosphatochelys*, new genus**

Type Species: *Phosphatochelys tedfordi*, new species.

Distribution: Paleocene of Morocco.

Etymology: Allusion to the phosphatic sediments in which the skull was found.

Diagnosis: A member of the Bothremydidae known only from the skull; skull small as in *Taphrosphys* and *Bothremys*, not large as in *Arenila*, *Azabbaremys*, and *Nigeremys*; orbits facing anterolaterally as in *Azabbaremys*

not dorsally; preorbital part of skull very short, shorter than in *Azabbaremys* and *Taphrosphys*; prefrontal larger than in other bothremydids; prefrontal-parietal contact present in contrast to all other turtles; jugal-quadrate contact present as in *Azabbaremys*; postorbital wall open as in *Azabbaremys* and *Taphrosphys*; postorbital very short in contrast to *Azabbaremys*; quadratojugal-parietal contact present as in *Taphrosphys* but absent in all other bothremydids; premaxilla short as in *Azabbaremys* in contrast to long as in *Arenila* and *Nigeremys*; labial ridge deeper than in any other bothremydid; maxillary triturating surface parallel sided as in *Azabbaremys*, not triangular as in *Bothremys* Group; maxilla-quadrate separated only by a narrow cheek emargination; palate strongly arched as in *Azabbaremys*; palatine not exposed extensively on triturating surface; antrum postoticum moderate in size not absent as in *Azabbaremys*; pterygoideus muscle attachment area flat not concave; anterolaterally facing trough developed on pterygoid, parietal, and quadrate extending anterior for foramen nervi trigemini ventrolaterally to condylus mandibularis unique to this taxon; foramen posterius canalis carotici interni formed by pterygoid and quadrate; supraoccipital-quadrate contact seen in *Bothremys* absent; foramen stapedio-temporale on anterior surface of otic chamber close to foramen nervi trigemini and not visible in dorsal view.

Phosphatochelys tedfordi, new species

TYPE SPECIMEN: AMNH 30008, complete skull without lower jaws. Gift from François Escuillié who purchased the specimen in France.

TYPE LOCALITY: Oued Zem, Ouled Abdoun Basin, Morocco.

HORIZON: Thanetian phosphates, late Paleocene. The skull has been dated by shark teeth included in the surrounding matrix which indicate Thanetian age (Cappetta, personal commun.).

DIAGNOSIS: Same as for genus.

ETYMOLOGY: For Dr. Richard H. Tedford, in recognition of his lifelong contributions to vertebrate paleontology in general and to the American Museum of Natural History in particular.

DESCRIPTION

The type skull of *Phosphatochelys tedfordi*, AMNH 30008 (figs. 26.1, 26.2), has a premaxilla-condyle median length of 68.0 mm, a maximum width of 69.0 mm, and a height from condylus mandibularis of the quadrate to the top of the skull roof of 47.5 mm.

PREFRONTAL

Both prefrontals in AMNH 30008 are present and nearly complete with clear sutures. A small amount of the ventral process seems to be broken on both sides. The left prefrontal is completely clear of matrix but the right has some matrix on its ventral surface.

The prefrontal in *Phosphatochelys* is a relatively large element, larger even than in *Azabbaremys* and much larger than in pelomedusids and *Araripemys*. The prefrontal forms a distinct, anterior process on its ventral surface.

The contacts of the prefrontal in *Phosphatochelys* are with the maxilla anterolaterally, the frontal posteromedially, the parietal posterolaterally, and with the other prefrontal anteromedially. The parietal-prefrontal contact of *Phosphatochelys* is unusual and, in fact, unique among pleurodires and cryptodires. It is not even approached by any other bothremydid, which generally have large prefrontals. Unlike most pelomedusids in which the prefrontals meet on the midline for their entire length, *Phosphatochelys* has a midline length much shorter than its maximum length. The suture with the frontal is strongly convex anteriorly, quite different from the straight suture in *Azabbaremys* and other bothremydids. The median prefrontal contact length is less than the total prefrontal length, as in chelids, *Araripemys*, and FR 4922. This may be a primitive condition; however, its absence in *Azabbaremys* and other close relatives of *Phosphatochelys* makes this unlikely. The prefrontal in *Azabbaremys* has a distinct, anterior projection slightly subdividing the apertura narium externus.

Because of its large size and thickness, the prefrontal in *Azabbaremys* forms much of the roof of the fossa nasalis and fossa orbitalis. On the ventral surface, the prefrontal con-

tacts the parietal. The frontal is not exposed on the ventral surface. The ventral process of the prefrontal contacts the dorsal process of the maxilla as in other pelomedusoides. This contact area is quite narrow in *Phosphatochelys* in contrast to the broad contact in *Azabbaremys*. The entire snout area of *Phosphatochelys* is telescoped in comparison to *Azabbaremys*.

FRONTAL

Both frontals are present and complete with clear sutures. The frontal in *Phosphatochelys* is very unusual for pleurodires. It is small in size, widely separated from the orbital margin, and not exposed on the ventral surface in the cavum cranii. The frontal contacts the prefrontal anterolaterally, the parietal posterolaterally, and the other frontal medially.

PARIETAL

Both parietals are nearly complete, but some of the ventral surface is damaged or covered by matrix.

The dorsal plate of the parietal is large as in *Azabbaremys*, but it is nearly rectangular rather than an irregular quadrangle. It contacts the frontal anteromedially and the prefrontal anterolaterally. As mentioned (see Prefrontal), the broad prefrontal contact is unique among pleurodires and cryptodires. Also unique among pleurodires is the exposure of the parietal in the margin of the orbit. This condition is not approached by any other pleurodire or cryptodire. Laterally the parietal contacts the postorbital anteriorly and the quadratojugal posteriorly. The quadratojugal-parietal contact only occurs in *Phosphatochelys* and *Taphrosphys* among the Bothremydidae. Although it also occurs in FR 4922 and Podocnemididae, (including *Hamadachelys*), it seems to be an independent acquisition within the *Taphrosphys* Group of the Bothremydidae.

The posterior margin of the parietal along with the quadratojugal forms the posterior limits of the posterior temporal emargination. The temporal emargination in *Phosphatochelys* is not different in extent from *Azabbaremys*, but the margin in *Phosphatochelys* is transverse, while in *Azabbaremys* it is also straight but trends anterolaterally from the midline. This transverse edge is unique in Bothremydidae but a number of taxa (*Rosasia*, *Arenila*, *Zolhafah*) are incompletely known in the skull roof.

The processus inferior parietalis in *Phosphatochelys*, exposed only on the left side, is very thin as in *Azabbaremys* and enters the foramen nervi trigemini also as in *Azabbaremys*. The processus inferior parietalis contacts the pterygoid ventrally from the foramen interorbitale anteriorly to the foramen nervi trigemini posteriorly. The parietal also sends a process ventrally on the lateral side of the sulcus pterygopalatinus (Antunes and de Broin, 1988), which contacts the palatine anteriorly and the pterygoid posteriorly. This process as well as an enclosed sulcus pterygopalatinus is absent in *Azabbaremys*. As in *Azabbaremys*, the foramen interorbitale of *Phosphatochelys* is relatively small compared with other pelomedusoids. Posteriorly the parietal contacts the supraoccipital in a nearly vertical suture above the prootic contact.

JUGAL

Neither jugal is complete, but the left one is missing only part of its posterior edge.

The jugal of *Phosphatochelys* is widely exposed in the posteroventral margin of the fossa orbitalis, contacting the postorbital dorsally and the maxilla ventrally, all as in *Azabbaremys*. In *Phosphatochelys*, however, there appears to be a free posterior edge along the margin of the left jugal, indicating a cheek emargination. The right jugal is damaged posteriorly in this area. On the right side, the quadrate and maxilla meet. This may be due to postmortem distortion, and the rest of the skull also supports this interpretation. It seems likely then, that there was a narrow cheek emargination, as shown in the restored lateral view (fig. 26.3) with part of the jugal exposed on the margin of the emargination. Nonetheless, the dorsal placement of the quadratojugal and the close approximation of quadrate and maxilla is similar to *Azabbaremys*.

The medial process of the jugal is best preserved on the right side. It is barely visible in ventral view and does not extend onto the triturating surface. The posterior wall of the

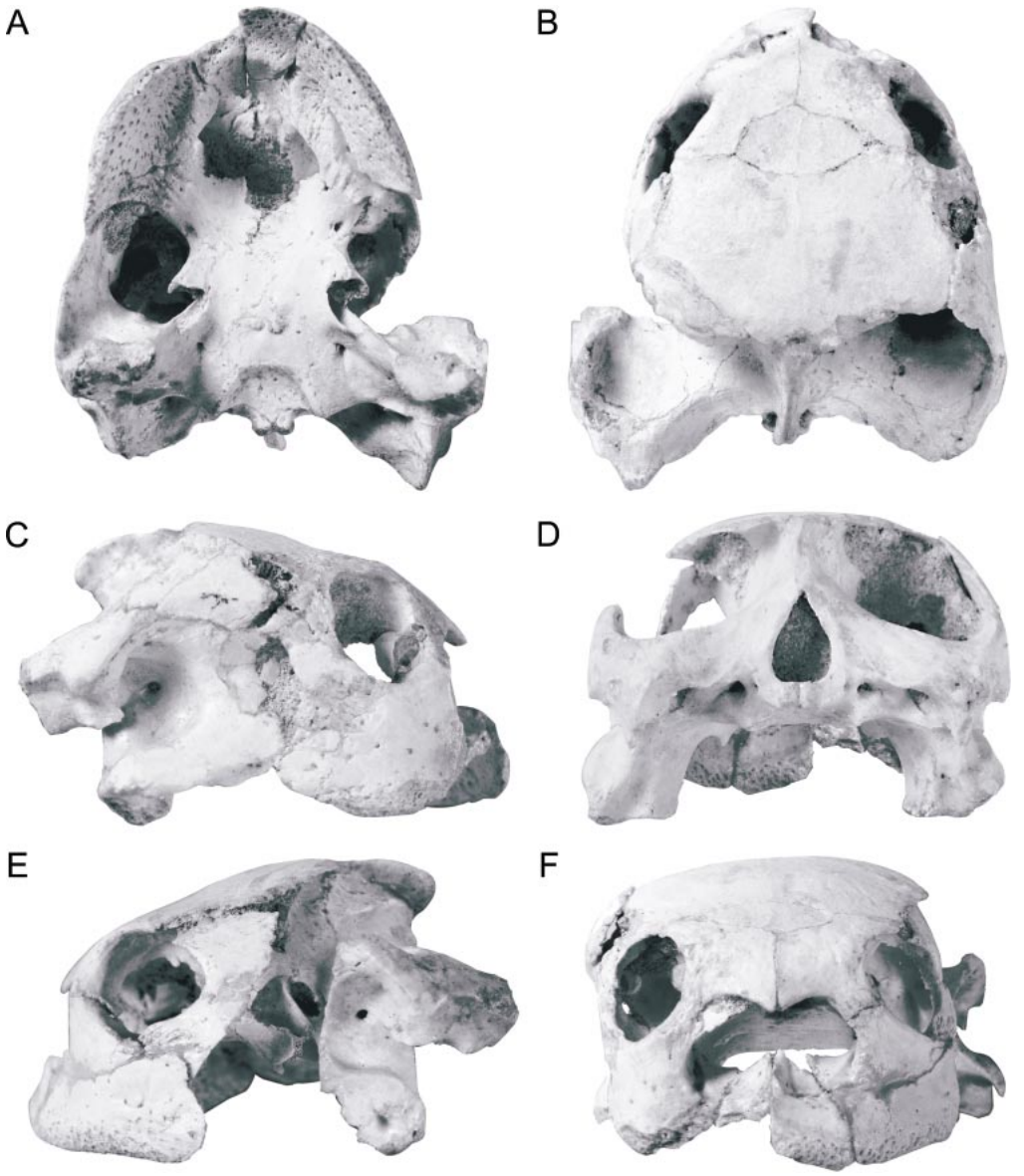

Fig. 26.1. *Phosphatochelys tedfordi*, n. gen. and n. sp., AMNH 30008, Phosphates of Oued Zem, Ouled Abdoun Basin, Thanetian, late Paleocene, Morocco. Skull: **A,** ventral view; **B,** dorsal view; **C,** right lateral view; **D,** occipital view; **E,** left lateral view; **F,** anterior view.

orbit is absent as in *Azabbaremys*, so the jugal has only a ventromedial process that reaches the maxilla and palatine in the orbital floor.

QUADRATOJUGAL

The quadratojugal in AMNH 30008 is present only on the right side. The quadratojugal is complete except along its anterior margin where some of its edge has been eroded.

In most turtles the quadratojugal is a large C-shaped element lying along the anterior margin of the quadrate on the cheek. This is the case in bothremydids like *Foxemys*, but in *Azabbaremys* and *Phosphatochelys*, the

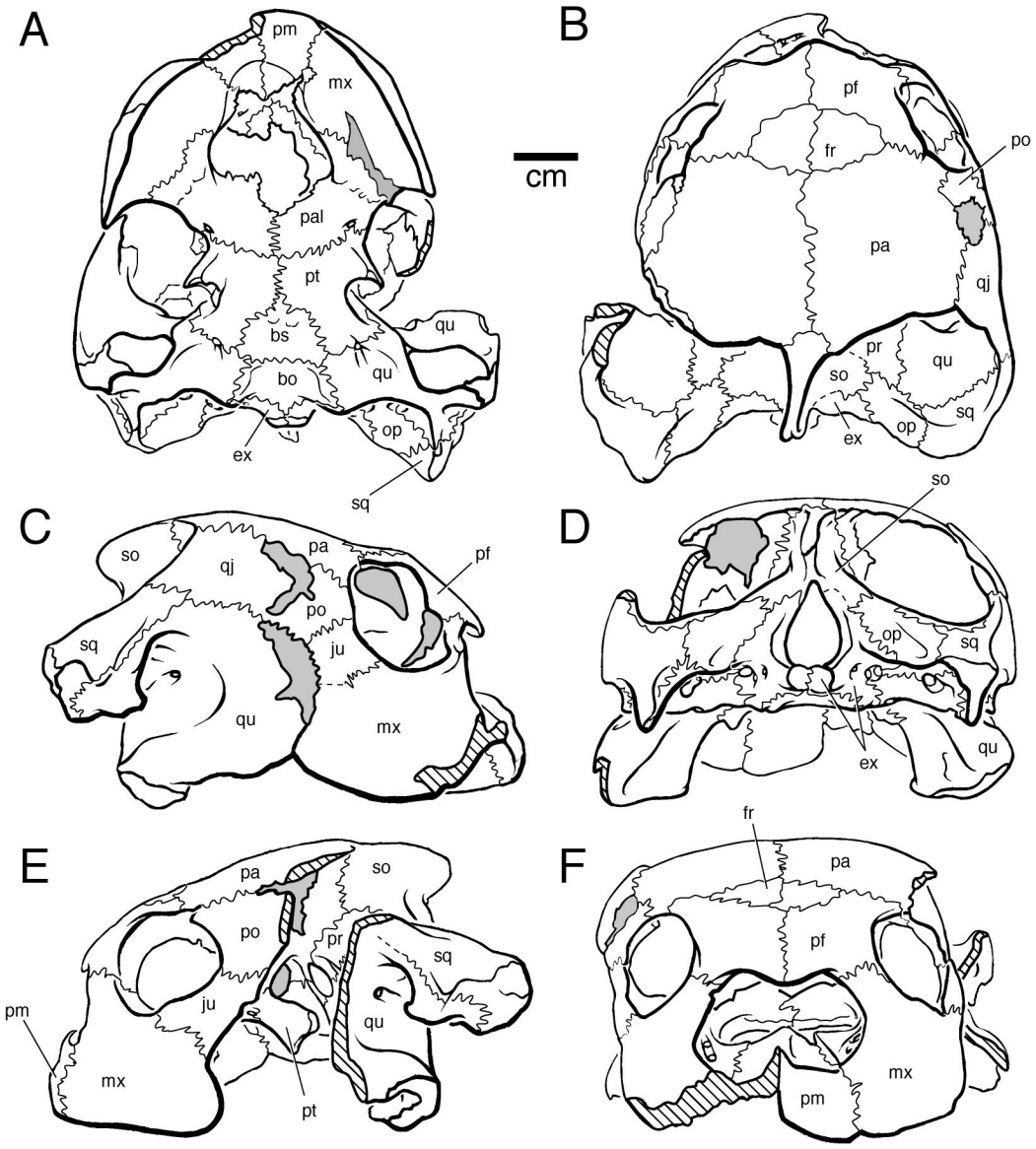

Fig. 26.2. *Phosphatochelys tedfordi*, n. gen. and n. sp., AMNH 30008, key to fig. 26.1.

quadratojugal lies well above the main body of the quadrate and there is a jugal-quadrate contact. *Azabbaremys* and *Phosphatochelys* differ, however, in the shape and position of the postorbital. In *Phosphatochelys* the postorbital is small and lies anterior to the quadratojugal, while in *Azabbaremys* it is large and lies above the quadratojugal.

The quadratojugal in *Phosphatochelys* contacts the parietal medially, the postorbital anteriorly, the quadrate ventrolaterally, and the squamosal posteroventrally. The area of the postorbital contact is damaged, but the fact of the contact is not doubtful. A quadratojugal-parietal contact also occurs in the podocnemidids *Erymnochelys* and *Peltocephalus*, but among bothremydids it is definitely known only in *Taphrosphys*. In *Taphrosphys*, the quadratojugal is more extensive ventrally, but whether or not a jugal-quadrate

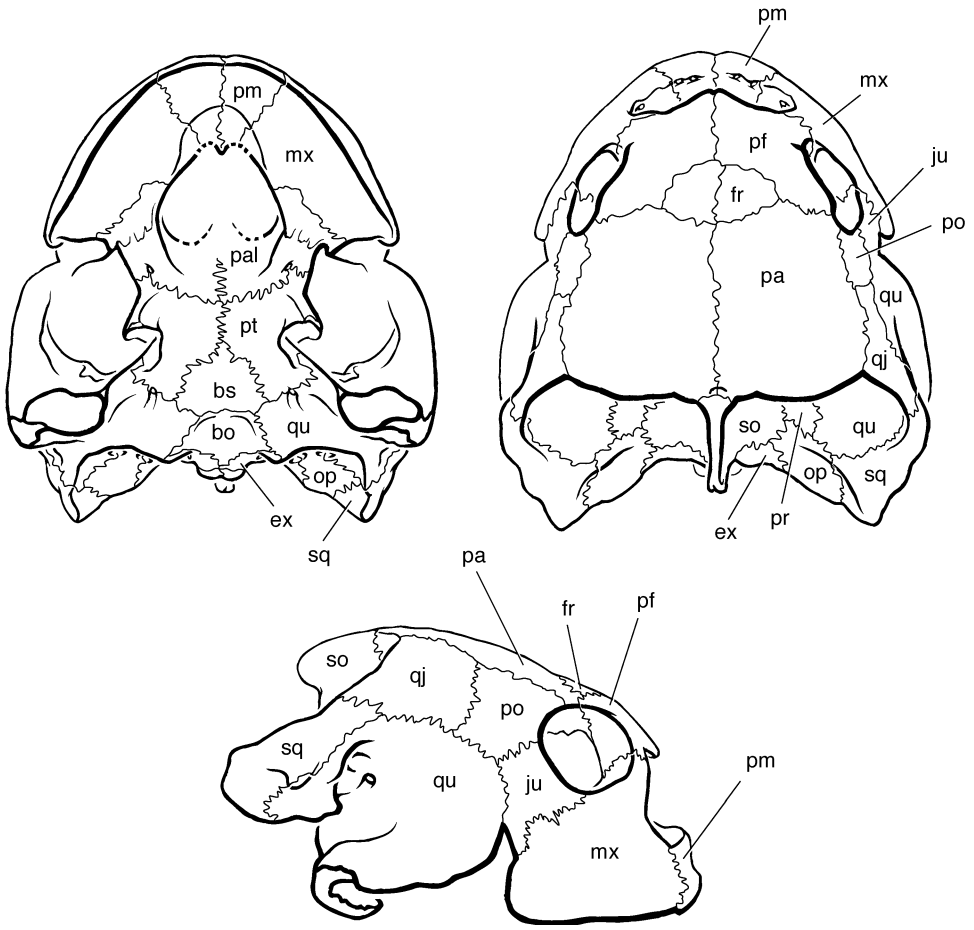

Fig. 26.3. *Phosphatochelys tedfordi*, n. gen. and n. sp., restored line drawings of skull.

contact is present is unknown so far. It is the pattern of a dorsally placed quadratojugal seen in such bothremydids as *Taphrosphys*, *Phosphatochelys*, *Azabbaremys*, and some undescribed species that argues for the identification of this bone as a quadratojugal.

Squamosal

Both squamosals are present, the right one is complete, the left one lacks some of its anterior process. The squamosal in AMNH 30008 is the usual cone-shaped element lying on the posterolateral corner of the quadrate. It contacts the opisthotic medially on the dorsal, medial, and ventral surfaces. A short process of the squamosal contacts the quadratojugal along the lateral edge of the temporal embayment as in *Azabbaremys*. In *Phosphatochelys*, there is a ventral, parasagittal flange or process extending from the posteroventral part of the bone. This is absent in *Azabbaremys*, but occurs in *Taphrosphys*.

Postorbital

The postorbital is present on both sides of AMNH 30008. The left one is nearly complete, only some of its posterior edge is damaged, but the right postorbital is damaged with its posterior margin missing. The internal surface is visible on the left side but only partially on the right.

The postorbital of *Phosphatochelys* is a roughly square element, contacting the parietal medially, the quadratojugal posteriorly, the quadrate posteroventrally, and the jugal anteroventrally. The absence of a frontal con-

tact, due to the prefrontal-parietal contact, is unusual and seems to be unique to *Phosphatochelys*. The short postorbital of *Phosphatochelys* is completely separated from the posterior temporal emargination by the parietal-quadratojugal contact, quite different from the long postorbital of *Azabbaremys* that reaches the temporal emargination. It is possible that a very narrow postorbital-prefrontal contact was present, but as preserved, the right side is eroded and the left side is broken at this point. Thus we have restored the postorbital with no prefrontal contact and a narrow orbital exposure of the parietal. We consider this to be equivocal, however.

In most bothremydids, the postorbital has a medial wall that contacts the jugal and palatine to form a strong posterior wall for the fossa orbitalis. In *Phosphatochelys*, *Azabbaremys*, and *Taphrosphys*, however, this wall is absent. In *Phosphatochelys*, the medial surface of the postorbital has a vertical ridge continuous with one from the jugal that represents the fossa orbitalis margin. A much lower ridge is present in *Azabbaremys*.

Premaxilla

Both premaxillae are present in AMNH 30008, but the right one lacks the labial ridge.

The premaxilla in *Phosphatochelys* forms a deep, acute labial ridge with a median notch in contrast to the hook seen in *Azabbaremys*. In *Azabbaremys* and many pelomedusoids, the ventral rim of the apertura narium externa protrudes well anterior to the labial ridge. But in *Phosphatochelys*, the lower rim of the apertura is distinctly recessed, unlike any other bothremydid, so that the labial ridge is the anteriormost part of the skull. In *Azabbaremys*, there is a median ridge with low troughs on either side communicating with the apertura narium externa. In *Phosphatochelys*, there is also a median ridge but it is acute, not blunt as in *Azabbaremys*, and there are no troughs. *Phosphatochelys* does have a low concavity on the premaxilla that produces the recessed shape of the lower rim of the apertura. Below the concavity on the anterior face in *Phosphatochelys*, there is a distinct pattern of the nutrient foramina presumably for the horny beak. These occur in a band along the ventral edge of the labial ridge, premaxilla, and maxilla that is slightly raised above the more dorsal parts of these bones. In *Azabbaremys*, *Taphrosphys*, and other bothremydids, the nutrient foramina are not so prominent on the outer surface of premaxilla and maxilla. The horizontal plate of the premaxilla forms the floor of the fossa nasalis, and in *Phosphatochelys*, these form an acute dorsal ridge on the midline absent in *Azabbaremys*.

On the ventral surface, the premaxilla in *Phosphatochelys* forms the anterior part of the very high and acute labial ridge, higher than in *Azabbaremys* or any other bothremydid. Also in contrast to *Azabbaremys* and other bothremydids, the horizontal part of the triturating surface in *Phosphatochelys* is very narrow, particularly on the premaxilla, where it is hardly developed at all. The lingual ridge might be identified as the very low, rounded edge separating the triturating surface proper from the median concavity that leads into the apertura narium interna. This concavity is large in *Phosphatochelys*, wider and more open posteriorly in comparison to *Azabbaremys*.

Maxilla

Both maxillae are present in AMNH 30008 and are slightly damaged. The left maxilla is nearly complete but has a horizontal break running through the main body; not much bone seems to be missing, however. The right maxilla is missing its anteriormost edge and has a broken area below the orbit. Both have the internal portion preserved.

In lateral view, the maxilla of *Phosphatochelys* contacts the premaxilla anteriorly, the prefrontal anterodorsally, and the jugal posterodorsally. It is more curved, convex anterolaterally, than the very flat maxilla of *Azabbaremys*, and has a relatively larger fossa orbitalis and apertura narium externa than in *Azabbaremys*. As preserved, the maxilla contacts the quadrate on the right side. Based on the apparent free edges of the maxilla and jugal on the left side and some distortion on the right side, we have restored *Phosphatochelys* with a narrow cheek emargination. The prefrontal-maxilla contact is best pre-

served on the left side. It is much narrower than in *Azabbaremys*.

The medial parts of the maxilla help form the fossa nasalis anteriorly and the fossa orbitalis posteriorly. The fossa nasalis is relatively large for a bothremydid and does not have the posterolateral pocket seen in *Azabbaremys*. Along the ventrolateral margin of the fossa nasalis is a deep groove beginning as a shallow groove on the premaxilla and running posterolaterally to the fossa orbitalis. This groove has two large foramina in it that open ventrolaterally into the main body of the maxilla. In *Podocnemis* and *Pelusios*, Albrecht (1976) described the canalis infraorbitalis and canalis alveolaris superior system that connects a series of foramina and contains the supramaxillary and superior alveolar arteries. The groove and foramina in *Phosphatochelys* seem to be part of this system. Although we have not seen it developed to this extent in any other pelomedusoids, other taxa do have foramina in the same place in the fossa nasalis that communicate with the alveolar canals.

In the floor of the fossa orbitalis, the horizontal plate of the maxilla contacts the palatine posteromedially and the jugal posterolaterally. The lower border of the orbital opening is relatively high above the orbital floor, resulting in a deep pocket, deeper than seen in *Azabbaremys* and much deeper than seen in *Bothremys*, *Foxemys*, *Podocnemis*, and pelomedusids.

The ventral portion of the maxilla bears the triturating surface and forms part of the palate. The labial ridge of *Phosphatochelys* is much deeper than in *Azabbaremys* or other bothremydids. The snout is unusually foreshortened and the labial ridge is very deep, resulting in a deep, horseshoe-shaped space. The flat portion of the triturating surface width is very small and not distinctly separated from the labial ridge or the lingual edge. The lingual ridge barely exists; it is just the rounded margin for the apertura narium interna. The triturating surface has the usual nutrient foramina but it is smooth, not corrugated as in *Azabbaremys*.

In ventral view, the maxilla contacts the premaxilla anteromedially, the jugal posteriorly, and the palatine posteromedially. The area around the premaxilla-maxilla suture is broken on both sides as the suture approaches the apertura narium interna. The vomer, presumably present, is missing and it is possible that the maxilla contacted the vomer; if not, it did come close to it. The jugal does not extend onto the triturating surface in *Phosphatochelys*. The palatine contact is also farther from the triturating surface than it is in *Azabbaremys*.

VOMER

There is no vomer present, possibly due to postmortem loss.

PALATINE

Both palatines are present but are missing some of the anterior margin, although the right seems to be nearly complete. Most of the dorsal surfaces are visible except posteromedially.

In ventral view (fig. 26.4), the palatine in *Phosphatochelys* is smaller than the unusually large palatine of *Azabbaremys*. The palatine-pterygoid suture is roughly transverse in *Phosphatochelys*, not concave anteriorly as in *Azabbaremys*. The edges of the apertura narium interna in *Phosphatochelys* are not completely preserved, but they seem to be more circular rather than triangular as in *Azabbaremys*. As in *Azabbaremys*, only a small part of the palatine enters onto the triturating surface. The palatine forms the roof of the choanal opening into the mouth, the apertura narium interna, and in *Phosphatochelys*, *Azabbaremys*, and *Nigeremys*, this roof is highly arched dorsally in contrast to the flatter surface of other bothremydids. The foramen palatinum posterius in *Phosphatochelys* is formed almost entirely by the palatine, but is very close to the pterygoid suture, and a small spur of the pterygoid may enter the foramen. The foramen palatinum posterius of *Phosphatochelys* is in a comparable position to that seen in *Azabbaremys*, but it is much more medial and closer to the apertura narium interna in *Phosphatochelys* than in *Azabbaremys* or other bothremydids.

The dorsal surface of the palatine is complex, as it is involved in the fossa orbitalis, the sulcus pterygopalatinus, and the postorbital wall. In *Phosphatochelys* as in *Azabbaremys* and *Taphrosphys*, the postorbital

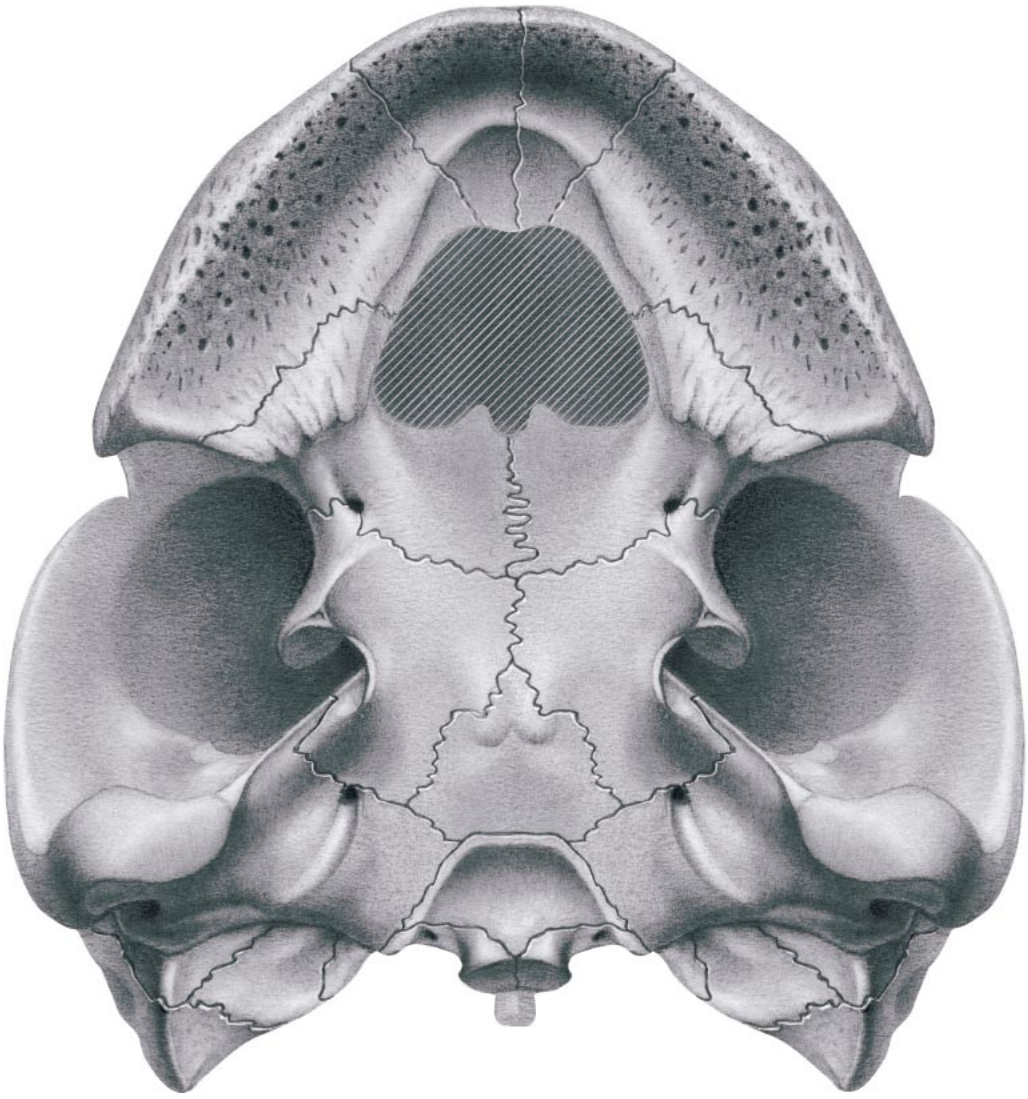

Fig. 26.4. *Phosphatochelys tedfordi*, n. gen. and n. sp., AMNH 30008. Partially restored ventral view of skull. See fig. 26.3 for bone names.

wall, so prominent in other bothremydids, is largely absent. In dorsal view, the palatine of *Phosphatochelys* is similar to *Azabbaremys* in forming most of the floor of the orbit and in having a broad anterolateral maxilla contact and a broad lateral jugal contact. The surface of the orbital floor is deeply concave, even more than in *Azabbaremys*. In contrast to *Azabbaremys*, *Phosphatochelys* has a completely enclosed sulcus pterygopalatinus. In *Azabbaremys*, the lateral wall of the sulcus is gone; in *Phosphatochelys* it is narrow but complete. Medially the palatines in *Phosphatochelys* contact each other in a relatively short suture, which may have been longer before postmortem damage.

Quadrate

Both quadrates are nearly complete. The left one lacks its anterior edge and the right one has some breakage along the jugal-maxilla contact.

The cavum tympani in *Phosphatochelys*

has a completely enclosed incisura columellae auris as in *Azabbaremys* and most bothremydids. Also as in *Azabbaremys*, the cavum is hemispherical and lacks a precolumellar fossa. However, *Phosphatochelys* has a well-developed antrum postoticum, larger than in *Taphrosphys sulcatus*, which is in strong contrast to *Azabbaremys*, which completely lacks an antrum postoticum. At the posterior margin of the cavum tympani in *Phosphatochelys* is a groove for the eustachian tube as in *Azabbaremys*. In *Azabbaremys*, this groove is open, but in *Phosphatochelys*, there is a well-developed ventral process or overhang that partially encloses the eustachian tube. As in *Azabbaremys*, there is a shelf along the ventral margin of the cavum tympani. It is very similar in size and shape in both *Phosphatochelys* and *Azabbaremys*.

In lateral view the quadrate of *Phosphatochelys* contacts the jugal anteriorly, the postorbital anterodorsally, the quadratojugal dorsally, and the squamosal posterodorsally. As preserved, there is a maxilla contact anteroventrally and this may have been the case in life although we have interpreted the presence of a narrow cheek emargination (see Maxilla).

In posterior view, the quadrate contacts the squamosal dorsolaterally, the opisthotic dorsally, the exoccipital medially, and the basioccipital ventromedially (not quite visible in occipital view). The quadrate and opisthotic combine to form a fully enclosed fenestra postotica, very similar to that in *Azabbaremys*. In the shelf leading into the fenestra, both dorsally and ventrally, are low spurs suggesting a division of stapedial artery and lateral head vein, but not distinct ridges as seen in *Taphrosphys*. As in *Azabbaremys*, the fenestra postotica of *Phosphatochelys* is widely separated from the foramen jugulare posterius by a well-developed opisthotic-quadrate contact. In *Phosphatochelys* and *Azabbaremys*, the quadrate contacts the exoccipital and basioccipital ventral to the foramen jugulare posterius. On the posterior surface of *Phosphatochelys* is a continuation of the groove, apparently for the eustachian tube, from the cavum tympani. This groove is roughly horizontal and is well defined dorsally by a shelf that has a slight ventral ridge resulting in an overhang partially enclosing the groove. Medially the groove flattens out and disappears.

In ventral view, the quadrate of *Phosphatochelys* contacts the pterygoid anteromedially, the basisphenoid medially, and the basioccipital posteromedially, as in *Azabbaremys* and other bothremydids. The quadrate and the basioccipital form the tuberculum basioccipital, which is higher and more prominent than in *Azabbaremys*. As in *Azabbaremys*, there is a narrow contact with the basisphenoid between the broader basioccipital and pterygoid contacts. The quadrate contacts the quadrate ramus of the pterygoid in a suture extending from the basisphenoid along the processus articularis of the quadrate as in *Azabbaremys* and other pleurodires.

The foramen posterius canalis carotici interni is formed in the pterygoid-quadrate suture, but more is formed by the quadrate than the pterygoid. In contrast to *Azabbaremys*, there is no contribution from the basisphenoid. There is a distinct groove on the quadrate leading anteriorly into the foramen posterius canalis carotici interni.

The processus articularis of the quadrate in *Phosphatochelys* is longer than in *Azabbaremys* so that the condylus mandibularis is much farther from the plane of the palate in *Phosphatochelys* than it is in *Azabbaremys*. This is presumably related to the very deep labial ridge in *Phosphatochelys*, although a lower jaw will be needed to demonstrate this.

The anterior face of the otic chamber can be seen on both sides, but it is best exposed on the left side. The quadrate enters into the margin of the foramen nervi trigemini along its posteroventral edge between the prootic and pterygoid. In *Azabbaremys* the quadrate does not enter the foramen nervi trigemini as preserved, but this region is damaged on both sides, and originally the quadrate may have been present. The foramen stapedio-temporalis in *Phosphatochelys* is very close to the foramen nervi trigemini, being separated from it only by narrow process of quadrate below and prootic above. The foramen stapedio-temporalis, formed ventrally by the quadrate and dorsally by the prootic, in *Phosphatochelys* is completely on the anterior surface of the otic chamber and not visible in dorsal view. This area is somewhat eroded in *Azabbaremys*, but to the extent it

is preserved, it is very similar to *Phosphatochelys*. There is a strong ridge that begins dorsally along the anterior margin of the foramen nervi trigemini and extends posteroventrally straight to the medial margin of the condylus mandibularis. This ridge is absent in *Azabbaremys*. On the anterior surface of the quadrate in *Phosphatochelys* is a low ridge, lateral to the foramen stapedio-temporalis, that runs roughly dorsoventrally and is presumably related to muscle attachments.

In dorsal view, the quadrate in *Phosphatochelys* contacts the prootic medially, the opisthotic posteromedially, and the squamosal posterolaterally. As in *Azabbaremys* and *Taphrosphys*, there is no quadrate-supraoccipital contact that is seen in the *Bothremys* Group.

Pterygoid

Both pterygoids are present and nearly complete. The processus trochlearis pterygoidei is displaced on the right side, but intact on the left. In ventral view, the pterygoid contacts are as in other bothremydids: the palatine anteriorly, the quadrate posterolaterally, the basisphenoid posteromedially, and the other pterygoid medially. The midline pterygoid contact is slightly longer than in *Azabbaremys*.

The foramen posterius canalis carotici interni (see Quadrate) lies in the pterygoid-quadrate suture midway between the basisphenoid and lateral edge of the quadrate. Nonetheless, the foramen is in a similar position in *Azabbaremys* despite the fact that the basisphenoid enters the foramen in *Azabbaremys*. The basisphenoid is much wider in *Azabbaremys* than in *Phosphatochelys* and that may be a factor. The pterygoideus muscle scar is weakly developed in *Azabbaremys*, but it is absent in *Phosphatochelys*. There is no indication at all of its presence. However, there is a dorsally directed trough formed by pterygoid and quadrate in *Phosphatochelys* that may have held an insertion for the M. pterygoideus. This trough has a sharp ridge on the quadrate as its lateral margin and the crista pterygoidea and processus inferior parietalis as its medial limits. It trends posteroventrally from the parietal down to the condylus mandibularis and is open anteriorly. As it reaches the ventral edge of the pterygoid, its posterior wall ends and only the lateral ridge reaches the condylus mandibularis. Thus, in ventral view, the end of the trough lies behind the processus trochlearis pterygoidei just lateral to the thin web of bone behind the processus. This structure developed to the extent seen in *Phosphatochelys* is not seen in other pleurodires. It is possible that this trough contains a division of the M. pterygoideus (Schumacher, 1973), probably either the pars ventrolateralis, or possibly the pars ventroposterior (seen in *Podocnemis*).

The processus trochlearis pterygoidei of *Phosphatochelys* is relatively well preserved on both sides; in many pleurodire fossils it is damaged due to the thin bone. In *Azabbaremys*, only part of one is preserved, but it is similar to that in *Phosphatochelys*. The processus in both genera extends posteriorly at an angle of roughly 30° from the midline. There is a low ridge along the ventrolateral margin of the processus in *Phosphatochelys* also as in *Azabbaremys*, but absent in pelomedusids. The base of the processus trochlearis pterygoidei contacts the parietal anterodorsally and the palatine anteroventrally. The foramen palatinum posterius (see Palatine) is formed almost entirely by the palatine, with a very narrow contribution from the pterygoid.

The crista pterygoidea in *Phosphatochelys* is completely covered with matrix on the right side and only partially exposed on the left. But the left side does show the anterior margin and the foramen nervi trigemini clearly. The crista pterygoidea in *Phosphatochelys* is narrow in comparison to *Bothremys* Group taxa, but it is not as narrow as in *Azabbaremys*. In *Azabbaremys*, both the processus inferior parietalis and the crista pterygoidea are roughly half the width of these walls in *Phosphatochelys*. The posterior edge of the crista pterygoidea forms the anteroventral margin of the foramen nervi trigemini in *Phosphatochelys*, as in *Azabbaremys*. In *Phosphatochelys*, in contrast to *Azabbaremys*, there is a high, thin ridge along the anterior margin of the foramen nervi trigemini, separating it from the more anterior part of the crista pterygoidea.

SUPRAOCCIPITAL

The supraoccipital in AMNH 30008 is nearly complete and well preserved, with all sides visible. The supraoccipital of *Phosphatochelys* underlies the two parietals on the midline but not to the extent seen in *Azabbaremys*, presumably related to the shorter parietals in *Phosphatochelys*, because the supraoccipitals in both *Phosphatochelys* and *Azabbaremys* are quite similar. The crista supraoccipitalis is complete in *Phosphatochelys* and short as in *Azabbaremys*, extending only slightly past the level of the condylus occipitalis. *Phosphatochelys* has a slightly shorter crista than in *Azabbaremys*. The blade of the crista is deeper in *Azabbaremys* than *Phosphatochelys*, but this seems to be related to the larger foramen magnum of *Phosphatochelys*, in turn presumably related to its smaller size.

The laterally projecting otic portion of the supraoccipital in *Phosphatochelys* contacts the prootic anterolaterally, the opisthotic laterally, and the exoccipital posterolaterally.

EXOCCIPITAL

Both exoccipitals are preserved in AMNH 30008, complete, free of matrix, and with clear sutures.

The exoccipital in *Phosphatochelys* forms all of the condylus mandibularis; the basioccipital enters the neck of the condyle and almost reaches the articulation surface, in contrast to the condyle in *Azabbaremys* where the basioccipital is more posterior. The exoccipitals are slightly eroded on the midline, or perhaps were not fully ossified, giving the occipital condyle a bilobate appearance as in BMNH R 16370, the type specimen of *Azabbaremys moragjonesi*. The foramen jugulare posterius is formed mostly by the exoccipital, with between a third and a half being formed by the opisthotic, in contrast to *Azabbaremys*, in which only a very narrow process of the opisthotic enters the foramen margin. The foramen jugulare posterius is entirely enclosed by bone, as in *Taphrosphys*, *Arenila*, and *Bothremys*, but in contrast to the open condition of *Foxemys* and *Polysternon*.

Between the foramen jugulare posterius and the condylus occipitalis are the two foramina nervi hypoglossi entirely formed by the exoccipital. Their positions differ significantly in *Phosphatochelys* and *Azabbaremys*. In *Phosphatochelys* the more medial foramen lies on the roughly flat posterior surface of the exoccipital and opens posterolaterally and is clearly visible in posterior view. The more lateral foramen lies within the entry to the foramen jugulare posterius and is so far within the margin that it is completely concealed in posterior view on the right side and only barely visible on the left. The more medial foramen nervi hypoglossi in *Phosphatochelys* is larger in diameter than the more lateral one. In *Azabbaremys*, both foramina are very close to one another, are the same size, and neither are close to the foramen jugulare posterius.

The exoccipital in *Phosphatochelys* contacts the supraoccipital dorsally, the opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally, as in *Azabbaremys* and other bothremydids.

BASIOCCIPITAL

The basioccipital in AMNH 30008 is complete and clearly defined. The basioccipital in *Phosphatochelys* contacts the basisphenoid anteriorly, the quadrates laterally, and the exoccipitals posteriorly, as in *Azabbaremys*. *Phosphatochelys* has a broadly curved anterior margin rather than the straight suture seen in *Azabbaremys*. The basisphenoid contact is smaller and the quadrate contact more extensive in *Phosphatochelys*. The basioccipital in *Phosphatochelys* makes up the medial half of the very low tuberculum basioccipitale. Between the paired tubercula is a median concavity that is deeper and more clearly defined than in *Azabbaremys*. The concavity in *Phosphatochelys* is almost exactly coincident with the basioccipital.

PROOTIC

Both prootics are present and complete; the left one is free of matrix, but the right one is covered anteromedially. Both have clear sutures.

The prootic in *Phosphatochelys* contacts the supraoccipital posteromedially, the parietal medially, the pterygoid ventrally (internal to the foramen nervi trigemini), the quad-

rate laterally, and the opisthotic posterolaterally. The prootic forms the dorsomedial margin of the foramen nervi trigemini, the parietal forms its anterodorsal margin, the pterygoid forms its anteroventral margin, and the quadrate its posteroventral margin. The foramen nervi trigemini is visible and complete on the left side of AMNH 30008 as well as the foramen stapedio-temporale. The two foramina are very close together in *Phosphatochelys* and only separated by contact of the prootic and quadrate. The prootic forms the dorsal half of the foramen stapedio-temporale, which lies entirely on the anterior face of the otic chamber and is not visible in dorsal view. This is the same condition in *Azabbaremys*, *Taphrosphys*, *Bothremys*, *Rosasia*, and *Foxemys*. The quadrate forms the lower half of the foramen stapedio-temporale.

Opisthotic

Both opisthotics are complete and well preserved with clear sutures in AMNH 30008. The opisthotic in *Phosphatochelys* has the usual bothremydid contacts: supraoccipital dorsomedially, prootic anteromedially, quadrate anterolaterally, squamosal posterolaterally, quadrate (again) ventrolaterally, and exoccipital posteromedially.

The opisthotic forms the roof of the fenestra postotica, the ventral and greater portion being formed by the quadrate. The fenestra in *Phosphatochelys* is oblong with small ridges distally presumably indicating the positions of the stapedial artery and lateral head vein (see Quadrate). The processus interfenestralis of the opisthotic forms the wall between the fenestra postotica and foramen jugulare posterius, contacting the quadrate ventrally. This wall is quite thick in *Phosphatochelys*, as it is in *Azabbaremys* and also *Bothremys*.

Basisphenoid

The basisphenoid is complete and clearly defined in AMNH 30008, but its dorsal surface is covered with matrix. The basisphenoid of *Phosphatochelys* is roughly triangular but nearly pentagonal, similar to *Taphrosphys* and distinct from *Azabbaremys*. It has a straight posterior contact with the basioccipital, posterolateral contacts with the quadrates, and anterolateral contacts with the pterygoids. The basisphenoid in *Phosphatochelys* is about as wide as long in contrast to the very short and wide basioccipital in *Azabbaremys*.

RELATIONSHIPS

Phosphatochelys is a pleurodire because it has these pleurodiran synapomorphies (Gaffney and Meylan, 1988): (1) processus trochlearis pterygoidei, (2) quadrate process below cranioquadrate space, (3) epipterygoid absent, and (4) foramen palatinum posterius behind orbit. It is also a member of the Pelomedusoides (Broin, 1988; Lapparent de Broin and Werner, 1998; Meylan, 1996; Tong et al., 1998) because it has these characters: (1) nasals absent, and (2) prefrontals meet on midline. *Phosphatochelys* is a member of the Bothremydidae based on these synapomorphies: (1) precolumellar fossa absent, (2) condylus occipitalis consisting only of exoccipitals, (3) foramen stapedio-temporale not visible in dorsal view, (4) eustachian tube and stapes separated by bone, (5) incisura columellae auris closed, and (6) exoccipital contacts quadrate. Within the Bothremydidae, *Phosphatochelys* can be allied with members of the *Nigeremys* Group: *Azabbaremys*, *Taphrosphys*, *Nigeremys*, and *Arenila* because it has an open postorbital wall and a dorsally arched palate.

ACKNOWLEDGMENTS

We wish to thank our pleurodiran associates, Drs. Peter Meylan and Roger Wood, for their support and help in this project. We are grateful to Valerie Storfer for the line drawings (figs. 26.2, 26.3), Brittany Degner for the photographs (fig. 26.1), and Frank Ippolito for the shaded palate (fig. 26.4). We very much appreciate the help of Judy Galkin in the preparation of the paper. Thanks to François Escuillié for providing the specimen, and Henri Cappetta (Montpellier, France) for data on shark teeth.

REFERENCES

Albrecht, P.W. 1976. The cranial arteries of turtles and their evolutionary significance. Journal of Morphology 149: 159–182.

Antunes, M.T., and F. de Broin. 1988. Le Crétacé terminal de Beira Litoral, Portugal: remarques stratigraphiques et écologiques, étude complémentaire de *Rosasia soutoi* (Chelonii, Bothremydidae). Ciências da Terra 9: 153–200.

Arambourg, G. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). Service Géologique du Maroc, Notes et Mémoires 92: 1–372.

Baur, G. 1891. Notes on some little known American fossil tortoises. Proceedings of the Academy of Natural Sciences of Philadelphia 43: 411–430.

Bergounioux, F.-M., and F. Crouzel. 1968. Deux tortues fossiles d'Afrique. Bulletin de la Société d'Histoire Naturelle de Toulouse 104: 1–2, 179–186.

Broin, F. de. 1988. Les tortues et le Gondwana. Examen des rapports entre le fractionnement du Gondwana au Crétacé et la dispersion géographique des tortues pleurodires à partir du Crétacé. Studies Palaeocheloniologiques 2(5): 103–142.

Buffetaut, E., and G. Wouters. 1979. *Atlantosuchus coupatezi* n. g. n. sp., un nouveau Dyrosauridé (Crocodylia, Mesosuchia) des phosphates montiens du Maroc. Bulletin Trimestriel de la Société Géologique de Normandie et desAmis du Muséum du Havre 66(4): 85–90.

Cavin, L., N. Bardet, H. Cappetta, E. Gheerbrant, S. M. Iarochene, and J. Sudre. 2000. A new Palaeocene albulid (Teleostei: Elopomorpha) from the Ouled Abdoun phosphatic basin, Morocco. Geological Magazine 137(5): 583–591.

Cope, E.D. 1864. On the limits and relations of the Raniformes. Proceedings of the Academy of Natural Science of Philadelphia 16: 181–183.

Cope, E.D. 1868. On the origin of genera. Proceedings of the Academy of Natural Science of Philadelphia 20: 242–300.

Gaffney, E.S. 1975. A revision of the side-necked turtle *Taphrosphys sulcatus* (Leidy) from the Cretaceous of New Jersey. American Museum Novitates 2571: 1–24.

Gaffney, E.S. 1977. An endocranial cast of the side-necked turtle, *Bothremys*, with a new reconstruction of the palate. American Museum Novitates 2639: 1–12.

Gaffney, E.S. 1979. Comparative cranial morphology of recent and fossil turtles. Bulletin of the American Museum of Natural History 164(2): 65–376.

Gaffney, E.S., D. de Almeida Campos, and R. Hirayama. 2001a. *Cearachelys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Early Cretaceous of Brazil. American Museum Novitates 3319: 1–20.

Gaffney, E.S., S. Chatterjee, and D.K. Rudra. 2001b. *Kurmademys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of India. American Museum Novitates 3321: 1–16.

Gaffney, E.S., and P.A. Meylan. 1988. A phylogeny of turtles. *In* M.J. Benton (editor), The phylogeny and classification of the tetrapods, Volume 1: Amphibians, reptiles, birds. Systematics Association Special Volume 35A: 157–219.

Gaffney, E.S., and P.A. Meylan. 1991. Primitive pelomedusid turtle. *In* J.G. Maisey (editor), Santana fossils: an illustrated atlas: 335–339. Neptune, NJ: T.F.H. Publications.

Gaffney, E.S., R.T.J. Moody, and C. Walker. 2001c. *Azabbaremys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Paleocene of Mali. American Museum Novitates 3320: 1–16.

Gaffney, E.S., and R. Zangerl. 1968. A revision of the chelonian genus *Bothremys* (Pleurodira: Pelomedusidae). Fieldiana, Geology 16: 193–239.

Gheerbrant, E., J. Sudre, and H. Cappetta. 1996. A Palaeocene proboscidean from Morocco. Nature 383: 68–70.

Gheerbrant, E., J. Sudre, H. Cappetta, and G. Bignot. 1998. *Phosphatotherium escuilliei* du Thanétien du Bassin des Ouled Abdoun (Maroc), plus ancien proboscidien (Mammalia) d'Afrique. Géobios 31(2): 247–269.

Hirayama, R. 1998. Oldest known sea turtle. Nature 392: 705–708.

Karl, H.-V., G. Tichy, and H. Ruschark. 1998. *Osteopygoides priscus* n. gen. n. sp. und die Taxonomie und Evolution der Osteopygidae (Testudines: Chelonioidea). Mitteilungen der Geologischen und Paläontologischen Landesmuseum Joanneum 56: 329–350.

Lapparent de Broin, F. de, and C. Werner. 1998. New late Cretaceous turtles from the western desert, Egypt. Annales de Paléontologie 84(2): 131–214.

Leidy, J. 1865. Memoir on the extinct reptiles of the Cretaceous formations of the United States. Smithsonian Contributions to Knowledge 14(6): 1–135.

Linnaeus, C. 1758. Systema naturae, 10th ed., Vol. 1. Stockholm. 824 pp.

Maisey, J.G. 1991. Santana fossils: an illustrated atlas. Neptune, NJ: T.F.H. Publications.

Meylan, P.A. 1996. Skeletal morphology and relationships of the Early Cretaceous side-necked turtle, *Araripemys barretoi* (Testudines: Pelomedusoides: Araripemydidae), from the Santana Formation of Brazil. Journal of Vertebrate Paleontology 16(1): 20–33.

Noubhani, A., and H. Cappetta. 1997. Les Orec-

tolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des Bassins à phosphate du Maroc (Maastrichtien-Lutétien basal). Systématique, biostratigraphie, évolution et dynamique des faunes. Palaeo-Ichthyologica 8: 327.

Schumacher, G.-H. 1973. The head muscles and hyolaryngeal skeleton of turtles and crocodilians. *In* C. Gans and T.S. Parsons (editors), Biology of the Reptilia, Vol. 4: 101–199.

Tong, H., and E. Buffetaut. 1996. A new genus and species of pleurodiran turtle from the Cretaceous of southern Morocco. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 199(1): 133–150.

Tong, H., E.S. Gaffney, and E. Buffetaut. 1998. *Foxemys*, a new side-necked turtle (Bothremydidae: Pelomedusoides) from the Late Cretaceous of France. American Museum Novitates 3251: 1–19.