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Source: American Museum Novitates, 2001(3320) : 1-16

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0082(2001)320<0001:AANSNT>2.0.CO;2

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3320, 16 pp., 3 figures February 27, 2001

Azabbaremys, a new Side-Necked Turtle (Pelomedusoides: Bothremydidae) from the Paleocene of Mali

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ABSTRACT

The Paleocene Teberemt Formation in eastern Mali has yielded the skull of a new genus of side-necked turtle, *Azabbaremys moragjonesi*, new genus and species. *Azabbaremys* is a pelomedusoid pleurodire belonging to the family Bothremydidae Baur, 1891, based on these characters: (1) precolumellar fossa absent, (2) occipital condyle 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, *Azabbaremys* is best resolved as a member of the group containing *Taphrosphys*, *Nigeremys*, and *Arenila* because it has a dorsally arched palate and an open postorbital wall.

INTRODUCTION

Kingston Polytechnic University and the Natural History Museum (then known as the British Museum [Natural History]) first joined forces in West Africa when Cyril Walker (BMNH) and Dick Moody (Kingston) were invited to participate in the ill-fated 1977–78 expedition to the upper Cretaceous deposits of northern Nigeria led by the late Beverly Halstead (University of Reading). This was a trip plagued by political intrigue and hostility (Halstead, 1979a), resulting in the arrest and detention of the expeditionists. The trip spanned Christmas

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1977 and was effectively terminated when Eric Buffetaut and Dick Moody decided it was futile to stay with the expedition, given the volatile situation, and returned to Europe. Their departure was subsequently reported in the Nigerian media as the deporation of two CIA agents ‘‘too dangerous to be held by the Nigerian authorities’’. In the meantime, Bev Halstead, Cyril Walker, and Jenny Halstead decided to remain with the intention of sorting out the problems. Their trip culminated in a 900-mile taxi drive to the outcrop, the rapid collection of some material, and the publication of several papers including the notification of two new species of turtles by Walker (1979), and their naming by Halstead (1979b). These specimens were retained by Ibaden University, but are now untraceable.

In the early eighties, Eric Buffetaut, Cyril Walker, and Dick Moody decided to return to West Africa but avoid ‘‘English-speaking’’ ex-colonies. The first Trans-Saharan-Sahel Expedition to Mali, a joint venture between Kingston Polytechnic, The Natural History Museum (BMNH), and the Centre National de la Recherche Scientifique took place in October 1981. The field area was centered on the area east of the northern Malian village of Tamaguilelt. The geological succession exposed in low-lying, tabular outcrops to the east of the Tilemsi Valley is composed of chalky and nodular late Cretaceous-early Eocene limestones, paper shales, and phosphates overlain by a thick sequence of terrestrial-lacustrine mudstones and siltstones (Moody and Sutcliffe, 1990, 1991, 1993). The 1981 expedition collected a range of incomplete fish and reptile material from the phosphates. A detailed investigation revealed, however, that a variety of well-preserved vertebrates were to be found in the older chalky limestones and in a thin, extensively bioturbated, ferruginous oolitic calcsandstone. From Tamaguilelt the expedition followed the outcrops toward and beyond In Fargas. Moving southeastward enabled the group to work an older horizon within the area known as the Iullemmeden Basin. In Fargas is difficult to describe. The region is wonderfully desolate and unpopulated, but a small well and a tiny oasis indicate a resting place for Touaregs and a nearby dissected plateau region extends around the edge of the Adrar des Iforas Precambrian Massif into Niger. The turtle skull described in the paper was found in the first of the chalky limestones encountered in the In Fargas area. This limestone has been subsequently named and dated by Moody and Sutcliffe (1993). Several turtle shells were recorded and one collected from this limestone.

This new turtle, *Azabbaremys moragjonesi,* from the Paleocene marine limestones near In Fargas, has characters relating it to the side-necked turtle family Bothremydidae. The Bothremydidae was first named in 1891 by George Baur with its type genus, *Bothremys* Leidy, 1865, from the late Cretaceous of New Jersey (Gaffney and Zangerl, 1968). The Bothremydidae are known from the early Cretaceous to the Miocene and are found on all the continents except Antarctica and Australia. Bothremydids had a body-size range from less than a foot to over 5 ft in length. Fossils of bothremydids occur in near-shore marine sediments as well as terrestrial freshwater units. Cranial diversity of the group supports the reinterpretation of pleurodires as being widespread and ecologically diverse, rather than more conservative. The original misconception is based on the more frequently preserved shells, which are unusually conservative, even for turtles.

Although Bothremydidae was named as early as 1891 by George Baur, the term fell into disuse for most of this century and the few included taxa, particularly *Bothremys* and *Taphrosphys,* were simply included in the Pelomedusidae. Antunes and Broin (1988) and Broin (1988) revived Bothremydidae, provided a new diagnosis, and added taxa, such as *Rosasia,* based on skulls and shells. 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 recognized as a more 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 is 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); and *Nigeremys* (Bergounioux and Crouzel, 1968; Lapparent de Broin and Werner, 1998). Other pelomedusoid skulls are *Araripemys* (Meylan, 1996) and an unnamed Santana genus (Gaffney and Meylan, 1991). A general treatment and description of pleurodire skulls, turtle skull morphology and terminology, and a literature review are 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. The contents of these groups are as follows: *Bothremys* Group—*Bothremys, Rosasia, Zolhafah, Foxemys*; *Nigeremys* Group—*Nigeremys, Arenila, Taphrosphys.*

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History
BMNH	British Museum (Natural History) (now known as The Natural History Museum)

ANATOMICAL ABBREVIATIONS

bo	basioccipital
bs	basisphenoid
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
(FIDE GAFFNEY AND MEYLAN, 1988)
HYPERFAMILY PELOMEDUSOIDES COPE, 1868
FAMILY BOTHREMYDIDAE BAUR, 1891

Azabbaremys, new genus

TYPE SPECIES: *Azabbaremys moragjonesi,* new species.

DISTRIBUTION: Paleocene of eastern Mali.

ETYMOLOGY: *Azabbar,* a monster in popular Mali folk stories in the Tamasheq language (from a suggestion by Mali resident, Mr. Ibrahim Litny, to whom we are grateful).

DIAGNOSIS

A member of the Bothremydidae known only from the skull; skull large as in *Nigeremys* and *Arenila,* not small as in *Taphrosphys* and *Bothremys*; orbits facing anterolaterally, not dorsally as in *Bothremys*; preorbital part of skull narrow as in *Nigeremys* and in contrast to *Bothremys*; jugal-quadrate contact present in contrast to all other described bothremydids; postorbital wall open as in *Taphrosphys,* in contrast to *Bothremys*; relatively long postorbital as in *Foxemys,* but in contrast to *Taphrosphys*; premaxilla relatively short as in *Taphrosphys,* not long as in *Nigeremys* and *Arenila*; labial ridge of maxilla relatively thin as in *Taphrosphys,* not thick as in *Nigeremys* and *Arenila*; maxillary triturating surface parallel sided as in *Arenila,* not triangular as in *Bothremys*; maxillary triturating surface covered with prominent toothlike crenellations not found in any other pleurodire; palatal pits seen in *Bothremys* absent; maxilla-quadrate contact present, no cheek emargination; palate strongly arched dorsally as in *Nigeremys*; palatine not exposed extensively on triturating surface; antrum postoticum completely absent not small as in *Bothremys*; attachment area for pterygoideus musculature flat as in *Taphrosphys,* not a deep concavity as in *Nigeremys* and *Arenila*; foramen posterius canalis carotici interni formed by pterygoid and quadrate as in *Bothremys*; supraoccipital-quadrate contact seen in *Bothremys* absent; foramen stapedio temporale placed on anterior surface of otic chamber close to foramen nervi trigemini and not visible in dorsal view.

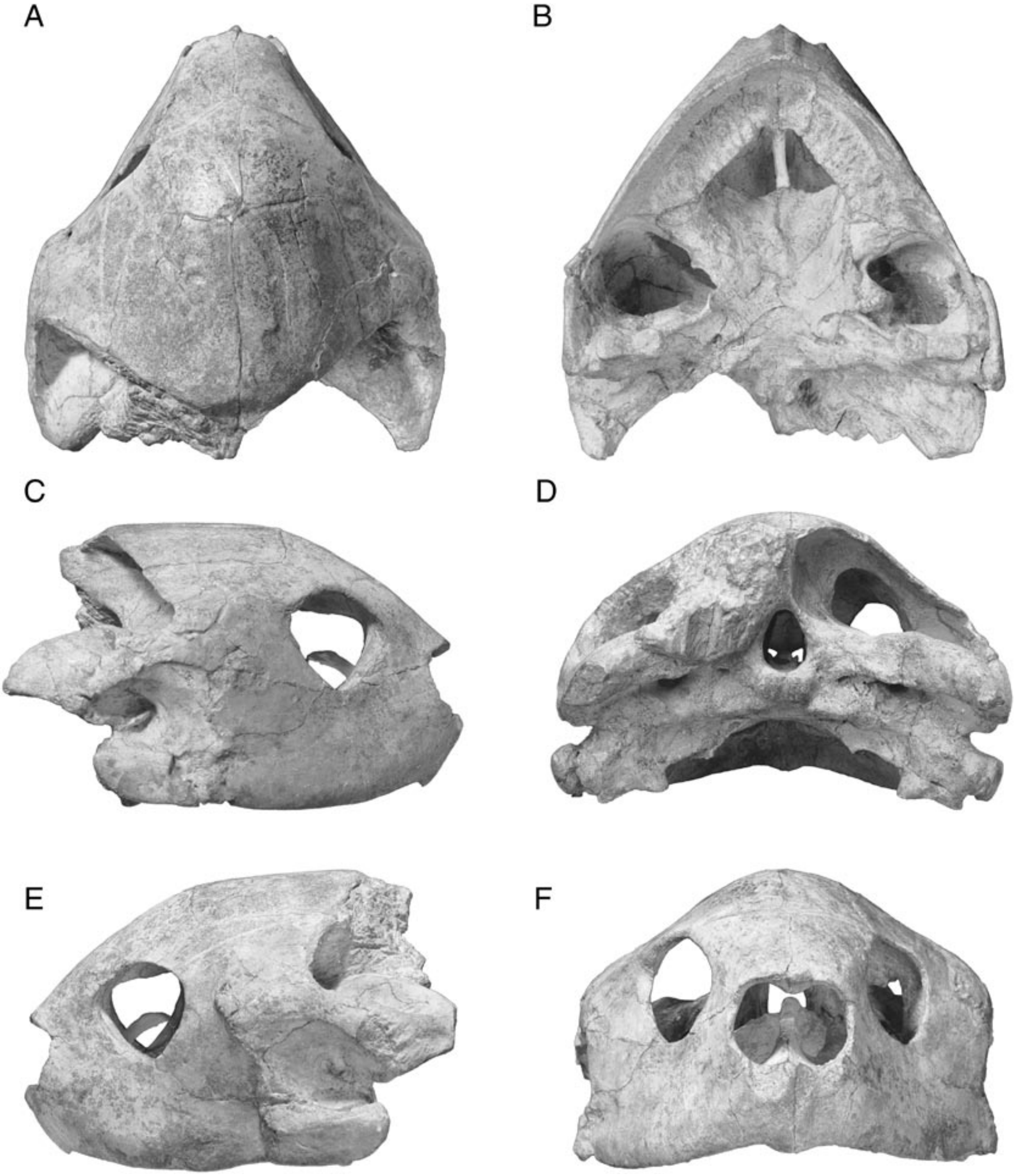

Fig. 1. *Azabbaremys moragjonesi*, n. gen. & sp., BMNH R 16370, Teberemt Formation, Paleocene, In Fargas, Mali. Skull, **A,** dorsal view; **B,** ventral view; **C,** right lateral view; **D,** occipital view; **E,** left lateral view; **F,** anterior view.

Azabbaremys moragjonesi, new species

TYPE SPECIMEN: BMNH R 16370, a complete skull without lower jaws.

TYPE LOCALITY: North of In Fargas near Samit, eastern Mali.

HORIZON: Teberemt Formation, Paleocene

DIAGNOSIS: Same as for genus.

ETYMOLOGY: Species apellation, *moragjonesi,* in memory of Ms. Morag Jones, a research student who participated in the discovery of this specimen; tragically, she died on the first Mali expedition.

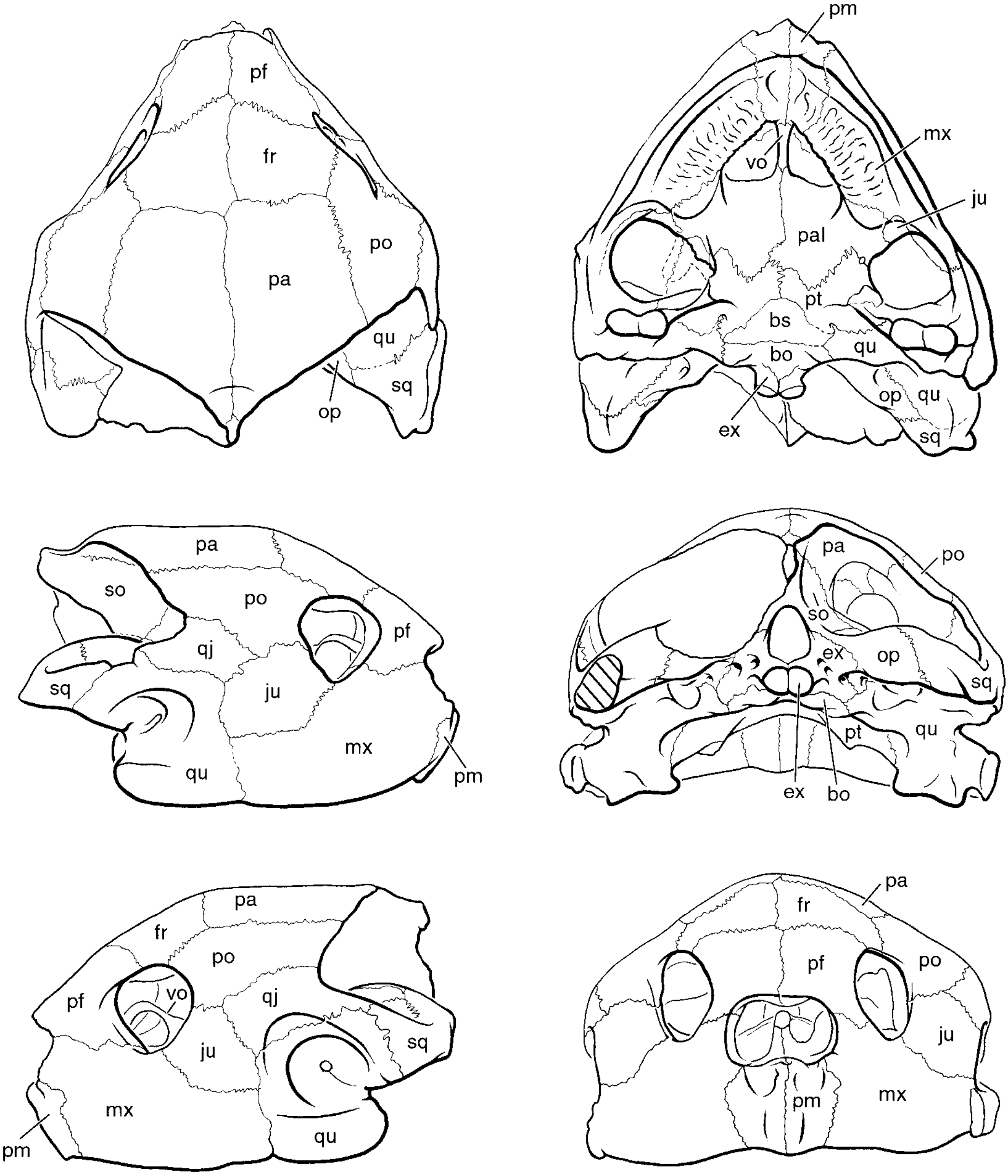

Fig. 2. *Azabbaremys moragjonesi,* n. gen. & sp., BMNH R 16370. Key for fig. 1.

DESCRIPTION

The type skull of *Azabbaremys moragjonesi,* BMNH 16370, has a premaxilla-condyle median length of 145.5 mm, a maximum width of 164.3 mm, and a height from condylus mandibularis of the quadrate to the top of the skull roof of 67.1 mm.

PREFRONTAL

Both prefrontals are present and complete. The sutures are clearly defined and the dorsal and ventral surfaces are visible.

The prefrontal in *Azabbaremys* is a relatively large element, forming most of the preorbital part of the skull in dorsal view. In

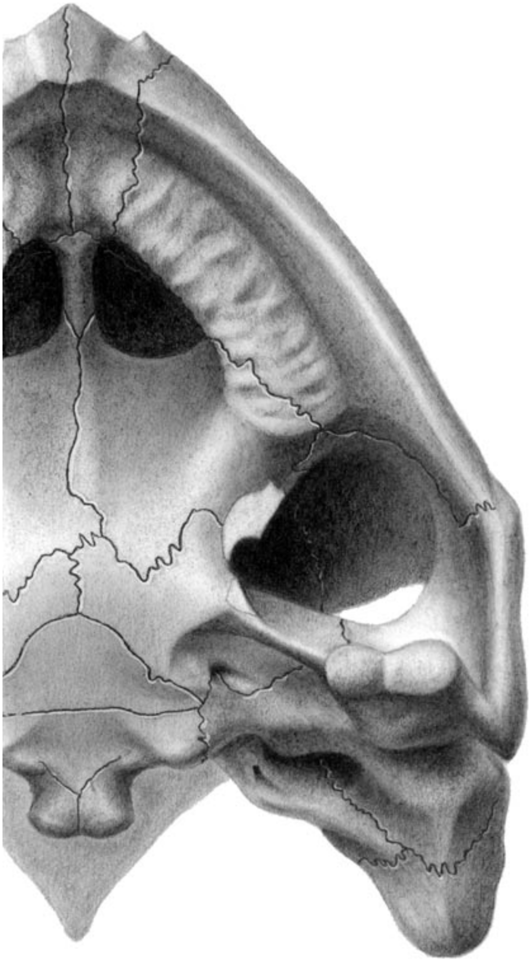

Fig. 3. *Azabbaremys moragjonesi*, n. gen. & sp., BMNH R 16370. Ventral view of skull partially restored by combining information from both sides of skull. See fig. 2 for bone identifications.

contrast to the small prefrontals of pelomedusids and *Araripemys*, many bothremydids have a broad preorbital area and a large prefrontal. The dorsal surface is convex, forming most of the distinctive dorsal protuberance of the nose found in *Azabbaremys*. The ventral surface is broadly concave, without a distinctly defined sulcus olfactorius.

The prefrontal of *Azabbaremys* forms the anterior margin of the fossa orbitalis as in other pelomedusoids; however, in *Azabbaremys* the prefrontal has a well-developed posteroventral portion that occupies the area formed by the maxilla in other pelomedusoids. This part of the prefrontal is comparable in extent to *Taphrosphys* and possibly *Arenila*, although the sutures are ambiguous in the latter. Ventrally the prefrontal contacts the maxilla in a nearly horizontal suture at the level of the ventral margin of the orbit. The anterior margin of the prefrontal forms the dorsal margin of the apertura narium externa, which is protuberant in *Azabbaremys* so that the dorsal margin overhangs the apertura, much as in *Taphrosphys*. The protuberance is broad, extending the entire width of the apertura. Medially the prefrontals meet on the midline, posteriorly each prefrontal contacts the frontal in a posterolaterally trending suture.

FRONTAL

Both frontals are present and complete. The sutures are clearly defined and the dorsal and ventral surfaces are visible.

The frontal in *Azabbaremys* contacts the prefrontal anteriorly, the other frontal medially, the parietal posteriorly, and the postorbital posterolaterally. It forms the dorsal margin of the fossa orbitalis between the prefrontal and postorbital contacts. The dorsal surface of the frontal in *Azabbaremys* is broadly convex, continuing the convexity formed by the prefrontal.

On the ventral surface the frontal forms a deep and well-developed sulcus olfactorius. The parasagittal ridge is low anteriorly, beginning as a continuation of the prefrontal ridge that divides the fossa orbitalis from the fossa nasalis. The sulcus olfactorius ridge deepens posteriorly as it merges into the processus inferior parietalis. The orbits of *Azabbaremys* are widely separated and the margins are almost vertical, a strong contrast with other bothremydids such as *Bothremys* and *Rosasia*, which have orbits that face primarily dorsally. *Nigeremys* and *Arenila* have orbits with a more lateral orientation, but do not approach the *Azabbaremys* condition.

PARIETAL

Both parietals are present and complete. Sutures are clear on the dorsal surface. The right parietal is visible ventrally, but the left has matrix on its ventral surface.

The dorsal plate of the parietal contacts the frontal anteriorly, the other parietal medially, and the postorbital laterally. The posterior edge of the parietal forms part of the anterior margin of the temporal emargination. The margin is a nearly straight edge trending anterolaterally along the parietal and continuing onto the postorbital. The temporal roof in *Azabbaremys* is relatively extensive, most of the otic chamber is covered in dorsal view. In comparison to other bothremydids, the roof in *Azabbaremys* is more extensive, although *Nigeremys* approaches it. Nonetheless, the size and shape of the parietal itself are quite similar in *Azabbaremys* and *Taphrosphys.* The processus inferior parietalis in *Azabbaremys* is present on both sides, with medial and lateral surfaces visible. It is unusually narrow, in strong contrast to pelomedusids, podocnemidids, and most bothremydids, but in common with *Taphrosphys.* The condition in *Arenila* and *Nigeremys* is indeterminate. The parietal extends ventrally, forming the processus inferior parietalis, and meets the crista pterygoidea of the pterygoid in a suture that drops anteroventrally from the foramen nervi trigemini to the edge of the processus inferior parietalis. The anterior margin of the processus forms the posterior margin of the foramen interorbitale. As a consequence of the high, arched palate, the deep sulcus olfactorius, and the short snout, the foramen interorbitale is relatively small in *Azabbaremys.*

Posteriorly the parietal in *Azabbaremys* lies above the supraoccipital as in other turtles. The prootic contacts the parietal from midway along the supraoccipital suture and extends anteroventrally to the foramen nervi trigemini. In *Azabbaremys* the foramen nervi trigemini is preserved but damaged on both sides. As preserved, the parietal narrowly enters the foramen margin dorsally. The pterygoid forms nearly all of the anterior and ventral margin, with the prootic forming the posterior margin. The complete extent of the foramen is not known posteriorly due to damage.

JUGAL

Both jugals are present and complete. The sutures are clearly defined and the internal and external surfaces are visible except for a small area on the inside of the left jugal.

The external or vertical plate of the jugal contacts the postorbital dorsally, the quadratojugal posterodorsally, the quadrate posteriorly, and the maxilla ventrally. Within the bothremydids the postorbital, quadratojugal, and maxilla contacts are always present, but the jugal-quadrate contact in *Azabbaremys* is unusual. This contact requires the quadratojugal to be withdrawn or retracted dorsally so that the jugal and quadrate meet. This condition occurs only in *Azabbaremys* among named bothremydids (it also occurs in *Peltocephalus* and *Erymnochelys* and in an undescribed bothremydid from Morocco). It is possible that the jugal in *Taphrosphys* contacts the quadrate, but this area is ambiguous. The jugal forms the posteroventral margin of the orbit in *Azabbaremys.* It is exposed to a greater extent than the published figures of the jugal in *Nigeremys* and *Arenila* (Lapparent de Broin and Werner, 1998). The medial process of the jugal in *Azabbaremys* forms part of the anterior temporal fossa wall, contacts the palatine medially, and the maxilla ventrally. The jugal does not extend on to the triturating surface in *Azabbaremys.* The jugal forms part of the floor of the fossa orbitalis, contacting the maxilla anteriorly and the palatine medially.

QUADRATOJUGAL

Both quadratojugals are present and complete, but both have some damage due to cracking, and the sutures are not all clear.

In most bothremydids the quadratojugal is a large element extending from the ventral margin of the cheek to the temporal emargination on the skull roof. In *Azabbaremys* the quadratojugal is smaller and retracted dorsally above the quadrate, not exposed on the cheek edge, but still entering the edge of the temporal emargination. *Rosasia* also has a retracted quadratojugal with no exposure on the cheek edge. The ventral edge of the quadratojugal in *Azabbaremys* contacts the quadrate. Just dorsal to this suture the edge of the concave cavum tympani extends up onto the quadratojugal. It is unusual in turtles to have the quadratojugal form a significant portion of the cavum tympani, and this does not occur in any other pleurodire.

SQUAMOSAL

Both squamosals are preserved but missing parts of their posterolateral margins. The right squamosal is more complete posteriorly, but it has breakage on its anterolateral process.

The squamosal in *Azabbaremys* is the usual cone-shaped element sitting on the posterolateral corner of the quadrate, as in most turtles. It contacts the opisthotic medially on the dorsal, posterior, and ventral surfaces. A short process of the squamosal contacts the quadratojugal along the lateral edge of the temporal emargination. All of these contacts are as in pelomedusids, bothremydids, and podocnemidids. The squamosal in *Azabbaremys* is cone-shaped and relatively smooth, not flat as in *Pelusios*. *Azabbaremys* also lacks the ventral, parasagittal flange or process of the squamosal characteristic of *Taphrosphys.*

POSTORBITAL

Both postorbitals are present and complete. The sutures are clearly defined and the internal surface is visible on the right side.

The postorbital in *Azabbaremys* is a large, quadrangular element contacting the frontal anteromedially, the parietal posteromedially, the jugal anterolaterally, and the quadratojugal posterolaterally. The postorbital forms the posterior margin of the orbit and the anterior margin of the temporal emargination. In most pelomedusoids, the postorbital has a medial and ventral process (Gaffney 1979: figs. 53, 54) that contacts the jugal and palatine to form a variably developed posterior wall of the fossa orbitalis. This is particularly large in the *Bothremys* Group, such as *Rosasia* (Antunes and Broin, 1988: fig. 4). In *Azabbaremys* this wall is absent (fig. 1F) and the medial and ventral surface of the postorbital is smooth. This condition is also seen in *Taphrosphys.*

PREMAXILLA

Both premaxillae are preserved in *Azabbaremys,* complete and visible on all surfaces.

The premaxilla in *Azabbaremys* forms a deep, acute labial ridge with a median ventral process forming a short hook. On the anterior surface this hook is continuous with a low ridge running on the midline dorsally to the ventral margin of the apertura narium externa. The ridge is unpaired, but at the ventral margin of the apertura, on either side of this ridge, are paired troughs that cut into the lower margin of the apertura narium externa. This premaxillary morphology is unique in turtles. The labial ridge on the premaxilla of *Azabbaremys* is relatively deep, in contrast to the shallower labial ridge in *Nigeremys. Nigeremys* also has a very wide and thick labial ridge with a blunt margin. In *Azabbaremys* and *Taphrosphys* the ridges are much thinner and more acute. The premaxillae are missing in *Arenila.*

The premaxillae in *Azabbaremys* form a relatively deep concavity on the midline just posterior to the labial ridge. *Nigeremys* also has a midline concavity that is hemispherical rather than triangular as in *Azabbaremys.* The posterior margins of the premaxillae enter the apertura narium interna in *Azabbaremys,* but are excluded from it in *Nigeremys* and *Arenila* by a vomer- maxilla contact.

The dorsal surface of the premaxilla in *Azabbaremys* forms the ventral margin of the apertura narium externa and the floor of the fossa nasalis. The apertura has paired grooves at the front that lead posteriorly into the shallow choanal channels that run posterolaterally from the fossa nasalis. Within the fossa the premaxillae on the midline are nearly flat anteriorly, but rise dorsally very quickly to form a high, median projection dividing the choanal channels and meeting the vomer.

MAXILLA

Both maxillae are complete and visible on all surfaces in *Azabbaremys.*

The maxilla in lateral view shows a relatively flat, deep, bladelike bone, forming most of the labial ridge, the ventral part of the fossa orbitalis, and the lateral part of the fossa nasalis. The prefrontal and premaxilla contacts are clear on both sides. The maxilla has a long, roughly horizonal suture, with the jugal behind the orbit. In more typical bothremydids such as *Bothremys* and *Rosasia,* the jugal contact is not as long.

In *Azabbaremys* the posterior end of the maxilla contacts the quadrate. In all other bothremydids, except for *Rosasia,* the maxilla contacts the quadratojugal, which lies between the maxilla and quadrate. In *Azabbaremys* the quadratojugal is small and placed above the quadrate. The maxilla-quadrate contact in *Azabbaremys* is broken slightly on both sides. On the right side it is slightly broken but not displaced. The suture on the external surface can be seen ventrally, beginning in a broken part of the cheek margin and extending dorsally into an area of some breakage with a slight amount of breakage in the sutural contact itself until it reaches the jugal. On the internal surface of the right side, the maxilla-quadrate suture is less disturbed and altered only by a slight amount of overlap between the two bones. The left side is damaged by anterior-posterior pressure forcing the maxilla and quadrate past each other so that they overlap for about a centimeter. The break did not occur precisely in the suture between the two bones, and part of the maxilla-quadrate suture is clearly visible on the internal surface running dorsally from the ventral margin of the cheek.

The horizontal plate of the maxilla makes up the triturating surfaces, the floor of the fossa orbitalis, and the floor of the fossa nasalis. The fossa nasalis in *Azabbaremys* is a large chamber divided posteriorly into paired choanal channels leading into the apertura narium interna. Comparisons to other *Nigeremys* Group bothremydids is difficult; the fossa nasalis is largely missing in *Arenila,* obscured by matrix in *Nigeremys,* and not well preserved in *Taphrosphys.* The floor of the fossa orbitalis in *Azabbaremys* lies above the choanal channel and is angled anterodorsally, forming part of the arched palate seen in *Azabbaremys.* Only a small part of the orbital floor is actually made up of maxilla; most of it is palatine and jugal.

The maxilla bears most of the triturating surface in *Azabbaremys.* It is roughly parallel sided; the labial ridge is equidistant from the lingual margin, bordering the apertura narium interna throughout its length. There is a very small contribution of the palatine to the triturating surface posteromedially. The width of the triturating surface in *Azabbaremys* is narrower than in *Nigeremys* and *Arenila,* particularly anteriorly. In *Nigeremys* and *Arenila* the maxilla is broad enough to contact the vomer and prevent narial exposure of the premaxilla. In *Azabbaremys* the maxilla does not contact the vomer and the premaxilla does enter the apertura narium interna. It is likely that in *Taphrosphys* the maxilla does not contact the vomer either. The triturating surface in *Azabbaremys* is unusual in being very rugose and formed by a series of rough corrugations with the shape of small teeth. *Arenila, Nigeremys,* and *Taphrosphys* are smooth.

VOMER

The vomer was originally complete and well preserved in *Azabbaremys,* but it was broken off and lost after preparation. Fortunately, the cast of the skull preserves the vomer shape and position and a series of photos in the AMNH also record its morphology.

The vomer in *Azabbaremys* is a thin, curved element, extending dorsally and posteriorly from a high midline process formed by the premaxillae. The vomer shows that the palate in *Azabbaremys* was highly arched. The dorsal margin of the vomer has a narrow groove in it, the sulcus vomeri of cryptodires that bears the septum nasalis (Gaffney, 1979: 92). In *Nigeremys* and *Arenila* the vomer is dumbbell shaped in contrast to the thin columnar shape in *Azabbaremys.* In the former taxa the vomer is also unusually thick and robust. As originally preserved, the vomer in *Azabbaremys* was only attached anteriorly to the premaxillae. It tapers posteriorly and there is a gap between the posterior end of the vomer and the palatines. The palatines have an anterior margin that is thin and lacks an expanded area for the reception of the vomer. It is possible that the vomer did not actually contact the palatines. However, the anterior margin of the palatines and the posterior margin of the vomer are not finished edges and missing bone connecting them has been restored in figures 1–3.

PALATINE

Both palatines are preserved in *Azabbaremys,* but their posterolateral contacts are slightly damaged and not completely clear. All of the ventral surfaces are visible, but only some of the dorsal surfaces can be clearly determined.

The palatine in *Azabbaremys* is a relatively large element, forming a large proportion of the palate behind the apertura narium interna. If the published figures of ventral views of *Nigeremys* (Lapparent de Broin and Werner, 1998: fig. 4b, although sutures are doubtful) and *Arenila* (Lapparent de Broin and Werner, 1998: fig. 12a) are correct, the palatine in these forms is significantly smaller than in *Azabbaremys.* The palatine-pterygoid suture in these two taxa is shown as transverse, while in *Azabbaremys* it is sharply concave anteriorly. The apertura narium interna in *Azabbaremys* is a relatively large, triangular opening, larger than in *Arenila* and *Nigeremys.* In *Nigeremys* the apertura is clearly circular. In *Arenila* the restored line drawing (Lapparent de Broin and Werner, 1998: fig. 12a) shows the apertura as more or less triangular, but the photograph (Lapparent de Broin and Werner, 1998: plate 7, fig. 1) shows a nearly circular apertura quite similar to *Nigeremys.*

The lateral portion of the palatine in *Azabbaremys* is complex and helps form a unique morphology. The absence of a postorbital wall (see Postorbital, Jugal) considerably alters the usual pleurodire morphology in *Azabbaremys.* The palatine forms most of a ridge that extends between the inside of the cheek laterally and the base of the processus trochlearis pterygoidei medially. It is really the ventral remnant of the postorbital wall. The medial process of the jugal does not extend far enough medially to reach the pterygoid as in most other pleurodires. Instead, the palatine is widely exposed in the anterior wall of the fossa temporalis between the jugal and the pterygoid.

The palatine forms most of the floor of the orbit. This area is preserved and visible on both sides of *Azabbaremys,* but the right side is damaged along the lateral palatine suture and the left side is intact. The palatine extends from a free edge anteriorly, the margin of the apertura narium interna (actually the ill-defined foramen orbito-nasale), to the posterior free edge on the margin of the fossa temporalis. In nearly all other pleurodires in which it is determinable (except *Taphrosphys*) there is a postorbital wall, rather than a free margin posteriorly. Laterally the palatine contacts a short process of the jugal posterolaterally and a short process of the maxilla anterolaterally. Medially the palatine reaches the other palatine. The palatine and descending process of the prefrontal do not meet in the anteroventral part of the orbital floor; they are separated by the maxilla.

The palatine in the orbital floor of *Azabbaremys* is not a flat element. It is high medially and posteriorly. It slopes ventrally, forming a concavity deepest at the jugal and maxilla sutures. Posteromedially the palatine forms a dorsal process, unknown in any other pleurodires, just anterior to the contact of the pterygoid at the base of the processus trochlearis pterygoidei. This process marks the anterolateral limit of the pterygo-palatine channel, a structure that in *Azabbaremys* lacks the firm base seen in other pleurodires, due to the absence of the postorbital wall. Only a small part of the palatine enters the triturating surface in *Azabbaremys,* about the same as in *Arenila* and *Nigeremys.*

QUADRATE

Both quadrates are present and well preserved in *Azabbaremys.*

The cavum tympani in *Azabbaremys* has a completely enclosed incisura columellae auris as in *Nigeremys* and *Arenila.* The cavum tympani is nearly circular, with a distinct notch in its posteroventral edge, presumably for the eustachian tube. The incisura columellae auris in *Azabbaremys* is a small round hole for the stapes. On the right side of the skull a remnant of the stapes is present. The cavum tympani in *Azabbaremys* is completely smooth in the area of the antrum postoticum. Neither *Arenila* nor *Nigeremys* are well enough preserved to determine the presence of an antrum postoticum. However, the New Jersey species of *Taphrosphys* (*T. sulcatus*) does have an antrum postoticum, but the Cabinda skull lacks one as in *Azabbaremys.*

In lateral view the quadrate in *Azabbaremys* contacts the maxilla anteroventrally, the jugal anterodorsally, the quadratojugal dorsally, and the squamosal posterodorsally. Quadrate sutures are ambiguous in *Nigere-*

mys and the areas are missing in *Arenila*. The quadrate of *Azabbaremys* has a step or shelf at the ventral margin of the cavum tympani, just above the flat, vertical sheet forming the ventral margin of the quadrate. This shelf seems to be in *Nigeremys* also, although the area is not well preserved. It is indeterminant in *Arenila.* The quadrate ventral margin is a continuation of the ventral margin of the maxilla, resulting in a lateral profile for *Azabbaremys* that completely lacks any suggestion of a cheek emargination. *Nigeremys* has a shallow notch, possibly due to postmortem damage, in the cheek area. *Arenila* is missing bone in this region.

Posteriorly the cone-shaped squamosal fits onto the posterodorsal part of the quadrate. The medial part of the quadrate meets the other braincase elements and forms structures enclosing the associated soft parts. The quadrate and opisthotic combine to form the ovoid fenestra postotica containing the stapedial artery and lateral head vein. In some forms (such as *Taphrosphys*) the fenestra is subdivided around those structures, but in *Azabbaremys* this is not the case. However, the fenestra postotica is widely separated from the foramen jugulare posterius by a well-developed opisthotic-quadrate contact medial to the fenestra postotica. Also, in *Nigeremys* the fenestra postotica is an ovoid foramen and it is widely separated from the foramen jugulare posterius. In *Azabbaremys* the quadrate contacts the exoccipital and the basioccipital ventral to the foramen jugulare posterius on the occipital surface.

In ventral view the quadrate of *Azabbaremys* forms part of the very low but distinct tuberculum basioccipitalis with the basioccipital. The paired tuberculum is essentially absent in *Nigeremys* and, apparently, *Arenila.* The quadrate has a very narrow contact with the basisphenoid between the broader contacts with the basioccipital and pterygoid. The basisphenoid contact may also be narrow in *Arenila* (Lapparent de Broin and Werner, 1998: fig. 12a). In *Nigeremys* the sutures on the specimen are unclear (although the published figure, Lapparent de Broin and Werner, 1998: fig. 4, shows a very narrow basioccipital with what appears to be a narrow quadrate contact).

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 other pleurodires. The foramen posterius canalis carotici interni (see Pterygoid) is formed in the contact of three bones: pterygoid, quadrate, and basisphenoid. This is similar to the condition in *Taphrosphys* and the same as reported for *Arenila* and *Nigeremys.* Lateral to the foramen posterior canalis carotici interni, the quadrate has a long suture with the quadrate ramus of the pterygoid.

On the anterior face of the otic chamber the quadrate-pterygoid suture is visible on both sides but best seen on the right. As in other turtles, the quadrate forms the lateral margin of the foramen stapedio-temporalis. The margins of the foramen are eroded on both sides of *Azabbaremys,* but it is best preserved on the left side. The canalis stapedio-temporalis is free of matrix on the right side, so that the aditus canalis stapedio-temporalis can be clearly seen as well as can the foramen and canalis. As in *Nigeremys, Taphrosphys, Foxemys, Rosasia,* and *Bothremys,* the foramen stapedio-temporalis in *Azabbaremys* opens on the anterior face of the otic chamber, not more dorsally as in other pleurodires. The quadrate forms the ventral margin of the foramen stapedio-temporale and the ventral and anterior portion of the canalis cavernosus as it extends medially from the region just beneath the canalis stapedio-temporalis.

In *Azabbaremys* the region between the foramen stapedio-temporale and the processus inferior parietalis is eroded and missing some of the thin bone that covers the canalis cavernosus and forms the margins of the foramen nervi trigemini. The ventral portion of the more lateral part of this area is formed by the quadrate.

Pterygoid

Most of both pterygoids are present, but the processus trochlearis pterygoidei is broken on both. On the right side the processus is missing entirely, but on the left side the main body is present but displaced anteriorly. The distal portions of the processus are missing on the left side also. The dorsal structures of the pterygoid are visible but so affected by damage that some areas are missing.

Some of the dorsal surface sutures are unclear, although all of the ones on the ventral surface can be seen.

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 palatine contact is not transverse as in *Arenila* and *Taphrosphys* (*Nigeremys* is in doubt), but is curved and concave anteriorly. The midline pterygoid contact is relatively short compared to *Taphrosphys,* but *Arenila* has the pterygoids completely or nearly separated on the midline.

The foramen posterius canalis carotici interni lies at the contact of pterygoid, quadrate, and basisphenoid at the posterior edge of the pterygoid. The anterior margin of the foramen is formed by a C-shaped indentation of the pterygoid, while the quadrate and basisphenoid are narrow elongations exposed in the roof and the posterior edge of the foramen. The pterygoid underlies broader exposures of the quadrate and basisphenoid. When compared with the much simpler triple meeting of these three bones in *Taphrosphys,* it seems as if the pterygoid of *Azabbaremys* had been dragged posteriorly over the other two bones, pulling the foramen with it. *Arenila* also seems to have the foramen posterius canalis carotici interni formed at the juncture of pterygoid, quadrate, and basisphenoid. Anterior to the foramen in *Azabbaremys* is a shallow concavity formed mostly by the pterygoid, with an anteromedial margin that extends right across the pterygoid. This is the scar for the M. pterygoideus, very shallow in *Azabbaremys.* In *Arenila* and *Nigeremys* this concavity is much deeper and fully defined, with posteromedial walls completely lacking in *Azabbaremys.*

The processus trochlearis pterygoidei in *Azabbaremys* is preserved only on the left side and its distal margins are missing. Its base has been broken and the process displaced dorsally and anteriorly. As preserved, the processus is not extensive; it would appear to be similar in shape and extent to that in the living pelomedusids and smaller than in the podocnemidids. The orientation of the processus trochlearis pterygoidei in *Azabbaremys* is posterolateral, rather than mostly lateral as in many podocnemidids. The *Azabbaremys* processus differs from Pelomedusidae in having a ridge along its ventrolateral edge, rather than being curved. The processus trochlearis pterygoidei of *Nigeremys* is present on both sides but badly damaged. Nonetheless, it is consistent with what is known in *Azabbaremys. Arenila,* however, is figured (Lapparent de Broin and Werner, 1998: fig. 12 and plates 6, 7) as having a large processus trochlearis pterygoidei that is oriented directly posteriorly, a condition otherwise known only in chelids.

The foramen palatinum posterius is formed in the pterygoid-palatine suture in *Azabbaremys* as in most bothremydids. It is preserved only on the left side and faces ventrolaterally rather than ventrally, at least partially as a result of postmortem deformation. However, the arching of the palate in *Azabbaremys* is somewhat greater than in *Nigeremys* and *Arenila,* so that the curve from the palate around the base of the processus trochlearis pterygoidei is more pronounced. Also, the foramen palatinum posterius is located more laterally than in *Nigeremys* and *Arenila,* resulting in a foramen that opens more laterally into the fossa temporalis in *Azabbaremys* than in the others.

The anterior contacts of the pterygoid at the base of the processus trochlearis pterygoidei in *Azabbaremys* can be seen on the left side. The pterygoid-palatine contact wraps around the base of the processus from the foramen palatinum posterius dorsally to the edge of the pterygo-palatine channel. In the anterior wall of the fossa temporalis the pterygoid is clearly separated from the medial process of the jugal by the palatine. This is an unusual condition; in nearly all pleurodires the jugal contacts the pterygoid in this area. The entire postorbital wall that is formed by medial processes of the postorbital and jugal in all other pleurodires is absent in *Azabbaremys.* The enlarged palatine forms the only remaining anterior support for the base of the processus trochlearis pterygoidei in *Azabbaremys.* Unfortunately, this region is poorly preserved in *Nigeremys* and *Arenila,* but in *Taphrosphys* the wall is also absent.

The dorsal surface of the pterygoid bears the crista pterygoidea and forms the floor of the canalis cavernosus and foramen nervi trigemini. The crista pterygoidea is preserved and visible on both sides in *Azabbaremys.* It rises above the level of the pterygoid plate and meets the processus inferior parietalis, making up the lower third of the braincase wall. The crista plus processus are relatively narrow in comparison to such forms as *Podocnemis.* The foramen nervi trigemini has been eroded along its margins as well as the anterior margin of the processus inferior parietalis. However, the damage is not enough to significantly narrow this structure.

The bone, prootic plus pterygoid, making up the anterior wall of the canalis cavernosus, is eroded, opening up the canalis on both sides. Nonetheless, the relative positions of the foramen nervi trigemini and the foramen stapedio-temporale can be determined. These foramina are relatively close to each other, as in *Taphrosphys, Bothremys, Rosasia,* and *Foxemys.* The foramina are not determinable in *Arenila* and *Nigeremys* due to poor preservation.

SUPRAOCCIPITAL

The supraoccipital is present and nearly complete in *Azabbaremys,* but only the right side is visible; the left side is still covered with matrix.

The median section of the supraoccipital underlies the two parietals along the midline. Their mutual contact slopes anteroventrally. The crista supraoccipitalis in *Azabbaremys* is relatively short, comparable to that in living pelomedusids, but slightly longer than in *Taphrosphys.* Although incomplete, the crista in *Arenila* seems to be longer than in *Azabbaremys,* compared to the position of the condylus occipitalis. The crista supraoccipitalis in *Nigeremys* is similar in length to *Azabbaremys* but seems to be incomplete. The crista supraoccipitalis in *Azabbaremys* is deeper anteriorly and narrows to an acute posterior end. In *Taphrosphys* the end of the crista is curved and blunt. The very end of the crista is broken off in *Azabbaremys,* but it is already very narrow and is probably missing only a small section.

The laterally projecting otic portion of the supraoccipital in *Azabbaremys* contacts the prootic anterolaterally, the opisthotic laterally, and the exoccipital posterolaterally. In contrast to the *Bothremys* Group (*Foxemys, Rosasia, Bothremys*), there is no supraoccipital-quadrate contact.

EXOCCIPITAL

Both exoccipitals are preserved in *Azabbaremys*; they are complete, but only the right one is entirely free of matrix. Both have clear sutures.

The exoccipital in *Azabbaremys* contacts the supraoccipital dorsally, the opisthotic laterally, and the basioccipital ventrally and ventrolaterally. There is also a contact with the quadrate ventrolaterally between the basioccipital and opisthotic. This quadrate contact is found in all bothremydids and is absent in all other pelomedusoides.

The exoccipital in *Azabbaremys* forms all of the condylus occipitalis; the basioccipital enters the neck of the condyle. The exoccipitals make up the condyle in all of the described bothremydids. However, this cannot be substantiated in either *Nigeremys* or *Arenila* due to poor preservation, but Lapparent de Broin and Werner (1998) describe both taxa as having this feature. In *Azabbaremys* the exoccipitals are eroded on the midline, giving the condyle a bilobar appearance. The foramen jugulare posterius is formed almost entirely by the exoccipital, with a narrow section of opisthotic entering the foramen dorsolaterally. The foramen is entirely closed by bone, as in *Taphrosphys, Arenila,* and *Bothremys,* in contrast to the open condition in *Foxemys.* Between the foramen jugulare posterius and the condylus occipitalis are the two foramina nervi hypoglossi.

BASIOCCIPITAL

The basioccipital in *Azabbaremys* is complete and clearly defined.

The basioccipital is a wide but very short, triangular element in *Azabbaremys.* It makes up the medial half of the tuberculum basioccipitale along with the quadrate laterally. Its entire anterior length is a transverse contact with the basisphenoid. Posteriorly and dorsally, the basioccipital contacts the exoccipitals, reaching only the base of the condylus occipitalis. Between the paired tubercula basiocciptale is a shallow median concavity that extends slightly onto the basisphenoid. The basioccipital in *Nigeremys* is not clearly defined by sutures. This element in *Taphrosphys* is much larger, longer and just as wide. *Arenila* has a longer basioccipital also, and its anterior contact with the basisphenoid is curved and concave posteriorly.

PROOTIC

Both prootics are present and visible in *Azabbaremys*, although they are eroded in the area of the canalis cavernosus and the sutures are not clear everywhere.

The prootic in *Azabbaremys* contacts the supraoccipital posteromedially, the parietal medially, the pterygoid ventrally, the quadrate laterally, and the opisthotic posterolaterally. The prootic forms the medial margin of the foramen nervi trigemini, the parietal forms the anterodorsal corner, and the pterygoid forms the anterior and ventral margin. The foramen nervi trigemini as preserved is incomplete on both sides due to erosion of the medial margin exposing the canalis cavernosus. The prootic-pterygoid suture is gone in this area, so its position and the relative amount of prootic versus pterygoid contribution to the margin of the foramen nervi trigemini is not determinable. The foramen stapedio-temporale is formed in the prootic-quadrate suture and opens directly anteriorly as in most bothremydids. Although much of the bone between the foramen stapedio-temporale and the foramen nervi trigemini is eroded away, it can be seen that these structures were relatively close together as in *Taphrosphys* and *Bothremys*. The entire area of the prootic and its associated structures is unavailable for study in *Nigeremys* and *Arenila*.

OPISTHOTIC

The opisthotic is preserved complete on both sides of *Azabbaremys*. It is clearly defined and visible except on the dorsal area of the left side where it is covered with matrix.

The opisthotic has the usual contacts for bothremydids: 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 half of the fenestra is formed by the quadrate. The fenestra is an oblong oval, presumably the stapedial artery lying in the upper part and the lateral head vein in the lower part. The processus interfenestralis of the opisthotic forms the relatively thick lateral wall of the foramen jugulare posterius, contacting the exoccipital ventromedially and the quadrate ventrolaterally. A distinct foramen, probably the foramen externum nervi glossopharyngei, penetrates the middle of the processus interfenestralis. Above this foramen is a much smaller foramen, which could alternatively be interpreted as the foramen nervi glossopharyngei. Neither can be probed, so their identification is in doubt. Neither of these foramina are found in *Bothremys*.

BASISPHENOID

The basisphenoid is present and clearly defined in *Azabbaremys*.

The basisphenoid in *Azabbaremys* has the triangular shape typical for many bothremydids, wider than long, with a straight transverse posterior suture with the basioccipital, rather than the curved suture seen in *Arenila*. The lateral contact with the quadrate is relatively narrow. Anterolaterally the junction of basisphenoid, quadrate, and pterygoid forms the foramen posterius canalis carotici interni (see Pterygoid and fig. 3). The anterior contacts of the basisphenoid are with the pterygoids.

The dorsal surface of the basisphenoid can be seen inside the nearly cleaned out cavum cranii. An endocast has been made to facilitate this study. The dorsum sellae is relatively high, compared to living Pelomedusoides and *Bothremys*. A well-developed processus clinoideus rises on each side of the dorsum also in contrast to the lower processus clinoideus of *Bothremys* and living pelomedusoides. The dorsum sellae in *Azabbaremys* does not overhang the sella turcica, also in contrast to the above taxa. The sella turcica is shorter due to the very short rostrum basisphenoidale, in contrast to the longer sella and very long rostrum in *Bothremys* and the living Pelomedusoides. The rostrum basisphenoidale in *Azabbaremys* is very short, with a deep concave anterior face. On either side thin walls may represent ossified portions of the trabeculae. The entire dorsal basisphenoid morphology in *Azabbaremys* is a foreshortened version of that seen in other pelomedusoids. This is consistent with the ventral morphology, which also shows a foreshortened basisphenoid.

RELATIONSHIPS

Azabbaremys is a pleurodire because it has these synapomorphies for the Pleurodira (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 (sensu 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 meeting on midline. *Azabbaremys* can be identified as a member of the family Bothremydidae based on these synapomorphies: (1) precolumellar fossa absent, (2) occipital condyle 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, *Azabbaremys* can be allied with *Taphrosphys, Nigeremys,* and *Arenila,* the *Nigeremys* Group of Lapparent de Broin and Werner (1998), because it has an open postorbital wall and a dorsally arched palate. It also lacks the supraoccipital-quadrate contact, a synapomorphy of the *Bothremys* Group.

ACKNOWLEDGMENTS

We wish to thank our associates, Drs. Peter Meylan, Roger Wood, and Haiyan Tong, for their support and contributions to the pleurodire project. The data matrix and phylogenetic analysis has been a joint effort with them. We are grateful to Utako Kikutani for the photos and line drawings, and to Ed Heck for the shaded palate and other work on all the figures, and to William Lindsay for his expertise in the fine preparation of the specimen. We also appreciate the help of Judy Galkin in the preparation of the paper. Cyril Walker and Dick Moody would also like to thank Dr. John Hall and Margaret Hall for their hospitality and support during the trials and tribulations of the ill-fated Nigerian expedition.

REFERENCES

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). Ciênc. Terra 9: 153–200.
Baur, G.
1891. Notes on some little known American fossil tortoises. Proc. Acad. Nat. Sci. Philadelphia 43: 411–430.
Bergounioux, F.-M., and F. Crouzel
1968. Deux tortues fossiles d'Afrique. Bull. Soc. Hist. Nat. Toulouse 104: 1–2, 179–186, 3 figs.
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. Stud. Palaeochelonoiol. 2(5): 103–142.
Cope, E. D.
1864. On the limits and relations of the Raniformes. Proc. Acad. Nat. Sci. Philadelphia 16: 181–183.
1865. Third contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia 17: 185–198.
1868. On the origin of genera. Proc. Acad. Nat. Sci. Philadelphia 20: 242–300.
Gaffney, E. S.
1975. A revision of the side-necked turtle *Taphrosphys sulcatus* (Leidy) from the Cretaceous of New Jersey. Am. Mus. Novitates 2571: 24 pp.
1977. An endocranial cast of the side-necked turtle, *Bothremys,* with a new reconstruction of the palate. Am. Mus. Novitates 2639: 12 pp.
1979. Comparative cranial morphology of recent and fossil turtles. Bull. Am. Mus. Nat. Hist. 164(2): 65–376.
Gaffney, E. S., and P. A. Meylan
1988. A phylogeny of turtles. In M. J. Benton (ed.), The phylogeny and classification of the tetrapods. Vol. 1, Amphibians, reptiles, birds. Syst. Assoc. Spec. Vol. 35A: 157–219.
1991. Primitive Pelomedusid turtle. In J. G. Maisey (ed.)., Santana fossils: an illustrated atlas: 335–339. Neptune, NJ: TFH Publications.

Gaffney, E. S., and R. Zangerl
1968. A revision of the chelonian genus *Bothremys* (Pleurodira: Pelomedusidae). Fieldiana Geol. 16: 193–239.
Halstead, L. B.
1979a. The International Palaeontological Expedition to Sokoto State 1977–1978. Niger. Field Monogr. 1: 3–30.
1979b. A taxonomic note on new fossil turtles. Niger. Field Monogr. 1: 48–49.
Lapparent de Broin, F. de, and C. Werner
1998. New late Cretaceous turtles from the western desert, Egypt. Ann. Paléontol. 84(2): 131–214.
Leidy, J.
1865. Memoir on the extinct reptiles of the Cretaceous formations of the United States. Smithson. Contrib. Knowledge vol. 14, art. 6: 1–135.
Linnaeus, C.
1758. Systema naturae. 10th ed., vol. 1. Stockholm, 824 pp.
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. J. Vertebr. Paleontol. 16(1): 20–33.
Moody, R. T. J., and P. J. C. Sutcliffe
1990. Cretaceous-Tertiary crossroads of migration in the Sahel. Geol. Today Jan.–Feb.: 19–23.
1991. The Cretaceous deposits of the Iullemmeden Basin of Niger, central West Africa. Cretac. Res. 12: 137–157.
1993. The sedimentology and palaeontology of the Upper Cretaceous-Tertiary deposits of central West Africa. Mod. Geol. 18: 459–474.
Tong, H., E. S. Gaffney, and E. Buffetaut
1998. *Foxemys*, a new side-necked turtle (Bothremydidae: Pelomedusoides) from the Late Cretaceous of France. Am. Mus. Novitates 3251: 19 pp.
Walker, C. A.
1979. New turtles from the Cretaceous of Sokoto. Niger. Field Monogr. 1: 42–48.

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