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Kurmademys, a New Side-Necked Turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of India

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ABSTRACT

The Maastrichtian Kallamedu Formation of southern India near the village of Kallamedu, Tamil Nadu, has yielded skulls and postcrania of a new genus of side-necked turtle. *Kurmademys kallamedensis*, new genus and species, is based primarily on a single well-preserved skull. *Kurmademys* is a pelomedusoid pleurodire belonging to the family Bothremydidae Baur, 1891, with these bothremydid characters: (1) exoccipital-quadrato contact, (2) incisura collicularis closed by bone, and (3) eustachian tube and stapes separated by bone. *Kurmademys* is unique among known bothremydids in having extensive temporal emargination, a small postorbital, a large precollicular fossa, and a foramen posterius canalis carotici interni formed completely by the basisphenoid.

INTRODUCTION

Pleurodires, or side-necked turtles, are not part of the recent fauna of the Indian subcontinent, but they are known as fossils from the late Cretaceous into the Neogene. Their record in India, however, is very poor. Summaries of this record are in Wood (1970), de Broin (1987, 1988), and Jain (1986). Good skulls of the podocnemidid *Shweboemys* are known

from the Neogene of Burma and Pakistan (see Wood, 1970). A skull of a pleurodire, *Shweboemys pisdurensis*, has been described by Jain (1977, 1986) and an unnamed bothremydid has been mentioned in Singh et al. (1998). *Shweboemys pisdurensis* appears to be a broad-jawed podocnemidid related to *Shweboemys* and *Stereogenys* (Wood, 1970). The bothremydid skull (SD S/VPL 1125) is pres-

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ently being studied by Gaffney, Sahni, Singh, and Schleich. This skull is a bothremydid, but distinct from *Kurmademys*. The shell of pelomedusoids is notoriously conservative and inadequate to distinguish bothremydids from podocnemidids even when completely known. Thus, the Indian pleurodire record rests on the two skulls indicated above and the new material from Kallamedu.

Shweboemys pisdurensis consists of a skull, nearly complete shell material, and some postcranial elements from the Maastrichtian Lameta Formation at Pisdura and Dongargaon, in Maharastra State, central India. We have not seen this material, but the skull does appear to be similar to the described *Shweboemys* of Wood (1970). The unnamed bothremydid skull of Singh et al. (1998) is from the Maastrichtian intertrapean Green Tuff bed of Amboli Quarry, Jogeshwari, Bombay. Features of this specimen are noted in the comparisons below.

Although the 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), Broin de Lapparent 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). 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), and *Nigeremys* (Bergounioux and Crouzel, 1968; Lapparent de Broin and

Werner, 1998). Other skulls of pelomedusoids are *Araripemys* (Meylan, 1996), and an unnamed Santana genus (FR 4922) (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).

This paper is intended to name and briefly describe this new taxon. More detailed comparative descriptions and a systematic analysis are part of a larger project on pleurodires (Gaffney, Meylan, and Wood, 1997; Gaffney, Tong, Chatterjee, Moody and Hirayama, 1998).

We use Lapparent de Broin and Werner's (1998) informal reference to a *Bothremys* Group and a *Nigeremys* Group (which includes *Taphrosphys*). These continue to form monophyletic taxa in most of our current analyses. Contents of these groups are as follows: *Bothremys* Group—*Bothremys*, *Rosasia*, *Zolhafah*, *Foxemys*; *Nigeremys* Group—*Nigeremys*, *Arenila*, *Taphrosphys*.

Institutional Abbreviations

ISI	Indian Statistical Institute, Calcutta, India
FR	Forschungsinstitut Senckenburg, Frankfurt, Germany
AMNH	American Museum of Natural History, New York, USA

Anatomical Abbreviations

bo	basioccipital
bs	basisphenoid
ex	exoccipital
fpcci	foramen posterius canalis carotici interni
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



Fig. 1. Type locality of *Kurmademys kallamedensis*, ISI R152, near the village of Kallamedu, Tamil Nadu, southern India. The turtle material occurs here in a 6 in. thick pocket of fine grained sandstone and clay in the upper Maastrichtian Kallamedu Formation.

SYSTEMATICS

ORDER TESTUDINES LINNAEUS, 1758

MEGAORDER PLEURODIRA COPE, 1864 (FIDE
GAFFNEY AND MEYLAN, 1988)

HYPERFAMILY PELOMEDUSOIDES COPE, 1868

FAMILY BOTHREMYDIDAE BAUR, 1891

Kurmademys, new genus

TYPE SPECIES: *Kurmademys kallamedensis*,
new genus and new species.

DISTRIBUTION: Maastrichtian of central India.

ETYMOLOGY: *Kurma*, "turtle" in Sanskrit, in allusion to the second-stage incarnation of Lord Vishnu as a turtle in Hindu mythology.

DIAGNOSIS

A genus of bothremydid pleurodire with triangular skull, orbits dorsolaterally placed, not dorsally as in *Bothremys*; extensive temporal and cheek emargination similar to *Pelusios* and *Pelomedusa*, but unique among bothremydid; jugal enters orbit; postorbital

short in contrast to *Foxemys* and *Bothremys*; triturating surfaces triangular in contrast to narrow in *Nigeremys* Group, but not greatly expanded as in *Foxemys*, *Rosasia*, *Zolhafah*, and *Bothremys*; no pit in triturating surface in contrast to *Bothremys* and *Rosasia*; maxilla-quadrangle contact absent; palatine extensively exposed on triturating surface as in all *Bothremys* Group; antrum postoticum large in contrast to small in *Bothremys*; eustachian tube separated from stapes as in all other bothremydid; incisura columellae auris closed as in *Bothremys* and *Taphrosphys*; precolumellar fossa large as in pelomedusids, but unique among bothremydid; pterygoideus depression moderate as in *Rosasia*, not deep as in *Foxemys*; foramen posterius canalis carotici interni completely enclosed in basisphenoid unique among pelomedusoids; supraoccipital-quadrangle contact present as in all *Bothremys* Group; foramen stapedio-temporale visible in dorsal view in contrast to all other bothremydid.

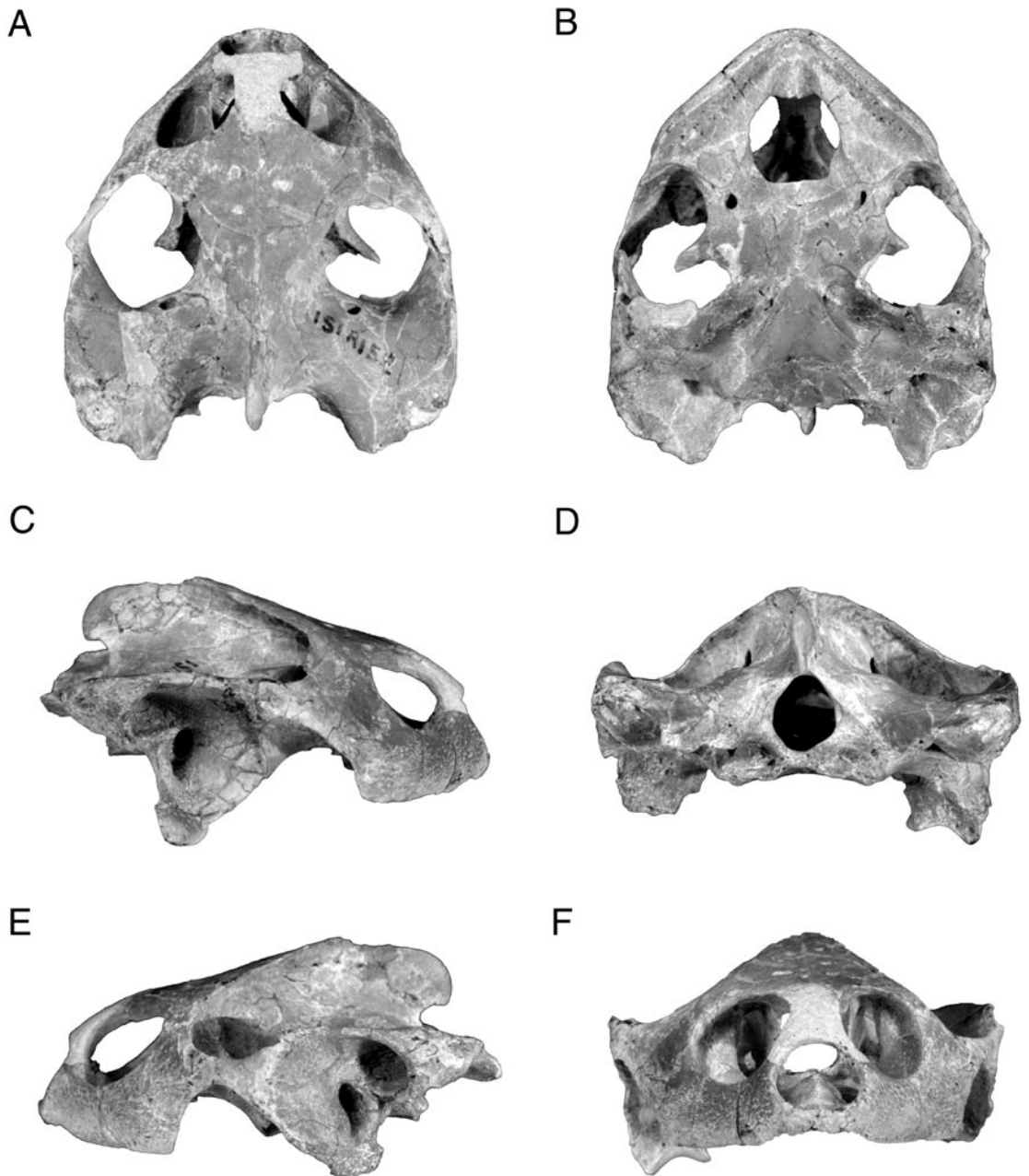


Fig. 2. *Kurmademys kallamedensis*, n. gen. & sp., ISI R152. A, dorsal; B, ventral; C, right lateral; D, posterior; E, left lateral; F, anterior.

Kurmademys kallamedensis, new species

TYPE SPECIMEN: ISI R152, a nearly complete skull lacking the dorsal part of the prefrontals, the posterior part of the crista su-

praoccipitalis, and part of the left quadratojugal.

TYPE LOCALITY: Near the village of Kallamedu, Tamil Nadu, southern India. Map of locality is in Sastry et al. (1972).

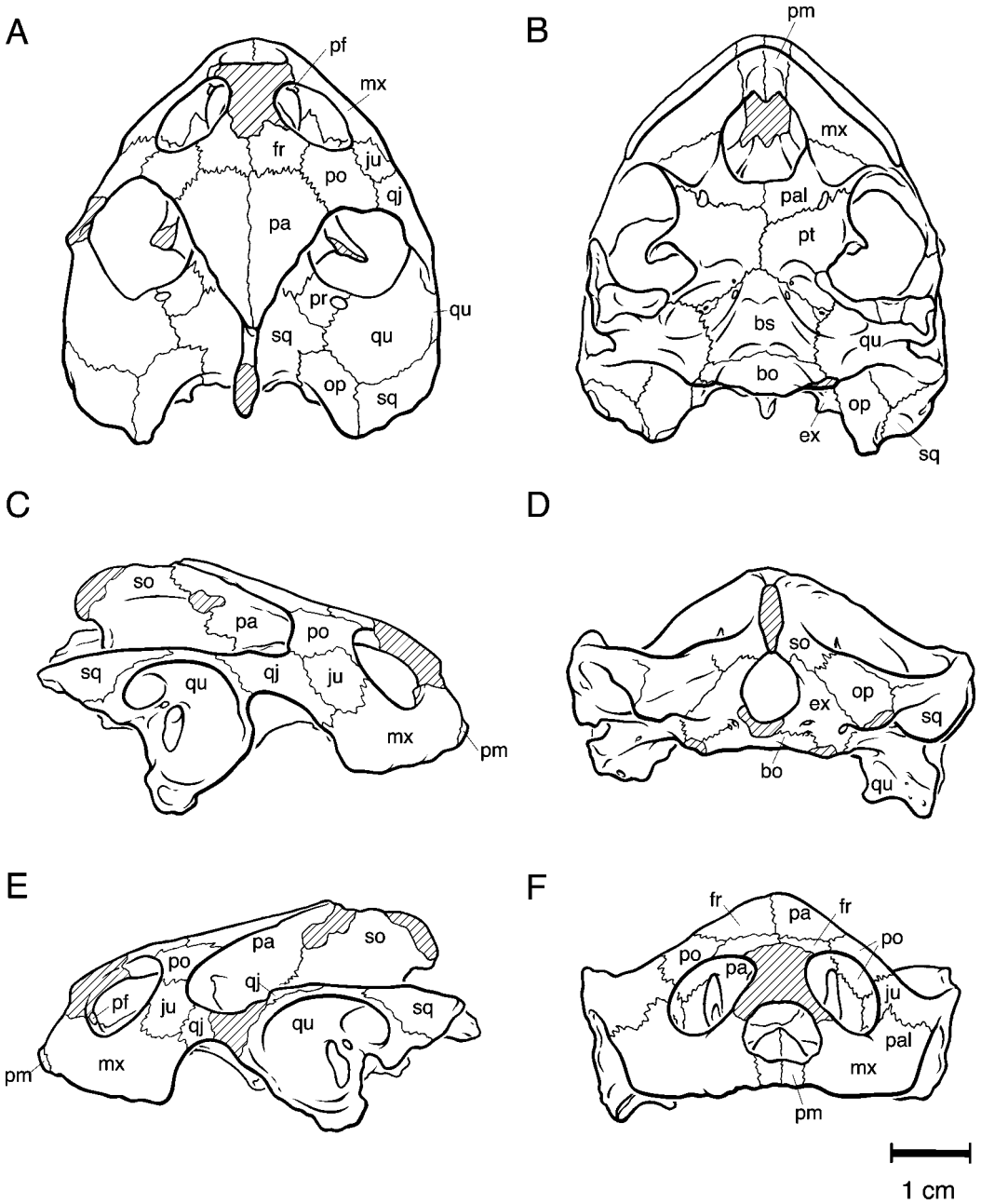


Fig. 3. Key for fig. 2.

HORIZON: Kallamedu Formation of the Ariyalur Group. Formation named and described by Sastry et al. (1972), who correlated it with the uppermost Maastrichtian; the Cretaceous-Tertiary boundary is its upper limit (Sastry et al.: 6). Dinosaurs have been

described from other exposures of the Kallamedu (Matley, 1929; Yadagiri and Ayyasami, 1987). The *Kurmademys* locality is a small pocket of fine-grained sandstone and clay, about 6 in. thick. It also contained crocodiles, gar scales, and freshwater gastropods

and bivalves and is interpreted as a freshwater pond deposit.

DIAGNOSIS: As for genus.

ETYMOLOGY: For the Kallamedu Formation.

REFERRED MATERIAL: ISI R155A, partial skull; ISI R155B, partial skull; ISI R155C, partial skull; ISI R158, partial skull; ISI R159, partial skull.

DESCRIPTION

The *Kurmademys kallamedensis* type skull, ISI R152 has a premaxilla-condyle median length of 47.2 mm, a maximum width of 49.4 mm, and a height from condylus mandibularis of the quadrate to the top of the skull roof of 28.2 mm.

The order of elements and the order of topics within elements follows Gaffney (1979). More general features of the pleurodire skull and explanations of terminology can also be found in Gaffney (1979) and are not repeated here.

Although at present six skulls of *Kurmademys* are known, the type specimen, ISI R152, forms the basis of this description, with a few contributions from the other specimens. The type skull is the best preserved and nearly complete. The other five skulls are not as well preserved and are not yet fully prepared.

PREFRONTAL

Almost all of both prefrontals are missing in the type skull, ISI R152. The only fragments of prefrontal remaining are the ventralmost tips of right and left prefrontals lying on the medial side of the maxillae in the anterior orbital walls. There is more of the right prefrontal than the left. The dorsal area of the prefrontals has been restored arbitrarily on ISI R152. However, ISI R158 has prefrontals preserved.

The shape and extent of prefrontal in *Kurmademys* is consistent with that seen in most other pelomedusoids, such as FR 4922. They meet for their entire length on the midline. There are no nasals.

FRONTAL

Both frontals are nearly complete in ISI R152, but their anteriormost margins are

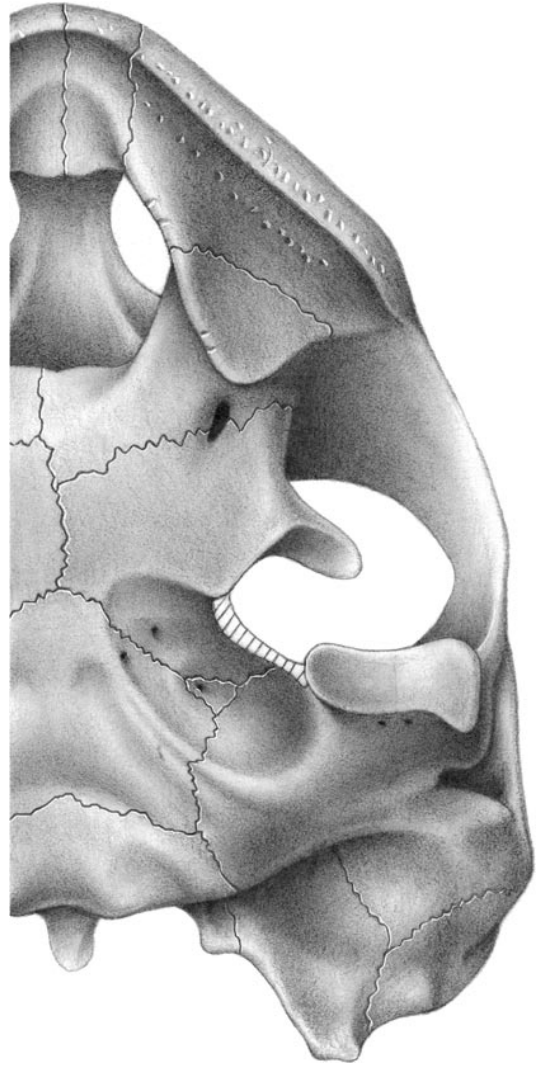


Fig. 4. *Kurmademys kallamedensis*, n. gen. & sp. Partially restored ventral view. See fig. 3 for bone identifications.

breaks rather than sutures, so the contact with the prefrontals is not determinable. However, the extent preserved is comparable to the frontal as seen in *Pelomedusa* and *Pelusios*, so it is not likely that much frontal is missing.

As in other pelomedusoids, the frontal of *Kurmademys* contacts the postorbital laterally and the parietal posteriorly. Its contacts and relative size are very similar to *Pelusios* and *Pelomedusa*. On the ventral surface the frontal of *Kurmademys* has a parasagittal

ridge separating fossa orbitalis from the sulcus olfactorius. The sulcus is slightly narrower anteriorly than in *Pelusios*, but widens posteriorly as in *Pelusios* and most pelomedusoids. The processus inferior parietalis meets the posterior edge of the frontal ridge dorsally as in FR 4922, without a ventral process as in *Pelusios*.

In other pelomedusoids, such as *Bauruemys*, FR 4922, and *Pelusios*, the frontal is thickened lateral to the sulcus olfactorius ridge and forms a wall for the fossa orbitalis anteriorly and a dorsal margin of the pterygo-palatine channel posteriorly. This wall is usually continuous with the posterior orbital wall laterally and ventrally. However, in *Kurmademys* the frontal is relatively thin and there is no distinct connection between the sulcus olfactorius ridge and the posterior orbital wall. The pterygo-palatine channel is relatively open dorsally, at the anterior end, in contrast to most other pelomedusoids, which have a more restricted ridge of bone here.

PARIETAL

Both right and left parietals are complete in ISI R152, except for small cracks and breaks.

The dorsal plate of the parietal is not extensive in *Kurmademys*. Anteriorly there is a transverse contact with the frontal, and laterally a contact with the postorbital. There is no contact between the parietal and quadratojugal; the postorbital is widely exposed along the edge of the temporal emargination. The temporal part of the parietal is about as extensive as in the living *Pelomedusa*, which is slightly more emarginate than most *Pelusios*.

The ventral wall of the parietal, the processus inferior parietalis, can be seen in both sides of ISI R152. The wall is similar to that in other pelomedusoids. The anterior margin of the wall is formed completely by the parietal and curves ventrally without the posterior indentation seen in some *Pelusios*. Ventrally the parietal contacts the pterygoid, which is low until it reaches the area anterior to the foramen nervi trigemini, where the pterygoid/parietal contact is more dorsal. The foramen nervi trigemini in *Kurmademys* is formed by the parietal, pterygoid, and pro-

otic as in most other pelomedusoids. Posteriorly the parietal contacts the supraoccipital and prootic as in other pleurodires. The parietal of *Kurmademys* also has a short ventral process below its lateral margin that contacts the dorsal process of the palatine in the lateral wall of the sulcus palatinoptyergoideus (Antunes and Broin, 1988).

JUGAL

The jugal in ISI R152 is preserved on both sides, but surrounding contacts are seen only on the right side.

The jugal is relatively small in *Kurmademys*, similar to *Pelusios* and *Pelomedusa*, and much smaller than in podocnemidids. The jugal is exposed in the posterior margin of the orbit, but its exposure is reduced by a posterodorsal process of the maxilla. Ventrally the jugal contacts the maxilla, and posteriorly the quadratojugal. The jugal is not exposed on the dorsal edge of the cheek emargination due to a contact of the quadratojugal and maxilla. This is unusual because *Kurmademys* has a cheek emargination at least as extensive as in *Pelomedusa* and *Pelusios*, and they have a large exposure of the jugal along this emargination.

The medial process of the jugal in ISI R152 is preserved and visible on both sides. It is basically similar to that area described by Gaffney (1979: figs. 53, 130) for *Pelusios*. The medial process of *Kurmademys* contacts the palatine medially and the maxilla anteriorly. The jugal forms part of the anterior wall of the adductor muscle chamber as in most pelomedusoids. The jugal contacts the postorbital medially and the pterygoid ventromedially. Ventrally the jugal contacts the maxilla. All of these contacts are quite similar to *Pelusios*.

QUADRATOJUGAL

The quadratojugal in ISI R152 is nearly complete on the right side. Some small parts of the dorsal and ventral margin are probably missing, but based on the tapering of the bone and on surrounding bones, very little of the quadratojugal is missing. On the left side, however, only the anterior part and a small fragment of the posterodorsal contact with the quadrate are preserved.

The quadratojugal of *Kurmademys* is unusually small for pelomedusoids, because the temporal and cheek emarginations are both extensive. *Kurmademys* is unique among bothremydids in having such a small quadratojugal and narrow temporal arch. The quadratojugal contacts the quadrate posteriorly, the postorbital anterodorsally, the jugal anteriorly, and the maxilla anteroventrally. The dorsal margin of the quadratojugal forms the lateral edge of the temporal emargination and the ventral margin forms the dorsal edge of the cheek emargination.

SQUAMOSAL

Both right and left squamosals are present in ISI R152 and both have some damage to their posterolateral margins, but are otherwise complete.

As in most turtles, the squamosal of *Kurmademys* is cone shaped, forming the posterolateral portion of the antrum postoticum. As in other turtles, the squamosal of *Kurmademys* fits onto the circular posterior end of the quadrate and contacts the opisthotic medially. *Kurmademys* has an extensive temporal emargination and the squamosal has no contact with parietal or postorbital. The right side of ISI R152 also shows that, although the squamosal has a narrow anterior process lying on the quadrate, the process does not reach the quadratojugal. In *Pelusios* and *Pelomedusa* there is usually a contact between the quadratojugal and squamosal, although there is some individual variation with some specimens having a very slight contact or no contact. However, none of the specimens of *Pelusios* or *Pelomedusa* available to us show the degree of reduction of quadratojugal and squamosal nor the extent of dorsal exposure of the quadrate seen in *Kurmademys*. This feature is unique to *Kurmademys*. The dorsolateral surface of the squamosal in *Kurmademys* is rounded, with no parasagittal ridge or wall seen in other Pelomedusoides. This ridge is a function of the degree of temporal emargination and is present to a varying extent in all other Pelomedusoides.

The antrum postoticum is preserved on both sides of ISI R152, and its internal extent is visible. The antrum is larger in *Kurmademys* than in any other Pelomedusoides. *Pe-*

lusios, *Pelomedusa*, and FR 4992 have a large antrum postoticum, but the antrum of *Kurmademys* is even larger. The size in FR 4992, *Pelusios*, and *Pelomedusa* is interpreted as the primitive condition for Pelomedusoides, because this is the condition in chelids. The *Kurmademys* condition is tentatively interpreted as a unique autapomorphy of this genus, because our current analyses show *Kurmademys* deep within the Bothremydidae.

POSTORBITAL

The postorbital is preserved on both sides of ISI R152. The posterior edge of the left postorbital is missing bone when compared with the more complete right postorbital.

The size and relations of the postorbital in *Kurmademys* are very similar to the postorbital in *Pelusios* and *Pelomedusa*. The postorbital of *Kurmademys* lies between the orbit anteriorly and the temporal margin posteriorly and forms part of the margins of those openings. Medially the postorbital contacts the frontal anteriorly and the parietal posteriorly. Laterally the postorbital contacts the jugal anteriorly and the quadratojugal posteriorly. All of these contacts are as in *Pelusios* and *Pelomedusa*. FR 4922 differs in having a broad contact of the parietal and quadratojugal posterior to the postorbital.

The ventral process of the postorbital is also similar to that in *Pelusios* and *Pelomedusa*. As exposed in the anterior wall of the temporal fossa, the postorbital contacts the parietal medially, the pterygoid ventrally, and the jugal laterally. On the right side, which is better preserved than the left side, there is a small contact between the parietal and pterygoid, preventing exposure of the postorbital in the pterygo-palatine channel at this point. In the posterior wall of the fossa orbitalis, the ventral process of the postorbital contacts the dorsal process of the palatine medially in a sloping suture. Laterally the postorbital contacts the jugal. The medial surface of the ventral process of the postorbital forms the lateral wall and the lateral part of the roof of a relatively short pterygo-palatine channel.

PREMAXILLA

Both premaxillae are present in ISI R152 and are nearly complete.

Laterally the premaxilla contacts the maxilla in a parasagittal suture, and it contacts the other premaxilla medially. The posterior margin of the premaxilla forms at least part of the apertura narium interna, but has a broken edge medially. The broken edge does not show a sutural surface anywhere and there is no fragment of a vomer, but it is possible that one was present. The premaxilla in FR 4922 has a process of the maxilla lying behind it, but this is absent in ISI R152. The dorsal surface of the premaxilla forms part of the floor of the fossa nasalis. In *Kurmademys* the premaxillae curve dorsally to form a sharply rising median ridge in the fossa. This median ridge is present in other pelomedusoids, but it is lower and smaller than in *Kurmademys*.

The ventral surface of the premaxilla bears the continuation of the labial ridge. The labial ridge of *Kurmademys* is narrower than in *Pelusios* and lacks the anterior projection of the margin of the apertura narium externa in that form. This area between the apertura narium externa and labial ridge is very thin in *Kurmademys*, similar to FR 4922. *Kurmademys* has a shallow median notch similar to *Pelusios* and wider than in FR 4922. In contrast to *Pelusios* and *Pelomedusa*, *Kurmademys* has a posterior extension to the premaxilla that bears a distinct, ventrally facing concavity on the midline that is the ventral surface of the dorsal ridge in the fossa nasalis. Lower jaws of *Kurmademys* show a marked symphyseal hook. The flat part of the triturating surface narrows considerably from the maxilla to form a narrow shelf between the concavity and the labial ridge. This morphology is also seen in *Bothremys* and *Rosasia* as well as *Neochelys* and some generalized cryptodires like baenids. There is no sign of a foramen praepalatium.

MAXILLA

Both maxillae of ISI R152 are complete except for the distal ends of the dorsal processes, which are missing.

The vertical or alveolar plate of the maxilla is deep and fairly massive, not narrow as in FR 4922, but similar to *Podocnemis*. The maxilla forms the apertura narium externa anteriorly and it is wider at its base than in FR 4922, similar to most other pelomedu-

soids. The apertura is not produced anteriorly as in *Pelusios* and *Podocnemis*. The dorsal process of the maxilla in *Kurmademys* is thinner than in *Pelusios* and *Pelomedusa* and is similar to FR 4922. The ventral margin of the orbit, is formed by the maxilla, which has a dorsal process along the posterior margin of the orbit reducing the contribution made by the jugal to the orbit. Forms such as FR 4922 and *Podocnemis* have a posterodorsal process, but it is separated from the orbit by the jugal. *Pelusios* and *Pelomedusa* do not have this process, but its expression is variable in pelomedusoids. The posterior edge of the maxilla forms the margin of the cheek emargination. Between the cheek emargination and the jugal, the maxilla contacts the quadratojugal.

The horizontal plate of the maxilla is exposed in the orbital floor where the maxilla contacts the palatine medially and forms a small part of the border of the large foramen orbito-nasale. Posteriorly the maxilla contacts the jugal.

The triturating surfaces of *Kurmademys* are narrow anteriorly and widely expanded posteriorly. The maxilla itself, however, tapers posteriorly, so that the palatine forms the posterior and medial portion of the triturating surface. The triturating morphology is similar to that in *Foxemys*, which is also narrow anteriorly and expanded posteriorly, with a significant contribution from the palatine. In both skulls the narrow, anterior part has a raised medial edge along the lingual ridge. They differ in that *Foxemys* has a slight pinching of the snout anteriorly, as in *Rosasia*; this is absent in *Kurmademys*, where the snout is straight. *Foxemys* has two accessory ridges, absent in *Kurmademys*.

The triturating surface in *Kurmademys* is raised anteriorly along the margin of the apertura narium interna. The posterior expanded area is slightly concave. There are no accessory ridges on the triturating surface, which ends posteriorly in a V-shaped margin completely formed by the palatine.

VOMER

There is no vomer present nor are there sutural surfaces remaining for a vomer. However, the bone edges in this area are not en-

tirely complete, and the morphology surrounding the apertura narium interna is very close to that in *Foxemys*, which has a well-developed vomer. Thus it is quite possible that one was present in *Kurmademys*.

PALATINE

Both palatine bones are present in ISI R152, but are missing some of the anterior edges that form the margin of the apertura narium interna and the possible vomerine contact.

The anterolateral part of the palatine in *Kurmademys* contacts the maxilla and forms the posteromedial part of the triturating surface. The triturating surface is a low platform that ends in a V-shaped margin completely formed by the palatine. *Foxemys* is similar to *Kurmademys* in this area. The palatine forms the posterior margin of the apertura narium interna, but most of this margin is missing in ISI R152. The choanal grooves are barely discernible in *Kurmademys*; they are better defined in *Foxemys*. The foramen palatinum posterius is formed in the palatine-pterygoid suture by both bones (fig. 4), as in *Foxemys* and in contrast to FR 4922, *Pelusios*, *Pelomedusa*, and *Podocnemis*, in which most of the foramen is in the palatine. As in other pleurodires, there is a median contact with the other palatine and a transverse, posterior contact with the pterygoid. On the dorsal surface both right and left palatines are visible and free of matrix. The palatine forms the medial part of the orbital floor and the lateral margin of the large foramen orbito-nasale.

Posteriorly the palatine of *Kurmademys* has a large dorsal process forming the lateral wall of the pterygo-palatine channel. This process contacts the jugal laterally, the post-orbital dorsolaterally, and the parietal dorsomedially. The process tapers dorsally, so that its medial edge is higher than its lateral edge. The medial edge forms that lateral margin of the adductor channel. This dorsal process of the palatine reaches the parietal in the postorbital wall, which is quite unusual and has not been found so far in other pelomedusoids. The posterior wall of the orbit is complex in pelomedusoids and particularly so in *Kurmademys*. Behind the dorsal process of the palatine is the ventromedial process of

the postorbital and a short ventral process of the parietal, all visible on the posterior surface of the postorbital wall.

QUADRATE

Most of both quadrates are complete and free of matrix. Part of the medial area of the left quadrate is broken and partially restored with something awful.

The squamosal lies at the posterolateral corner of the quadrate and its relations and contacts with the quadrate in *Kurmademys* are similar to those in *Pelusios* and *Pelomedusa*. The quadrate exposure along the lateral edge of the temporal emargination prevents contact of squamosal and postorbital. Anteriorly the quadrate contacts the quadratojugal, but the contact is relatively small because of the extensive temporal and cheek emargination. The quadratojugal contact is smaller in *Kurmademys* than in *Pelusios*, *Pelomedusa*, or FR 4922.

Most of the quadrate is involved in the formation of the cavum tympani and its two spaces, the antrum postoticum and the precollumellar fossa. The antrum postoticum of *Kurmademys* is unusually large for pelomedusoids; it is as large as the antrum in *Emydura*, the presumed primitive condition for pelomedusoids. The antrum of *Kurmademys* is swollen to completely fill the area inside the space formed by squamosal and quadrate. The precollumellar fossa is also deep and very large in *Kurmademys*, and also comparable in size to primitive chelids. However, other pelomedusoids, such as *Pelusios* and *Pelomedusa*, also have a large precollumellar fossa. In many features, the cavum tympani of *Kurmademys* is more primitive than in other bothremydids.

The other feature of interest in the cavum tympani is the incisura columellae auris, which still has the stapes present in the right quadrate of ISI R152. The incisura is reduced to a completely closed, small foramen containing only the stapes in *Kurmademys*, in contrast to the open incisura of *Foxemys*. *Artenila*, *Zolhafah*, *Bothremys*, and *Taphrosphys* have the closed incisura as in *Kurmademys* but in *Araripemys*, FR 4922, and chelids, it is open. The combination of a completely closed incisura columellae auris with

a gigantic antrum postoticum is a combination unknown so far in pleurodires. The quadrate of *Kurmademys* has a kidney-shaped cavum tympani as in *Bothremys*. Although the incisura columellae auris is completely closed by bone, behind it is a groove formed in the quadrate for the eustachian tube. Dorsally the groove slopes up to a horizontal, straight-edged ridge that separates the eustachian tube surface from the opening for the stapedial artery in the fenestra postotica.

The medial contact of the quadrate is with the prootic anteriorly. As in nearly all other turtles, the prootic and quadrate form the foramen stapedio-temporale. The foramen stapedio-temporale is certainly placed more anteriorly in *Kurmademys* than in *Emydura*, but not any more anteriorly than in FR 4922 or *Pelusios* and *Pelomedusa*. The canalis stapedio-temporalis can be followed posteriorly on the right side to the aditus canalis stapedio-temporalis, which is partially divided from the rest of the fenestra postotica, showing the entry of the stapedial artery into the skull. A separate canal for the stapes itself is present from the incisura columellae auris to the aditus canalis stapedio-temporalis as in *Bothremys* and *Taphrosphys*.

Behind the prootic there is a contact with the supraoccipital in ISI R152 (fig. 3A), that intervenes between the usual opisthotic-prootic contact. This contact also occurs in all other *Bothremys* Group taxa. The opisthotic contact appears to be reduced in favor of expansion of the supraoccipital contact when compared with a more generalized pleurodire like *Pelusios*. The quadrate-opisthotic contact is anteromedial to posterolateral in *Kurmademys*, between the supraoccipital and squamosal.

On the ventral surface the quadrate in *Kurmademys* contacts the pterygoid anteromedially from the base of the condylus mandibularis along the anterolateral edge of the processus articularis, as in most pleurodires, such as *Emydura* and *Pelusios*. *Kurmademys* has a medial process of the quadrate as in other pleurodires, that contacts a narrowly exposed prootic, and broadly contacts the basisphenoid. Behind the basisphenoid, the quadrate has a broad contact with the basioccipital. Dorsal to that the quadrate contacts

the exoccipital. The basioccipital contact of the quadrate characterizes the Bothremyidae plus Podocnemididae, but the exoccipital contact is more restricted, found so far only in the Bothremyidae.

The medial contacts of the quadrate include the opisthotic and prootic as in other turtles. The roof of the fenestra postotica (aditus canalis stapedio-temporalis) has a low parasagittal ridge showing the passage of the more lateral stapedial artery from the more medial (and ventral) lateral head vein. This ridge is largely formed by the quadrate, with the opisthotic contributing medially. The fenestra postotica of *Kurmademys* is subdivided by bony partitions, so that the lateral head vein and stapedial artery are separated from the more medial parts of the fenestra postotica. The opisthotic forms this wall dorsally and the quadrate forms it ventrally. On both sides of ISI R152 the contact of these two bones is broken, and a small amount of compression is visible on the left side. The quadrate also forms the ventral margin of a small opening medial to the one just described, but lateral to the foramen jugulare posterius, which seems to be a remnant of a more open fenestra postotica. In the Bothremyidae in general the fenestra postotica is strongly subdivided and separated by bony partitions. In *Kurmademys* the bony partitions are thinner and some are probably represented by cartilage or thin bone, allowing the collapse and breakage of foramen edges during fossilization. There is a well-developed quadrate-exoccipital contact medially as in *Bothremys*; this is considerably more extensive than the small contact in FR 4922.

The presumed foramen chorda tympani inferius is present on the posterior surface of the processus articularis, roughly similar in position to *Podocnemis*. Because of glue and crud on the right quadrate, this is only visible on the left.

PTERYGOID

Both pterygoids are preserved in *Kurmademys* and both are nearly complete. Most of the thin pterygoid flange extending ventrally from the quadrate process is missing from both pterygoids; the right one is more preserved than the left.

On the ventral surface the pterygoid contacts the palatine in a roughly transverse suture that trends slightly anterolaterally. The foramen palatinum posterius is formed in the palatine-ptyerygoid suture as in nearly all bothremydids. Medially the pterygoids meet on the midline for a bit less than half their length. They are separated posteriorly by the triangular basisphenoid.

As in all pleurodires, there is a laterally projecting processus trochlearis pterygoidei. In *Kurmademys* the processus does not extend at a sharp right angle as in the Santana bothremydids (Gaffney et al., in press), but is only slightly less than a right angle, much as in *Foxemys*. It is not as acute as in chelids and *Araripemys*. The flange or web that extends ventrally from the base of the processus trochlearis pterygoidei along the quadrate process in all pleurodires is mostly missing in *Kurmademys*. The portion preserved is consistent with that seen in other bothremydids.

The posterolaterally extended quadrate processus in *Kurmademys* is narrower and longer than in FR 4922, *Araripemys*, pelomedusids, and chelids. In these groups the process is relatively flat and more horizontal, while in *Kurmademys* and some other bothremydids, such as *Foxemys*, it is narrower and more vertical. This condition seems to be related to the presence of a ventrally concave depression in the posterolateral part of the pterygoid in these forms (fig. 4). This depression is presumably the pterygoideus muscle attachment site. In *Kurmademys* the depression is shallower than in *Nigeremys* and *Foxemys*, but it covers a larger area. Its margins are not as well defined in *Kurmademys* as it is in those taxa. There is no development of an overhang of this depression by the pterygoid as in the Podocnemididae.

The foramen posterius canalis carotici interni in *Kurmademys* lies entirely within the basisphenoid (fig. 3B); the pterygoid does not participate in its formation as it does in many other bothremydids. The *Kurmademys* condition is unique within pelomedusoids. The posterior margin of the pterygoid contacts the narrowly exposed prootic between the basisphenoid and quadrate contacts.

Most of the dorsal surface of the pterygoid is visible in *Kurmademys*, although the re-

gion inside the cavum cranii is variably obscured by pieces of matrix. The crista pterygoidea is relatively low. The pterygoid forms the ventral margin of the foramen nervi trigemini as in other bothremydids, but the foramen is not placed very close to the foramen stapedio-temporale as it is in many other bothremydids, such as *Bothremys* and *Foxemys*. The pterygoid forms the floor of the sulcus palatinoptyerygoideus, which lies between the side wall of the cavum cranii and the processus trochlearis pterygoidei.

The anterior contacts of the pterygoid at the base of the processus trochlearis pterygoidei are visible on both sides of ISI R152. The pterygoid plus the palatine and jugal form the postorbital wall, as exposed posteriorly in the adductor muscle chamber. The pterygoid has a very narrow contact with the parietal medially, broader contacts with the postorbital more laterally, and with the jugal most laterally.

SUPRAOCCIPITAL

The supraoccipital in ISI R152 is complete ventrally and anteriorly, but is missing the posterior part of the crista supraoccipitalis.

The supraoccipital in turtles is Y-shaped, with paired lateral projections forming the medial part of the cavum labyrinthicum on each side. In cryptodires and most pleurodires the supraoccipital has a tripartite suture, with the prootic and opisthotic visible on the dorsal surface of the otic chamber. It is unusual to find that in a group of bothremydids—the *Bothremys* Group of Lapparent de Broin and Werner (1998)—the supraoccipital contacts the quadrate and separates the prootic from the opisthotic. In *Kurmademys* this unusual condition is present. The supraoccipital on the right side has a broad contact with the quadrate laterally and separates the prootic from the opisthotic. On the left side the supraoccipital is complete and separates the prootic and opisthotic, but the quadrate is damaged. This degree of quadrate contact by the supraoccipital is similar in *Kurmademys*, *Bothremys*, *Foxemys*, and *Rosasia*. The contact is absent in *Taphrosphys* and indeterminate in *Zolhafah*, *Nigeremys*, and *Arenila*.

The crista supraoccipitalis is usually relatively short in bothremydids. In *Kurmademys*

it is broken posteriorly and its length is indeterminate.

EXOCCIPITAL

Both exoccipitals are preserved and only lack the condylus occipitalis, although there is some breakage around the posterior foramina.

The exoccipital contacts the supraoccipital dorsally, the opisthotic dorsolaterally, the quadrate ventrolaterally, and the basioccipital ventrally. The quadrate-exoccipital contact occurs in all Bothremydidae and is absent in other pleurodires.

Dorsomedially the exoccipital forms the lateral and ventral margin of the foramen magnum. Ventromedially the exoccipital presumably participates in the formation of the condylus occipitalis, but this structure is broken off at its base in ISI R152, so the presence or absence of the basioccipital in the condylus is not determinable. The foramen jugulare posterius in *Kurmademys* is formed entirely by the exoccipital. The bone surrounds most of the foramen, but on each side the foramen is open laterally due to the presence of a narrow fissure. This fissure is different in shape on both sides and may be due to breakage, in which case the original condition of the foramen would be closed. *Kurmademys* has two foramina nervi hypoglossi as in all other pelomedusoids; they lie near the base of the condylus occipitalis, ventrolateral to the foramen magnum. The more dorsal foramen is formed entirely within the exoccipital, but the more ventral one is formed in the exoccipital-basioccipital suture.

BASIOCCIPITAL

The basioccipital in ISI R152 is nearly complete. A small amount of breakage is visible on each tuberculum basioccipitale and the broken condylus occipitalis does not clearly show basioccipital sutures.

The basioccipital of *Kurmademys* has a broad, transverse contact with the basisphenoid anteriorly. Posterolaterally the basioccipital contacts the quadrate, and posterodorsally there is a broad contact with the exoccipitals. The tuberculum basioccipitale is formed about equally by the quadrate and ex-

occipital. A shallow, median concavity lies between the paired tuberculae and is formed almost entirely by the basioccipital.

PROOTIC

Both prootics in ISI R152 are preserved; the right one is nearly complete and the left one has a partially eroded dorsal surface.

The prootic is exposed on the dorsal and anterior surface of the otic chamber with the following contacts: the parietal medially, the quadrate laterally, the supraoccipital posteriorly, and the pterygoid ventrally. There is no prootic-opisthotic contact in *Kurmademys*. The foramen stapedio-temporale is formed in the prootic-quadrate suture. In contrast to all other bothremydids, the foramen opens anterodorsally rather than anteriorly. It is visible in dorsal view in *Kurmademys*, but in other bothremydids it is barely or not visible in dorsal view. The position of the foramen stapedio-temporale in *Kurmademys* is very similar to that in pelomedusids and chelids. The foramen nervi trigemini is formed by the prootic dorsolaterally, the parietal dorsomedially, and the pterygoid ventrally. The foramen is best preserved on the right side; the left foramen nervi trigemini is larger and has broken edges.

On the ventral surface of ISI R152, the prootic is exposed where the three bones (the pterygoid, basisphenoid, and quadrate) meet (fig. 4). This is in the deepest part of the concavity formed by these bones. The concavity is presumed to be for the pterygoideus muscle attachment. The prootic is exposed and has a very similar shape on both sides, so this is not interpreted as a consequence of preservation or an artifact. The prootic has a distinct foramen, here interpreted as the foramen nervi facialis (VII), for the facial nerve, always closely associated with the prootic ossification. The form of the prootic exposure in *Kurmademys* is not like that in any other pleurodire. The primitive condition of the ventral prootic exposure occurs in chelids, pelomedusids, and *Araripemys*, all of which have a large prootic exposure with the foramen posterius canalis carotici interni in the prootic. In all bothremydids, podocnemidids, and FR 4922 the prootic does not contain the internal carotid as it does in chel-

ids and pelomedusids. In FR 4922 the prootic is partially exposed in a narrow space between the basisphenoid and quadrate, similar to the primitive position found in chelids and pelomedusids, but is distinctly posterior to the prootic, as exposed in *Kurmademys*. It is likely that the prootic exposure in *Kurmademys* is not a retention of a primitive state, but is an autapomorphy of this genus, probably related to the development of the pterygoideus concavity that removed covering elements. Small areas of the prootic are variably exposed in other bothremydids skulls due to erosion or the development of the concavity.

OPISTHOTIC

Both opisthotics are preserved in ISI R152; the right one is nearly complete and the left one is missing a small part anteriorly.

In dorsal view, the opisthotic has these contacts: supraoccipital anteromedially, the squamosal laterally, and the exoccipital posteromedially. There is no prootic-opisthotic contact. The opisthotic in *Kurmademys* ends posteriorly at about the same level as the squamosal; it does not extend posteriorly beyond the squamosal as in pelomedusids, *Araripemys*, and FR 4922. Ventrally the opisthotic forms the roof and some of the subdivisions of the fenestra postotica. In ISI R152 the opisthotic divides the fenestra postotica into two portions: a more lateral one that seems to have contained the stapedial artery and lateral head vein, and a more medial one with unknown contents. The medial foramen has a finished dorsal margin, although as preserved, the ventral margin is broken. Presumably the more medial foramen just held cartilage as in living turtles with an open fenestra postotica (Gaffney, 1979).

BASISPHEOID

The basisphenoid is complete and well preserved in ISI R152. The cavum cranii is largely free of matrix and some of the dorsal surface of the basisphenoid is visible.

The basisphenoid in *Kurmademys* is not strongly triangular as in other bothremydids but is more pentagonal. It is a relatively large element, wider than long. The anterior con-

tact with the pterygoids trends posterolaterally and anteromedially, and the angle this suture makes with the midline is similar to that in *Foxemys* and *Zolhahafah*. At the anterolateral corner of the basisphenoid, between the pterygoid and quadrate contacts, is a short contact with the prootic. In nearly all bothremydids the prootic is covered, so this contact is unusual. The lateral margin of the basisphenoid is a long, parasagittal contact with the quadrate. This contact in *Kurmademys* is longer than in any other bothremydids; *Foxemys* and *Polysternon* most closely approach it. Posteriorly the basisphenoid has a transverse contact with the basioccipital.

In contrast to all other bothremydids, in *Kurmademys* the foramen posterius canalis carotici interni is formed completely by the basisphenoid, without participation of the pterygoid. However, the foramen is very close to the pterygoid suture, particularly on the right side. The foramen posterius canalis carotici interni in *Kurmademys* is also placed farther anteromedially than in any other bothremydids. This could be explained morphologically by a reduced ossification of the canalis caroticus internus posteriorly. The canalis in all bothremydids travels anteromedially and slightly dorsally to enter the sella turcica. If the canalis in a form like *Bothremys* (which has the foramen posterius canalis carotici interni placed far posterolaterally) were to be exposed by the removal of bone ventrally, the foramen would appear to migrate anteromedially along the path of the canalis caroticus internus. It is possible that this condition could result from the development of a deep pterygoideus muscle concavity, which is formed directly ventral to the canalis caroticus internus. Although *Kurmademys* has a distinct pterygoideus concavity, it is relatively shallow compared to such forms as *Foxemys*, and *Foxemys* does not have the foramen posterius canalis carotici interni placed anteromedially.

The dorsal surface of the basisphenoid in *Kurmademys* has the dorsum sellae and sella turcica visible. The dorsum sellae overhangs the sella turcica and has the foramen anterius canalis carotici interni also hidden in dorsal view and lying at the posterolateral corner of the sella turcica. There is a small processus clinoides on the left side; the right one is

broken. The shape and general proportions of the dorsum sellae and sella turcica are similar to those in *Pelusios*. The degree of overhang of the dorsum sellae, however, is greater in *Kurmademys* than it is in *Pelusios*. The rostrum basisphenoidale is fused into a single structure, but its anterior end shows the two ossified trabeculae rather than the single rostrum seen in *Pelusios*. There is no sign of a foramen nervi vidiani in the left sulcus cavernosus. The right side still has some matrix.

RELATIONSHIPS

Kurmademys is a pleurodire because it has these synapomorphies of the group listed by Gaffney and Meylan (1988) as diagnostic for the Pleurodira: (1) processus trochlearis pterygoidei present, (2) quadrate process below cranio-quadrate space, (3) epipterygoid absent, (4) foramen palatinum posterius behind orbit, and (5) pelvis suturally attached to carapace and plastron (based on shell material from same locality ascribed to *Kurmademys*). It is a member of the Pelomedusoides (sensu Broin, 1988; Meylan, 1996; Lapparent de Broin and Werner, 1998; Tong et al., 1998), which is equivalent to the Pelomedusidae in the classical sense (sensu Gaffney and Meylan, 1988) because it has these characters: (1) nasals absent, (2) prefrontals meeting on midline, and (3) splenial absent (based on lower jaws from same locality ascribed to *Kurmademys*). *Kurmademys* can be identified as a member of the family Bothremydidae based on its possession of the following characters: (1) exoccipital-quadrate contact, (2) incisura columellae auris closed by bone, and (3) eustachian tube and stapes separated by bone. Within the Bothremydidae, *Kurmademys* can be allied with *Bothremys*, *Rosasia*, *Foxemys*, and *Zollhafah* (the *Bothremys* Group of Lapparent de Broin and Werner, 1998) on the basis of these characters: (1) triangular triturating surfaces, (2) supraoccipital-quadrate contact, (3) maxilla-quadratojugal contact, and (4) palatine widely exposed on triturating surface.

Kurmademys is unique among known bothremydids in having extensive temporal emargination, a small postorbital, a large precolumellar fossa, and a foramen posterius canalis carotici interni formed completely by

the basisphenoid. *Foxemys*, *Polysternon*, *Rosasia*, *Zollhafah*, and *Bothremys* can be united by having a foramen stapedio-temporale very close to the foramen nervi trigemini and a broad preorbital part of the skull, features absent in *Kurmademys*.

Kurmademys has characters in common with the *Bothremys* Group, but the state of the current analysis shows only a few steps from *Kurmademys* as the sister group to the *Nigeremys* Group plus *Bothremys* Group. The addition of as yet undescribed taxa will help to resolve its phylogenetic position.

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