Kinkonychelys, A New Side-Necked Turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of Madagascar

Authors: Gaffney, Eugene S., Krause, David W., and Zalmout, Iyad S.

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Kinkonychelys, A New Side-Necked Turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of Madagascar

EUGENE S. GAFFNEY,[1] DAVID W. KRAUSE,[2] AND IYAD S. ZALMOUT[3]

ABSTRACT

The type specimen of *Kinkonychelys rogersi*, n. gen. et sp., is the first turtle skull to be described from the pre-Holocene fossil record of Madagascar. This specimen, a nearly complete cranium, along with several referred specimens (a series of maxillae and a partial lower jaw), was recovered from the Maastrichtian Maevarano Formation in the Mahajanga Basin of northwestern Madagascar. A braincase with the diagnostic characters of *Kinkonychelys*, but differing in the position of the jaw articulation, formation of the foramen nervi facialis, and a number of other characters, was found in the same rock unit and is provisionally identified as belonging to *Kinkonychelys* sp., a presumed distinct, but closely related species, too incomplete to be diagnosed at present.

Kinkonychelys is a bothremydid because it has the diagnostic characters of an exoccipital-quadrate contact and a fully enclosed incisura columellae auris (Gaffney et al., 2006). *Kinkonychelys* belongs to the tribe Kurmademydini, previously known to include only *Sankuchemys* and *Kurmademys* from the Late Cretaceous of India, because it has a deep fossa pterygoidea, a foramen stapediotemporale facing dorsally, a jugal not retracted from the orbit, a deep fossa precolumellaris, and a large, wide antrum postoticum. *Kinkonychelys rogersi* and *Kinkonychelys* sp. both possess a unique form of the overlapping fossa pterygoidea.

A cladistic analysis of *Kinkonychelys* reveals that it is nested within the tribe Kurmademydini of Gaffney et al. (2006) and is related to the other taxa in the tribe as follows: (*Sankuchemys* (*Kinkonychelys*+*Kurmademys*)). The discovery of a Malagasy bothremydid of Maastrichtian age that is nested within the Indian members of the Kurmademydini supports the hypothesis of a

[1] Division of Paleontology, American Museum of Natural History, (esg@amnh.org).
[2] Department of Anatomical Sciences, Stony Brook University, Stony Brook, New York 11794-8081, USA (David.Krause@stonybrook.edu).
[3] Department of Geosciences and Museum of Paleontology, the University of Michigan, Ann Arbor, Michigan 48109-1079, USA (zalmouti@umich.edu).

connection between Madagascar and the Indian subcontinent that persisted into the late stages of the Late Cretaceous.

INTRODUCTION

Early in their history, probably before the Late Triassic (see Gaffney et al., 1987; 2006; 2007, for supporting literature), turtles split into two main groups, cryptodires and pleurodires. Many species of both groups survived to populate the Recent fauna, but pleurodires are less diverse than cryptodires and are more restricted geographically, living at present only in the southern hemisphere. However, during the past few years, the fossil record of pleurodires has revealed a much greater taxonomic diversity and broader geographic distribution within the Pelomedusoides (Gaffney et al., 2006). The Cretaceous and Paleogene fossil records demonstrate that pleurodires were widespread, reaching all major landmasses except central Asia and Antarctica, and occupying at least the littoral marine realm, as well as diverse freshwater environments. The recently discovered morphological diversity of pleurodire skulls (Gaffney et al., 2006, and references therein) also demonstrates a level of ecological diversity previously unknown.

Madagascar figures significantly in pleurodire evolution. Its extant pleurodire fauna has one of the more unusual endemics, *Erymnochelys madagascariensis* (Grandidier, 1867), a member of the Podocnemididae with controversial relationships (Gaffney, 1988; Gaffney and Meylan, 1988; Noonan, 2000; Noonan and Chippendale, 2006; Romano and Azevado, 2006; Vargas-Ramírez et al., 2008), and three species of Pelomedusidae also occurring on the African mainland: *Pelomedusa subrufa* (Bonnaterre, 1789; [fide ICZN opinion 1463, 1987] Lacépède, 1788, made unavailable; Iverson, 1992), *Pelusios castanoides* Hewitt (1931), and *Pelusios subniger* (Bonnaterre, 1789) (Iverson, 1992, for distribution maps and synonymies; Raxworthy, 2003). The fossil pleurodire record of Madagascar (Lapparent de Broin, 2000; Gaffney and Forster, 2003), essentially restricted to the Late Cretaceous (but see Samonds et al., in press, for report of unidentified Eocene turtles), includes a close relative of *Erymnochelys madagascariensis* but also shows the presence of a number of species of the extinct family Bothremydidae. Until

now, however, there have not been bothremydid specimens of sufficient quality from Madagascar to include in a phylogenetic analysis. The lower jaw fragment described by Gaffney and Forster (2003) is very different in shape and much larger than a taxon that could be identified with *Kinkonychelys*.

Reconnaissance fieldwork in the Lac Kinkony Study Area of the Mahajanga Basin, northwestern Madagascar (fig. 1), conducted jointly by Stony Brook University and the Université d'Antananarivo during the austral winter of 2007, yielded a well-preserved cranial specimen of a new genus and species of Bothremydidae. Discovery of this skull allowed identification of several more fragmentary specimens (several isolated cranial fragments including parts of maxillae as well as a partial lower jaw) discovered during previous expeditions in the Berivotra Study Area that are here referred to this new taxon. The primary objective of this paper is to describe and name this new genus and species and place it into both phylogenetic and biogeographic context. Reconnaissance fieldwork in the Masiakakoho Study Area in 2005 yielded a basicranium of a closely related form that is also described here, and provisionally placed in the same genus. All of the specimens were recovered from the Maevarano Formation, named and described by Rogers et al. (2000).

The Maevarano Formation is Maastrichtian in age and was deposited in a highly seasonal, semiarid climate as sediments were washed from the crystalline highlands that run down the north-south axis of the island northwestward toward the Mozambique Channel (Rogers et al., 2000, 2007; Rogers and Krause, 2007). In addition to turtles, the vertebrate fauna of the Maevarano Formation includes fishes, frogs, lizards, snakes, crocodiles, nonavian dinosaurs, birds, and mammals (see Krause et al., 2006, for recent review), several of them represented by nearly complete, exquisitely preserved skulls and skeletons. Prior to the report of Gaffney and Forster (2003) of a nearly complete lower jaw of cf. *Erymnochelys* sp. and a dentary fragment of an indeterminate genus and species of Bothremydidae, no turtle remains had been identified from
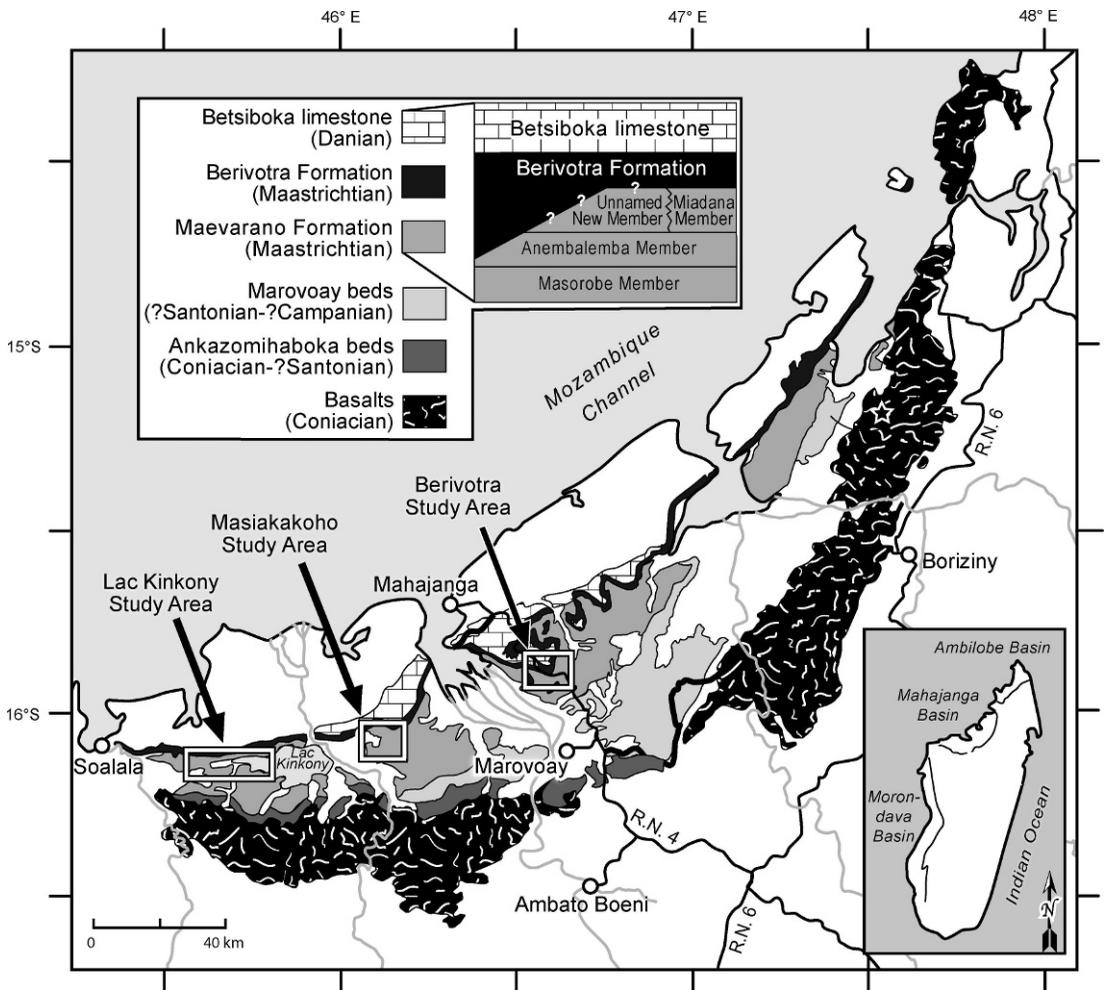
Fig. 1.   Outcrop map of Upper Cretaceous and Paleocene strata in the Mahajanga Basin of northwestern Madagascar indicating the Lac Kinkony, Masiakakoho, and Berivotra Study Areas from which specimens of *Kinkonychelys* were collected in the Maevarano Formation. [L. Nash, del.]

the Maevarano Formation despite the indications that they were represented by abundant fragmentary material and had been reported from that rock unit well over a century ago (e.g., Depéret, 1896; see Gaffney and Forster, 2003, for a review of pleurodire records from Madagascar).

The cranial morphology of turtles is described and depicted in Gaffney (1979), with an introduction to pleurodire cranial morphology in Gaffney et al. (2006). The anatomical terminology used here is available in an illustrated glossary (Gaffney, 1972, 1979). Of additional relevance here are the descriptions

in Gaffney et al. (2006) of the Kurmademydini bothremydids *Kurmademys* (Gaffney et al., 2001) and *Sankuchemys* (Gaffney et al., 2003), the forms most closely related to *Kinkonychelys*.

This report is based primarily on two specimens: a nearly complete skull, UA 9748, the holotype of *Kinkonychelys rogersi*, n. gen. et sp., and a braincase, FMNH PR 2446, identified as *Kinkonychelys* sp. Although they are described separately, the descriptions are comparative and include information on both (see figures and table 1 for comparative information).

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York, U.S.A.
FMNH	The Field Museum, Chicago, U.S.A.
ISI	Indian Statistical Institute, Kolkata, India
UA	Université d'Antananarivo, Antananarivo, Madagascar

ANATOMICAL ABBREVIATIONS

ap	antrum postoticum
bc	basis columellae
bo	basioccipital
bs	basisphenoid
ca	columella auris
cc	canalis cavernosus
co	condylus occipitalis
ct	cavum tympani
del	delineator, primary artist of figure
ex	exoccipital
facci	foramen anterius canalis carotici interni
faf	fossa acusticofacialis
fc	foramen cavernosum
fja	foramen jugulare anterius
fjp	foramen jugulare posterius
fnf	foramen nervi facialis
fnt	foramen nervi trigemini
fo	fenestra ovalis
fpc	fossa precolumellaris
fpcci	foramen posterius canalis carotici interni
fpo	fenestra postotica
fpt	fossa pterygoidea
fst	foramen stapediotemporale
fr	frontal
ica	incisura columellae auris
ju	jugal
mx	maxilla
op	opisthotic
pa	parietal
pal	palatine
pf	prefrontal
po	postorbital
pr	prootic
pt	pterygoid
qu	quadrate
rb	rostrum basisphenoidale
rlo	recessus labyrinthicus opisthoticus
rlp	recessus labyrinthicus prooticus
so	supraoccipital
VIII	foramen nervi acusticus
XII	foramen nervi hypoglossum

SYSTEMATICS

ORDER TESTUDINES LINNAEUS, 1758

INFRAORDER PLEURODIRA COPE, 1864

HYPERFAMILY PELOMEDUSOIDES COPE, 1868

FAMILY BOTHREMYDIDAE BAUR, 1891

TRIBE KURMADEMYDINI GAFFNEY, TONG, AND MEYLAN, 2006

TYPE GENUS: *Kurmademys* Gaffney, Chatterjee, and Rudra, 2001

INCLUDED GENERA: *Kurmademys* Gaffney, Chatterjee, and Rudra, 2001; *Sankuchemys* Gaffney et al., 2003; and *Kinkonychelys*, n. gen. et sp.

DISTRIBUTION: Late Cretaceous (Maastrichtian) of peninsular India and Madagascar.

Kinkonychelys, new genus

TYPE AND ONLY INCLUDED SPECIES: *KINKONYCHELYS ROGERSI*, n. gen. et sp.

DISTRIBUTION: Late Cretaceous of Madagascar.

ETYMOLOGY: Named for the Lac Kinkony (pronounced "kin-KOON-ee") Study Area, in which the type specimen was recovered, and *chelys*, "turtle."

DIAGNOSIS: A member of the bothremydid tribe Kurmademydini distinguished from all other members by absence of prootic exposure ventrally; presence of foramen nervi facialis formed by pterygoid, basisphenoid, and quadrate; relatively thick labial ridge in contrast to thin labial ridge; more posteriorly placed condylus mandibularis; fossa pterygoidea with overlapping medial ridge; condylus occipitalis formed entirely from exoccipitals rather than exoccipitals plus basioccipital. Further differs from *Kurmademys* by jugal reaching cheek margin and absence of palatine-parietal contact in septum orbitotemporale; and from *Sankuchemys* by deep fossa pterygoidea, absence of accessory triturating ridges, and relatively short basioccipital.

Kinkonychelys rogersi, new species

TYPE SPECIMEN: UA 9748, a nearly complete skull, including the basicranium, but

missing the premaxilla, vomer, squamosal, and quadratojugal (figs. 2–4, 8; table 2).

TYPE LOCALITY: MAD 07-25 (latitude 16°7′14.5″S, longitude 45°44′10.7″E) in the Lac Kinkony Study Area (fig. 1). MAD 07-25 lies approximately 2 km north of the western end of Lac Kinkony and 4.9 km northeast of the village of Antongomena.

HORIZON: Unnamed member, Maevarano Formation, Maastrichtian, Upper Cretaceous. UA 9748 was excavated in situ from facies that represent a new and soon to be described member of the Maevarano Formation that crops out above typical exposures of the Masorobe and Anembalemba Members. This new unit, which yields abundant, well-preserved fossils of aquatic taxa (ray-finned fishes, turtles, crocodyliforms) and nonavian dinosaurs, is exposed in an outcrop belt that extends along the northwest shore of Lac Kinkony and continues westward for several km toward the town of Soalala. The turtle skull was collected from the upper few centimeters of a bed of gray silty claystone intercalated immediately beneath a bed of white calcareous sandstone that shows evidence of tidal influence. In a regional sense, the stratigraphy of this new unit indicates that it likely correlates with the Miadana Member, and thus is somewhat younger than the well-known exposures of the Anembalemba Member in the Berivotra Study Area to the west (Rogers et al., 2000).

DIAGNOSIS: As for genus.

ETYMOLOGY: Named for Raymond R. Rogers, discoverer of the type specimen, in recognition of his important discovery but also of his many contributions to knowledge of the stratigraphy, sedimentology, and taphonomy of Upper Cretaceous strata of the Mahajanga Basin.

REFERRED MATERIAL: The following specimens, all recovered from the Anembalemba Member of the Maevarano Formation in the Berivotra Study Area, are also assigned to *Kinkonychelys rogersi*: FMNH PR 2650, left maxilla with partial jugal and palatine from locality MAD 05-04; FMNH PR 2651, partial left maxilla from locality MAD 96-03; FMNH PR 2652, partial left maxilla from MAD 99-31; FMNH PR 2653, right ramus of lower jaw, lacking articulation, from locality MAD 99-31; UA 8652, left maxilla from locality MAD 93-18; and UA 8655, partial right maxilla and jugal from locality MAD 93-18.

DESCRIPTION

Figures 2–4, 8

PREFRONTAL

PRESERVATION: Both prefrontals are present in UA 9748 but are cracked through their ventral processes, although most of the processes are preserved attached to the maxillae.

CONTACTS: As in other Kurmademydini, the contacts of the prefrontal in UA 9748 are with the other prefrontal on the midline, the maxilla anteroventrolaterally, and the frontal posteriorly.

STRUCTURES: The dorsal margin of apertura narium externa in UA 9748 is slightly protruding as in *Kurmademys*, ISI R 159 (Gaffney et al., 2006: fig. 61). The dorsal margin of the orbit and the interorbital distance in *Kinkonychelys* is also similar to that in *Kurmademys*. The sulcus olfactorius is preserved on the ventral surface of the prefrontal in UA 9748; it and the roof of the fossa nasalis are slightly wider than in *Kurmademys*. The anteroventral process of the prefrontal forms the edge of foramen orbitonasale, as in other pleurodires.

FRONTAL

PRESERVATION: Both frontals are present in UA 9748 but have broken margins along some of their lateral surfaces. The dorsal contacts are clear but some of the ventral edges are missing posteriorly.

CONTACTS: As in other Kurmademydini, the contacts of the frontal in *Kinkonychelys* are with the other frontal on the midline, the prefrontal anteriorly, the postorbital posterolaterally, and the parietal posteriorly.

STRUCTURES: Although the anterolateral margin of the frontal is broken away on both sides, it is very likely that it entered the orbital margin. On its ventral surface the frontal shows the sulcus olfactorius, which is slightly wider in *Kinkonychelys* than it is in *Kurmademys*.

PARIETAL

PRESERVATION: Both parietals are present in UA 9748 but have much of their edges
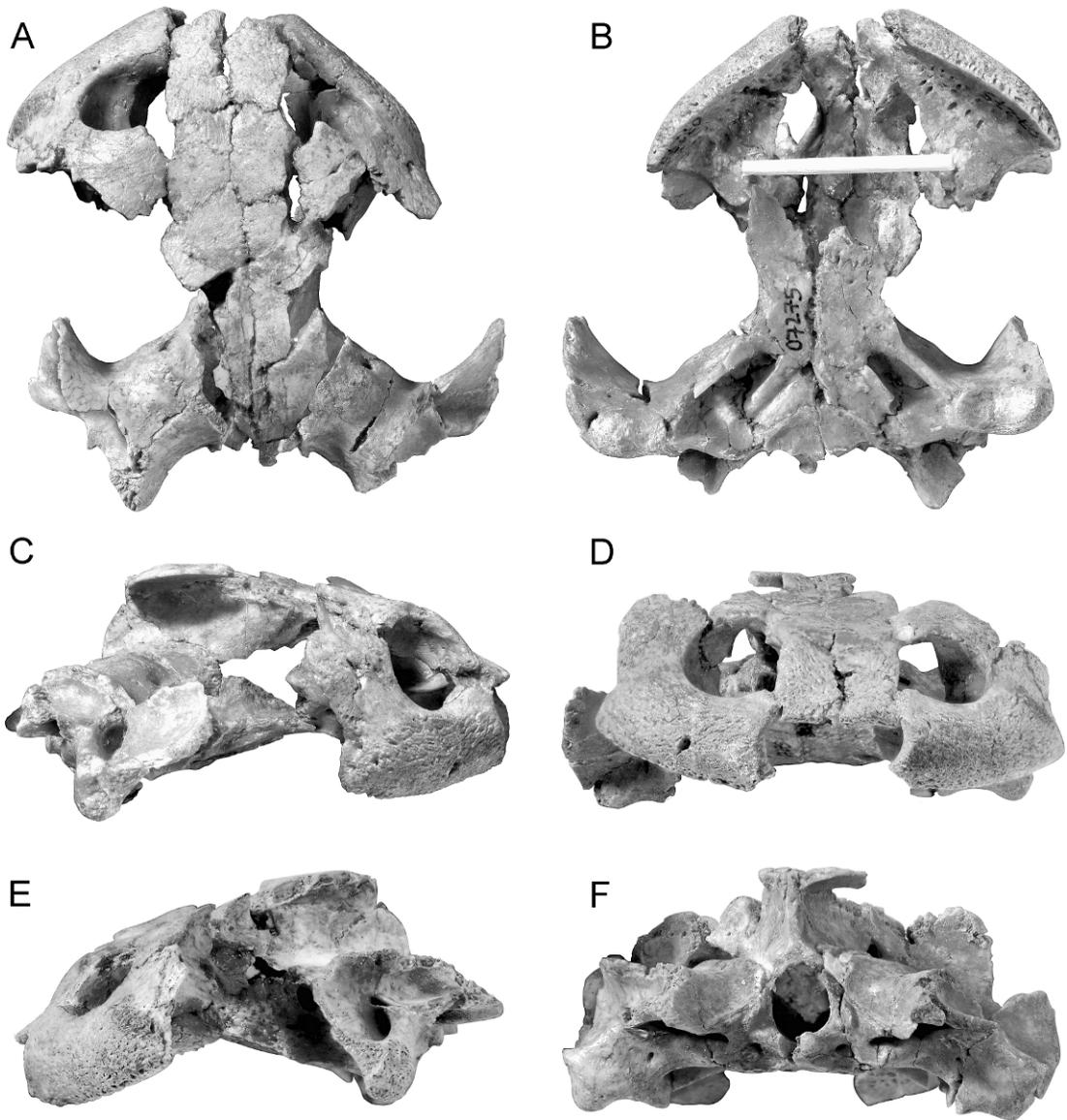
Fig. 2.   *Kinkonychelys rogersi*, n. gen. et sp. UA 9748, holotype skull. A, Dorsal; B, ventral; C, right lateral; D, anterior; E, left lateral; F, posterior. [C. Li, del.]

broken. The dorsal plate lacks its lateral edges for most of its length. There is a natural margin along the more posterior edge of the right parietal and this indicates a deep emargination (see below).

CONTACTS OF DORSAL PLATE: As in *Kurmademys*, the contacts of the parietal dorsal plate in UA 9748 are with the other

parietal on the midline, the frontal anteriorly, and the postorbital laterally.

STRUCTURES OF DORSAL PLATE: The extent of the temporal emargination in UA 9748 is poorly preserved, but a small natural edge on the right parietal shows that there was an extensive emargination, similar to or the same as in other Kurmademydini.
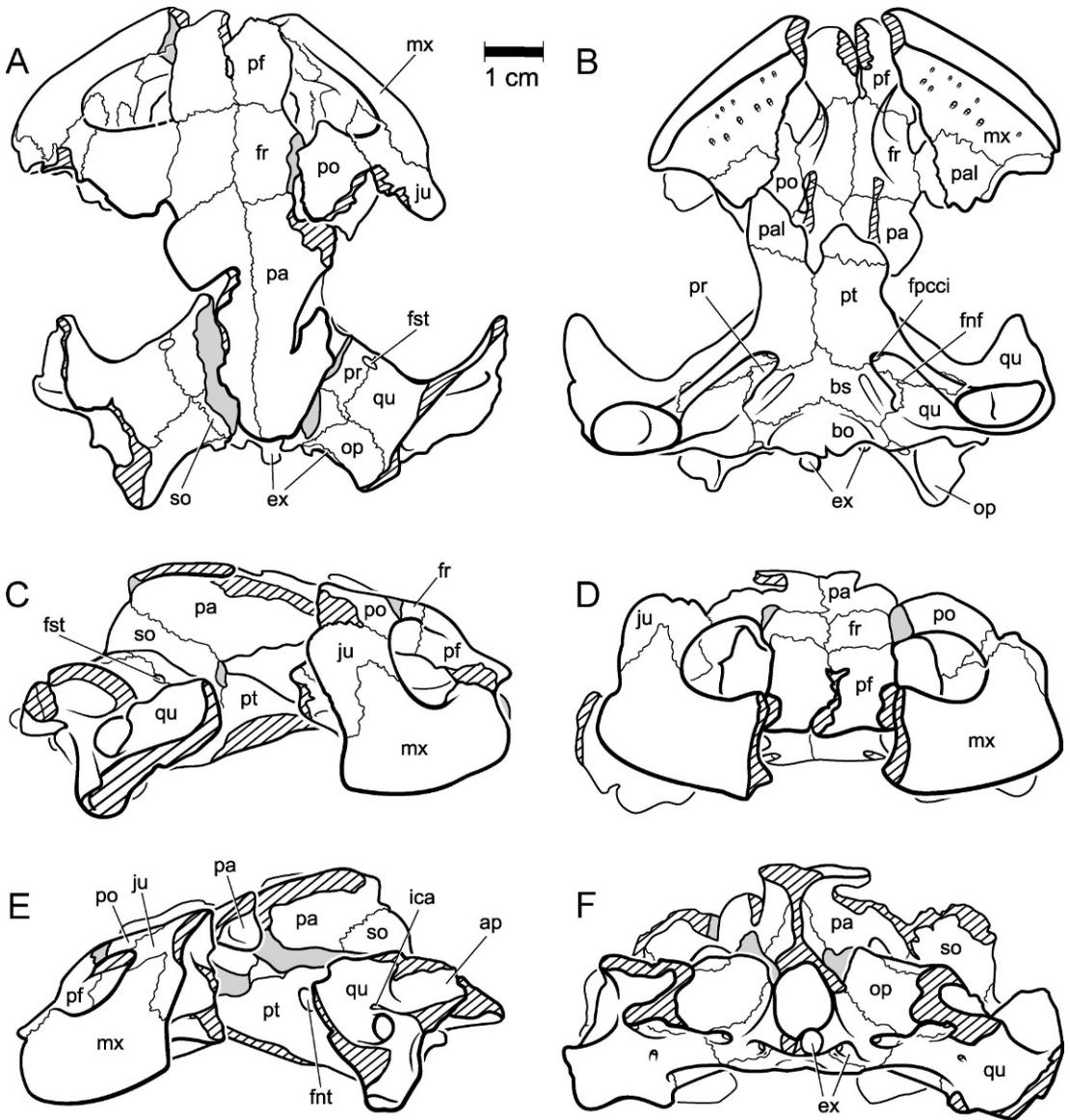
Fig. 3. *Kinkonychelys rogersi*, n. gen. et sp. UA 9748, holotype skull. A, Dorsal; B, ventral; C, right lateral; D, anterior; E, left lateral; F, posterior. Key to Fig. 2. [C. Li, del.]

The ventral process lateral to the sulcus palatinopterygoideus is represented in UA 9748 only by the base, and its extent and contacts are not determinable.

CONTACTS OF PROCESSUS INFERIOR PARIE-TALIS: In UA 9748 the processus is broken away along its base on both sides, but most of the ventral contacts are visible as fragments on the crista pterygoidea. The processus contacts the pterygoid ventrally, the prootic posteroventrally, and the supraoccipital posteriorly. The anteroventral contact with the palatine seen in *Kurmademys* is not determinable in UA 9748.

STRUCTURES OF PROCESSUS INFERIOR PARIE-TALIS: The foramen nervi trigemini in UA 9748 is bordered by the parietal anterodor-

sally, the prootic dorsolaterally, and the pterygoid ventrally, as in other bothremydids.

JUGAL

PRESERVATION: Both jugals are present, but neither is complete and both lack their posterior areas and most of the internal contacts.

CONTACTS OF LATERAL PLATE: The jugal in UA 9748 contacts the maxilla anteroventrally and the postorbital dorsally. Possible quadratojugal and quadrate contacts are indeterminate.

STRUCTURES OF LATERAL PLATE: The jugal in *Kinkonychelys* forms the posterior part of the orbital margin, as in the other Kurmademydini, but it has a greater orbital exposure than in the other taxa. Although the posterodorsal part of the jugal is missing in UA 9748, the posteroventral part is intact on both sides and shows the cheek margin. There is clearly a jugal exposure along the cheek, in contrast to *Kurmademys*, and the degree of cheek emargination, while not determinable posteriorly in UA 9748, is higher, anteriorly at least, in *Kinkonychelys* than in *Kurmademys* and probably in *Sankuchemys*.

CONTACTS OF MEDIAL PROCESS: In the floor of the orbit (dorsal view), the jugal in UA 9748 contacts the maxilla anteriorly and laterally and the palatine medially, in a suture pattern very similar to that in *Kurmademys*. In the septum orbitotemporale (i.e., the postorbital wall) the jugal contacts the postorbital dorsomedially, the palatine ventromedially, the pterygoid posteriorly, and the maxilla ventrally.

STRUCTURES OF MEDIAL PROCESS: The jugal forms part of the posterior wall of the fossa orbitalis, which in UA 9748 has a posterior enlargement that is diagnostic for bothremydids (Gaffney et al., 2006).

QUADRATOJUGAL

PRESERVATION: The quadratojugals are not preserved.

SQUAMOSAL

PRESERVATION: Both squamosals are missing, although some of the sutural surfaces remain on the preserved quadrates and opisthotics.

POSTORBITAL

PRESERVATION: Both postorbitals are present, although they lack their posterior limits and some of their ventral margins.

CONTACTS OF LATERAL PLATE: The postorbital in UA 9748 contacts the frontal anteromedially, the jugal ventrally, and the parietal posteromedially. The lateral views of UA 9748 in figure 3 are somewhat misleading, as the frontal does enter the orbital margin, but in these figures the (displaced) postorbital appears to exclude the frontal.

STRUCTURES OF LATERAL PLATE: The postorbital in UA 9748 forms the dorsal part of the orbital margin, as in the other Kurmademydini. The degree to which or even whether it entered the temporal margin is not determinable, although presumably it did, based on the small edge of parietal preserved.

CONTACTS OF MEDIAL PROCESS: In the septum orbitotemporale, facing the fossa orbitalis, the postorbital contacts the frontal dorsomedially, the jugal ventrolaterally, and the parietal medially. There is no palatine contact as seen in *Kurmademys*. In the septum orbitotemporale, facing the fossa temporalis, the postorbital contacts the parietal dorsomedially and the jugal ventrolaterally. Possibly there was a pterygoid contact, now broken away. There is no palatine contact.

STRUCTURES OF MEDIAL PROCESS: The postorbital forms part of the roof and lateral wall of the sulcus palatinopterygoideus and septum orbitotemporale, as in other bothremydids.

PREMAXILLA

PRESERVATION: The premaxillae are not preserved.

MAXILLA

PRESERVATION: Both maxillae are present and nearly complete in UA 9748. Their edges are missing at the premaxillary sutures and the pterygoid and palatine contacts are mostly broken edges. Additionally, there are five referred maxillae (FMNH PR 2650, FMNH PR 2651, FMNH PR 2652, UA 8652, and UA 8655) that probably belong to this species.

CONTACTS OF VERTICAL PLATE: The maxilla in UA 9748 contacts the premaxilla (presumably) anteromedially, the jugal posterodorsally, and the prefrontal anterodorsally.

STRUCTURES OF VERTICAL PLATE: The maxilla forms a distinct ridge separating the fossa orbitalis from the external surface of the skull, as in *Kurmademys* and in contrast to other bothremydids such as *Bothremys*. The ridge is more rounded in UA 9748 and more acute in
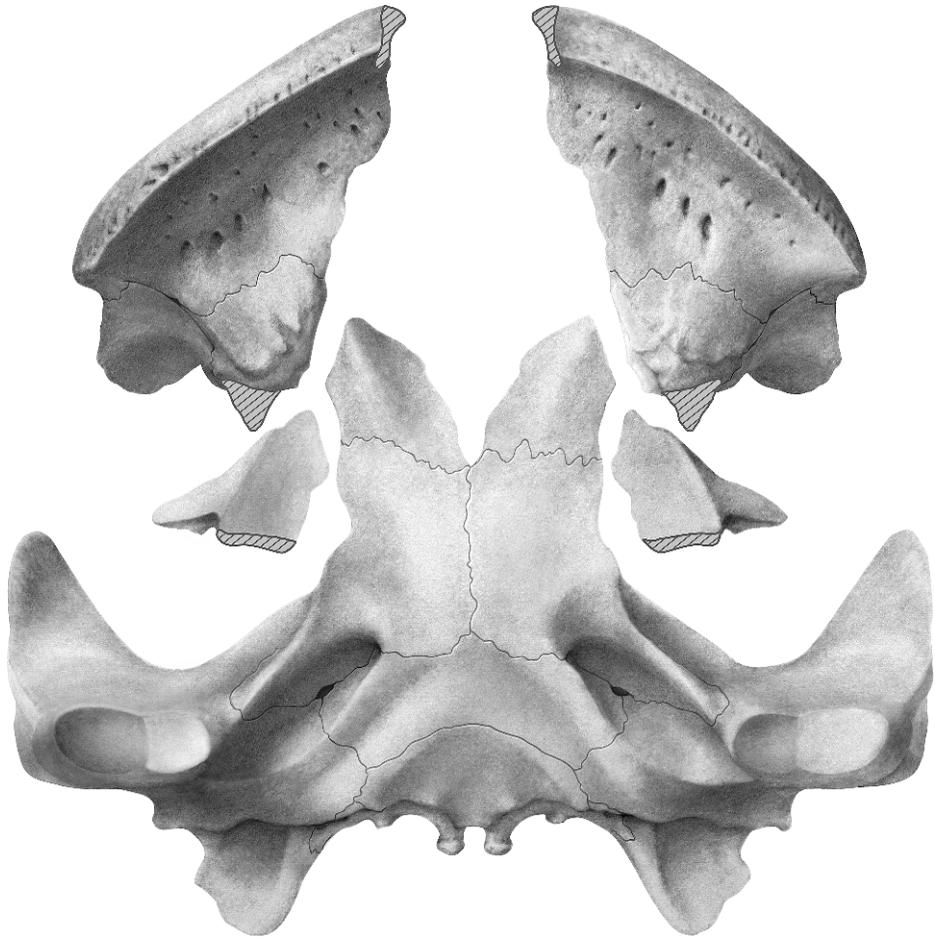
Fig. 4. *Kinkonychelys rogersi*, n. gen. et sp. UA 9748, holotype. Partially restored ventral view of skull. [C. Li, del.]

Kurmademys. The extent and shape of the apertura narium externa and foramen orbitonasale are not determinable, but the preserved areas are consistent in morphology with those of *Kurmademys*. The maxilla forms the ventral part of the anterior cheek emargination.

CONTACTS OF HORIZONTAL PLATE: The maxilla in UA 9748 contacts the palatine posteromedially and the jugal posterolaterally.

STRUCTURES OF HORIZONTAL PLATE: The triturating surface of *Kinkonychelys* is very similar to that in *Kurmademys*. It is triangular, wide posteriorly, and with no pits or ridges. The palatine makes up a significant part of it posteromedially, as in *Kurmademys*. The labial ridge in UA 9748 is thicker and less acute than in *Kurmademys*.

VOMER

PRESERVATION: The vomer is not preserved.

PALATINE

PRESERVATION: The palatines are incomplete in UA 9748 and not as well preserved as the other cranial elements. Those portions of the palatines forming part of the triturating surfaces are preserved, but they are broken off close to the maxillae on both sides. On the right side, some of the palatine is attached to the right pterygoid, extending anteriorly to form a broad area of contact between these two pieces of the right palatine. However, the more complex contacts of the bone are either missing or poorly preserved.

TABLE 1
Comparison of Tribe Kurmademydini Skulls

	Kinkonychelys rogersi UA 9748	*Kinkonychelys* sp. FMNH PR 2446	*Kurmademys kallamedensis*	*Sankuchemys sethnai*
Locality	Madagascar	Madagascar	India	India
Age	Maastrichtian	Maastrichtian	Maastrichtian	Maastrichtian
qj-mx contact behind orbit	absent, ju reaches cheek margin	?	yes	no
pal-pa contact in septum orbitotemporale	no	?	yes	?
Triturating surface	wide	?	wide	narrow
Labial ridge	thicker	?	thinner	thinner
Accessory ridge on triturating surface	absent	?	absent	present
Fossa precolumellaris	ventral to incisura columallae auris	anterior to incisura columallae auris	ventral to incisura columallae auris	?
Condylus mandibularis	more posterior	more anterior	more anterior	more anterior
Fossa pterygoidea	present	present	present	probably present
Fossa pterygoidea with medial BS overlap	yes	yes	no	?
Foramen posterius canalis carotici interni in bs medial wall	yes	yes	yes	no
Foramen posterius canalis carotici interni	pt+bs	pt+bs	bs	pt+bs
Condylus occipitalis	ex	ex	ex+bo	?
PR exposed ventrally	no	yes	yes	yes
Foramen nervi facialis	pt+bs+qu	pr+bs+qu	pr	pr
Foramen jugulare posterius	ex	ex+op	ex	?
Basioccipital	shorter	shorter	shorter	longer
Foramen stapediotemporale visible in dorsal view	yes	yes	yes	no (probably due to damage)

CONTACTS: The palatine contacts the maxilla anterolaterally, the other palatine medially, and the pterygoid posteriorly. There does not seem to be a parietal or postorbital contact.

STRUCTURES ON DORSAL AND VENTRAL SURFACES: The palatine forms the medial part of the fossa orbitalis floor and the lateral edge of the apertura narium interna. There is no dorsal process to the parietal as in *Kurmademys* (the *Sankuchemys* condition is unknown). The anterior margin of the foramen palatinum posterius can be seen on the right palatine, presumably the posterior edge of the foramen was formed by pterygoid. The palatine forms the posteromedial part of the triturating surface, as in other Kurmademydini (Gaffney, 2006).

QUADRATE

PRESERVATION: Both quadrates are present in UA 9748, but the left one is more complete. The left one has its anterior limits marked by broken edges while the right one has a section of natural edge showing some of the cheek emargination. Between the two quadrates, nearly all of the cavum tympani and quadrate portion of the antrum postoticum can be determined. The medial parts of both quadrates are preserved, although the right one has some breakage around the fossa pterygoidea.

CONTACTS ON LATERAL SURFACE: Due to lack of preservation, the only definite lateral surface contact of the quadrate in UA 9748 is with the squamosal posterodorsally. However, extensive cheek and temporal emargination suggest that the only other likely contact is with the quadratojugal anterodorsally, as in *Kurmademys*, which has a very similar skull emargination.

STRUCTURES ON LATERAL SURFACE: As stated above, the best estimate for cheek and

TABLE 2
Measurements of *Kinkonychelys rogersi* (see Gaffney et al., 2006: fig. 315)

	A	B	C	D1	D2	E	F	G	H	I	J1	J2	K	L	M	N	O
UA 9748	53.9[a]	60.04	13.04	11.09	12.8[a]	15.05	indet.	30.00	41.05	indet.	11.8	11.0[a]	24.00	9.01	15.05	15.8[a]	53.05

[a]Damaged.

temporal emargination in *Kinkonychelys* suggests an extensive degree for both, similar to that seen in *Kurmademys*.

The cavum tympani is almost completely known for UA 9748. The incisura columellae auris is completely enclosed by bone and separated from the eustachian tube, both bothremydid synapomorphies (Gaffney et al., 2006). There is a narrow groove extending posteriorly on a ridge from the incisura to the sulcus eustachii on the back of the quadrate, a feature of *Kurmademys* and *Galianemys* (Cenomanian, Morocco). The antrum postoticum is incomplete due to the absence of much of the squamosal, but its width and depth can still be determined from the quadrate portions. The cavum tympani of *Kinkonychelys* is most similar to that in *Kurmademys*.

The fossa precolumellaris is large, deep, and well defined in *Kinkonychelys*; the condition occurring in Pelomdusoides outgroups but found only in *Kurmademys* among the Bothremydidae (unknown for *Sankuchemys*). The two *Kinkonychelys* specimens, UA 9748 and FMNH PR 2446, differ significantly in the position of this fossa. In UA 9748 it is ventral to the incisura columellae auris, but in FMNH PR 2446, it is anterior to the incisura. To our knowledge, this degree of variation is unknown within a single species among the Recent species of podocnemidids.

CONTACTS ON DORSAL AND ANTERIOR SURFACE: As in other Pelomedusoides the contacts of the quadrate in *Kinkonychelys* are with the prootic anteromedially, the opisthotic posteromedially, the supraoccipital medially, and the squamosal posteriorly and posterolaterally.

STRUCTURES ON DORSAL AND ANTERIOR SURFACE: One of the more obvious characters of bothremydids is the unusual migration of the foramen stapediotemporale from the dorsal surface of the otic chamber onto the anterior surface. *Kurmademys* is unique among bothremydids in having the primitive position of the foramen on the dorsal surface, but *Kinkonychelys* exhibits this condition as well.

CONTACTS ON VENTRAL SURFACE: As in other bothremydids, the quadrate contacts in UA 9748 are with the pterygoid anteromedially, the basisphenoid medially, and the basioccipital posteromedially. In *Kurmademys* and *Sankuchemys* the prootic is exposed ventrally and

contacts the quadrate medially. This is also the case in FMNH PR 2446, the specimen referred below to *Kinkonychelys* sp. In *Kinkonychelys rogersi*, however, the prootic is covered, mostly by a thin flange of quadrate (visible in the broken area of the right side), so it is not exposed ventrally.

STRUCTURES ON VENTRAL SURFACE: The quadrate forms the lateral wall of the fossa pterygoidea (see Pterygoid). The condylus mandibularis in *Kinkonychelys* lies close to the level of the condylus occipitalis, more posterior than the condylus mandibularis in the other Kurmademydini, which is much more anterior with respect to the condylus occipitalis.

CONTACTS ON POSTERIOR SURFACE: As in other bothremydids, the contacts in *Kinkonychelys* are with the squamosal dorsolaterally, the opisthotic dorsomedially, the exoccipital medially, and the basioccipital ventromedially.

STRUCTURES ON POSTERIOR SURFACE: The quadrate forms the lateral portion of the fenestra postotica, which in UA 9748 is closed medially by the exoccipital. There is a low ridge separating the lateral head vein and stapedial artery. The foramen chorda tympani inferius lies on the posterior face of the condylus mandibularis.

PTERYGOID

PRESERVATION: The pterygoids in UA 9748 are both present but incomplete anterolaterally. A processus trochlearis pterygoidei is present but has no definite contact with the main pterygoid pieces.

CONTACTS ON VENTRAL SURFACE: As in other bothremydids, the pterygoid in *Kinkonychelys* contacts the palatine anteriorly, the other pterygoid anteromedially, the basisphenoid posteromedially, and the quadrate posterolaterally.

STRUCTURES ON VENTRAL SURFACE: The processus trochlearis pterygoidei, while associated with this specimen, cannot be definitely articulated with it, so its angle cannot be determined with certainty.

The fossa pterygoidea, the depression for attachment of the pterygoideus muscle (see Gaffney et al., 2006), is deep and well defined in UA 9748. Although the depth of the fossa is about the same in both *Kurmademys* and *Kinkonychelys*, its shape differs. In *Kinkony-*

chelys the fossa is deeper anteriorly in the area of the foramen posterius canalis carotici interni whereas in *Kurmademys* it becomes shallow anteriorly. Medially the basisphenoid overhangs the fossa and the foramen posterius canalis carotici interni in UA 9748 (and in FMNH PR 2446 of *Kinkonychelys* sp.), but there is no such overhang in *Kurmademys*. In *Kurmademys* the prootic is exposed in the roof of the fossa but not in *Kinkonychelys*.

The foramen posterius canalis carotici interni in UA 9748 is formed between the basisphenoid medially and the pterygoid laterally. In *Kurmademys* the foramen is almost completely within the basisphenoid but very close to the pterygoid, and in *Sankuchemys* it is between the basisphenoid and pterygoid. In FMNH PR 2446 it is also formed between the bones. Just lateral to the foramen posterius canalis carotici interni in UA 9748 is a small foramen completely in the pterygoid that is probably for the vidian nerve. This is also the condition in *Kurmademys* (Gaffney et al., 2006: fig. 63). The facial nerve is always contained within the prootic bone in pleurodires, although this is frequently covered by other bones and not visible on the skull surface (Gaffney et al., 2006). In *Kurmademys* and *Sankuchemys* the prootic is exposed and the foramen nervi facialis is visible on the ventral surface. However, in UA 9748 the pterygoid has a flange that extends medially to cover the prootic and the exit of the facial nerve, so that the foramen nervi facialis is formed between the pterygoid laterally and the basisphenoid medially, with a small piece of quadrate entering the foramen posteriorly. This can be seen completely preserved only on the left side of UA 9748, but some of the internal details are visible on the damaged right side.

Another feature of the fossa pterygoidea in UA 9748 is the small overhang formed by the basisphenoid along the medial margin of the fossa. This is not seen in *Kurmademys*, but it is seen in FMNH PR 2446 and seems to be related to the greater depth of the fossa anteriorly in these two taxa.

CONTACTS ON DORSAL SURFACE: The area around the base of the processus trochlearis pterygoidei is damaged or missing in UA 9748 and the contacts are not preserved. The other pterygoid contacts are with the parietal anterodorsally, the prootic posterodorsally, the

quadrate posterolaterally, the palatine anteriorly, and the basisphenoid medially, as in other bothremydids.

STRUCTURES ON DORSAL SURFACE: Although the anterior edges of the pterygoids are broken, the right crista pterygoidea is nearly complete and the left one is mostly complete. The foramen nervi trigemini is formed at the posterior end of the crista and has the usual bones in its margin: the pterygoid ventrally, the parietal anterodorsally, and the prootic posterodorsally. Medial to the foramen nervi trigemini and the crista pterygoidea is the canalis cavernosus posteriorly and the sulcus cavernosus anteriorly. If a foramen caroticum laterale were present it would be in the sulcus cavernosus, but there is no sign of one. There is also no sign of the anterior opening of the vidian nerve, which should be in this area, but it is possible that the pterygoid is broken off too far posteriorly for the foramen to be preserved.

SUPRAOCCIPITAL

PRESERVATION: The supraoccipital is present in UA 9748, but only the ventral half is preserved; there is nothing of the crista supraoccipitalis left and no portion of the skull roof contribution.

CONTACTS: The supraoccipital in UA 9748 has contacts with the parietals dorsally and anteriorly, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipitals posteroventrally. Most bothremydids also have a lateral contact with the quadrate (Gaffney et al., 2006) and this seems likely in UA 9748. However, the area is damaged, so the character has been coded as "?" in the data set. This contact is actually a thin sheet of supraoccipital overlying the prootic and opisthotic and is easily damaged.

STRUCTURES: The foramen magnum is rimmed dorsally by the supraoccipital and ventrally by the exoccipitals. The crista supraoccipitalis is missing, but what is preserved is consistent with that of *Kurmademys*.

EXOCCIPITAL

PRESERVATION: Both exoccipitals are present but slightly damaged. The right one is missing more of the foramen magnum margin but has the condylus occipitalis preserved, while the left one is missing the condylus but

preserves most of the margin of the foramen magnum. The ventral and occipital areas are all present.

CONTACTS: As in other bothremydids, the contacts of the exoccipital in *Kinkonychelys* are with the supraoccipital dorsally, the opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally.

STRUCTURES: The condylus occipitalis in UA 9748 is made up of the exoccipitals only; the basioccipital does not contribute to it. This is determinable, even though only the right exoccipital has the condylus preserved, because the preserved portion of the exoccipital makes up half of the condyle. *Kurmademys* has the basioccipital in the condylus occipitalis, but FMNH PR 2446, the other Madagascar braincase, also has only the exoccipitals making up the condyle.

The foramen nervi hypoglossi is best seen on the right side of UA 9748 and it consists of three openings. The two more dorsal ones are recessed on a larger depression, and the third is more ventral, in the basioccipital suture. *Kurmademys* has two foramina on each side and no recess, as is the condition in FMNH PR 2446. These foramina tend to vary individually, so their systematic significance is dubious.

The foramen jugulare posterius is closed and completely formed by the exoccipital in *Kinkonychelys*, as it is in *Kurmademys*. In FMNH PR 2446, however, the opisthotic forms the lateral wall to close the foramen.

The fenestra postotica in UA 9748 is closed with a small portion of the exoccipital forming its most medial edge.

BASIOCCIPITAL

PRESERVATION: The basioccipital in UA 9748 is nearly complete, although the small triangular piece that would fit in the neck of the condylus occipitalis is broken off and there is a crack down the middle.

CONTACTS: As in the other bothremydids, the contacts of the basioccipital in *Kinkonychelys* are with the basisphenoid anteriorly, the quadrate laterally, the exoccipitals posterodorsally, and the quadrate laterally. The exoccipital-quadrate contact is a bothremydid synapomorphy (Gaffney et al., 2006).

STRUCTURES: The basioccipital does not form part of the condylus occipitalis, but does seem to enter its neck. The tuberculum

basioccipitale of the Kurmedemydini is very low but widely spaced and this is also the case for *Kinkonychelys*. The shape is very similar to that in *Kurmademys* but in contrast to the longer basioccipital of *Sankuchemys*.

PROOTIC

PRESERVATION: Both prootics are preserved in UA 9748. The right one is more damaged than the left, which is nearly complete. Some of the breakage of the right allows observation of internal morphology.

CONTACTS: As in the other bothremydids, the contacts of the prootic in UA 9748 are with the parietal dorsomedially, the quadrate laterally, the supraoccipital posterodorsally, and the pterygoid and basisphenoid ventrally. Possibly there is a contact with the opisthotic posteriorly, but this may be prevented by a supraoccipital-quadrate contact (see supraoccipital).

STRUCTURES: The prootic forms the anterodorsal margin of the foramen nervi trigemini and the medial margin of the foramen stapediotemporale, as in other bothremydids. As discussed elsewhere (see Pterygoid, Quadrate), the prootic of *Kinkonychelys* is unusual among the Kurmademydini in not being exposed in the roof of the fossa pterygoidea. As a result, the foramen nervi facialis, usually formed by the prootic, is formed by the pterygoid and basisphenoid in *Kinkonychelys*. Interestingly, in the very similar FMNH PR 2446 of *Kinkonychelys* sp., the prootic is exposed ventrally and forms the foramen nervi facialis along with the basisphenoid.

OPISTHOTIC

PRESERVATION: Both opisthotics are present in UA 9748; the left one is nearly complete, but the right one lacks its posterior end. The medial sutures are in broken areas and unclear.

CONTACTS: As in the other bothremydids, the contacts of the opisthotic in *Kinkonychelys* are with the supraoccipital anteromedially, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially. Possibly there is a prootic contact anteriorly (see Supraoccipital).

STRUCTURES: The foramen jugulare posterius in UA 9748 has no opisthotic contribution. The adjacent fenestra postotica is formed medially by the exoccipital, dorsally by the opisthotic,

and ventrally and laterally by the quadrate. As with the other basicranial elements, the internal structures, such as the cavum labyrinthicum, the hiatus acusticus, and the cavum acusticojugulare are visible, but do not differ significantly from previously described material of bothremydids (see Gaffney et al., 2006).

BASISPHENOID

PRESERVATION: Most of the basisphenoid is present in UA 9748, but on the midline some bone is missing and the right fossa pterygoidea has a broken roof with parts of the pterygoid, basisphenoid, and quadrate missing.

CONTACTS: On the ventral surface, the basisphenoid in UA 9748 has the usual bothremydid contacts with the pterygoids anterolaterally, the basioccipital posteriorly, and the quadrate laterally. The latter contact is a synapomorphy for the superfamily Podocnemidoidea (Podocnemididae+Bothremydidae) of Gaffney et al. (2006).

STRUCTURES ON VENTRAL SURFACE: The most obvious feature on the ventral surface of the basisphenoid is the prominent fossa pterygoidea, a feature also occurring in FMNH PR 2446 and *Kurmademys* but otherwise rare in bothremydids. In the anterior wall of the fossa, the foramen posterius canalis carotici interni in UA 9748 is formed medially by the basisphenoid, as in FMNH PR 2446. The medial wall and the small overhang of the fossa pterygoidea are also formed by the basisphenoid in UA 9748 (see Pterygoid).

CONTACTS ON DORSAL SURFACE: As in other bothremydids, the contacts of the basisphenoid in *Kinkonychelys* are with the pterygoid anterolaterally, the prootic laterally, the palatines anteriorly (only on the dorsal surface), and the basioccipital posteriorly.

STRUCTURES ON DORSAL SURFACE: Fortunately, there are specimens of both *Kurmademys* (Gaffney et al., 2006) and FMNH PR 2446 that show the dorsal surface of the basisphenoid for comparison with UA 9748. The rostrum basisphenoidale in UA 9748 and FMNH PR 2446 is broken off. The sella turcica is preserved and very similar to that of *Kurmademys* in being relatively wide with the foramen anterius canalis carotici interni at the posterolateral corners of the sella turcica. The processus clinoideus is a low process with the

foramen nervi abducentis (VI) penetrating its base, as in *Kurmademys*.

LOWER JAW

A lower jaw ramus, FMNH PR 2653, consisting mostly of the dentary, is readily identifiable as a bothremydid based on the very low labial ridge, the posteriorly rising lingual ridge forming a shallow concavity laterally, with a symphysis having a U-shaped concavity posterior to a narrow triturating surface (see Gaffney et al., 2006, for the lower jaw morphology of bothremydids). The ramus is very similar to those described for *Kurmademys* (Late Cretaceous, India) and *Cearachelys* (Early Cretaceous, Brazil), the presumed primitive condition for bothremydids. The position and shape of the coronoid bone is the same in both. The sulcus cartilaginis meckelii is anteriorly continuous with the symphyseal depression, also as in other bothremydids. Although it is impossible to be sure, it is very likely that this jaw belongs to *Kinkonychelys*, based on agreement in triturating surface shape and size.

DISCUSSION

Kinkonychelys is a bothremydid because it has the diagnostic characters of an exoccipital-quadrate contact and a fully enclosed incisura columellae auris (Gaffney et al., 2006). *Kinkonychelys* belongs to the tribe Kurmademydini, previously known to include only *Sankuchemys* and *Kurmademys* from the Late Cretaceous of India, because it has a deep fossa pterygoidea, a foramen stapediotemporale facing dorsally, a jugal not retracted from the orbit, a deep fossa precolumellaris, and a large, wide antrum postoticum. It agrees with FMNH PR 2446 of *Kinkonychelys* sp. (described below) in the form of the overlapping fossa pterygoidea, which is unique.

FAMILY BOTHREMYDIDAE BAUR, 1891

TRIBE KURMADEMYDINI GAFFNEY, TONG, AND MEYLAN, 2006

Kinkonychelys sp.

SPECIMEN: FMNH PR 2446, left half of braincase (figs. 5–8).

LOCALITY: MAD 05-63 (latitude 16°2′58.6″S, longitude 46°3′39.4″E) in the Masiakakoho Study Area (fig. 1). MAD 05-63 lies approximately 4.7 km south-southeast of the village of Masiakakoho and 36.2 km northeast of the type locality of *Kinkonychelys rogersi*.

HORIZON: Anembalemba Member, Maevarano Formation, Maastrichtian, Upper Cretaceous. FMNH PR 2446 was surface-collected on red, weathered slopes of the Masorobe Member immediately below the contact between the Masorobe Member and the overlying Anembalemba Member (fig. 1). After examining field relations and the distribution of bone, it was concluded that the specimen most likely eroded prior to discovery from the base of the Anembalemba Member, which at this locality is represented by a massive bed of poorly sorted, clay-rich sandstone ("facies 2" of Rogers et al., 2000). Fossils from facies 2 were entombed in massive debris flows during the rainy season (Rogers, 2005).

DESCRIPTION

Figures 5–8

QUADRATE

PRESERVATION: The left quadrate is preserved but lacks most of its lateral margins, retaining the more medial surfaces of the cavum tympani. The medial contacts and structures are present.

CONTACTS ON LATERAL SURFACE: Of these, only a small part of the probable suture with the squamosal is preserved.

STRUCTURES ON LATERAL SURFACE: No information on the temporal or cheek emargination is preserved. However, much of the cavum tympani can be determined. There is a completely closed incisura columellae auris with a eustachian tube separated from the stapes by bone, all diagnostic for bothremydids. As in *Kinkonychelys* and *Kurmademys*, the antrum postoticum is large and deep, the fossa precolumellaris is deep and well defined, and there is a remnant of the narrow trough on the ridge extending from the incisura columellae auris to the sulcus eustachii.

CONTACTS ON DORSAL, VENTRAL, POSTERIOR, AND ANTERIOR SURFACES: These quadrate contacts are determinable in FMNH PR
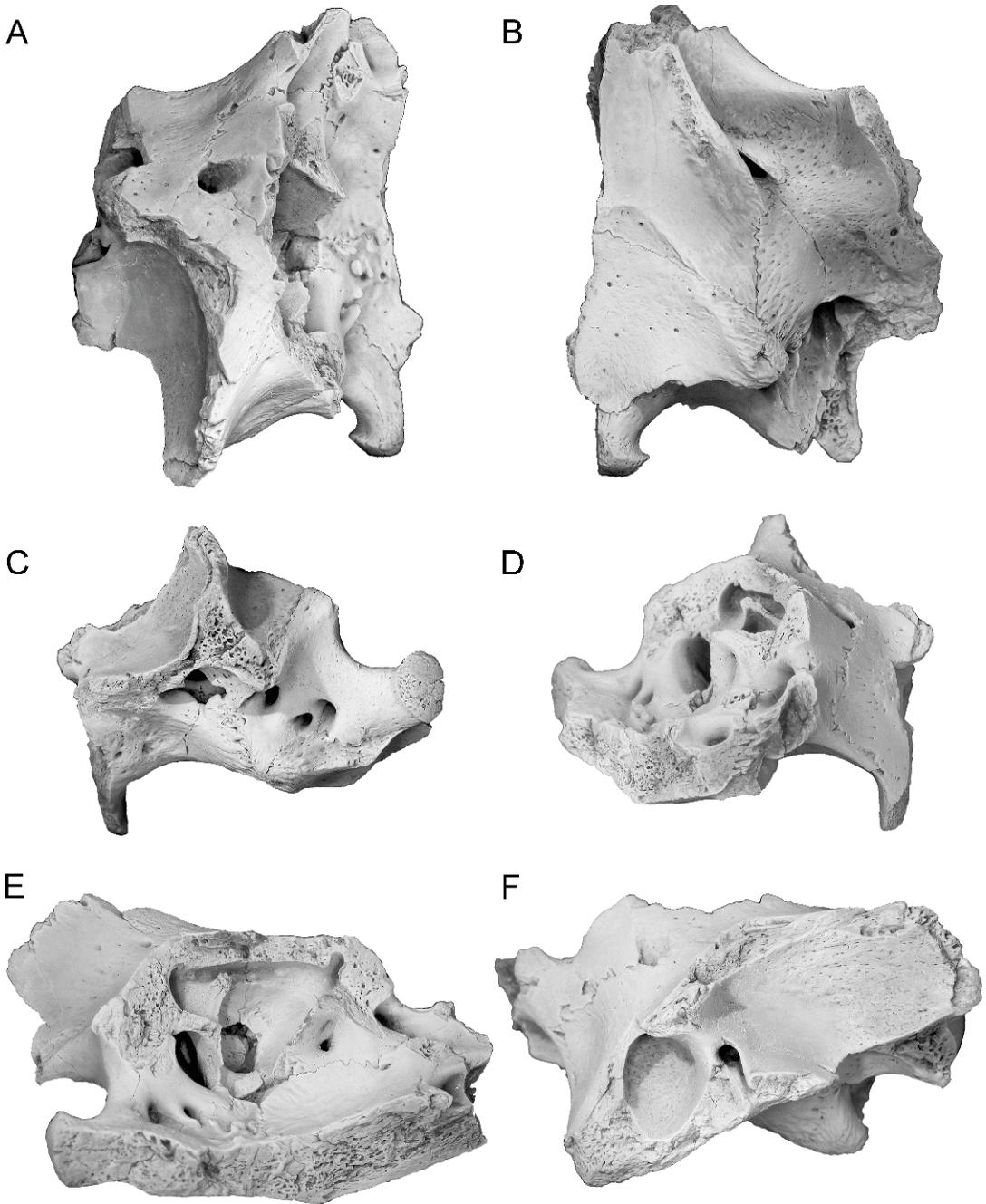
Fig. 5.   *Kinkonychelys* sp. FMNH PR 2446, partial braincase. A, Dorsal; B, ventral; C, posterior; D, anterior; E, medial; F, lateral. [I. Zalmout, del.]

2446: the prootic anteromedially, the opisthotic posteromedially, the pterygoid anteromedially, the basisphenoid medially, the basioccipital posteromedially, and the exoccipital medially. The exoccipital contact is synapomorphic for the Bothremydidae.

STRUCTURES ON DORSAL, VENTRAL, POSTERIOR, AND ANTERIOR SURFACES: The foramen
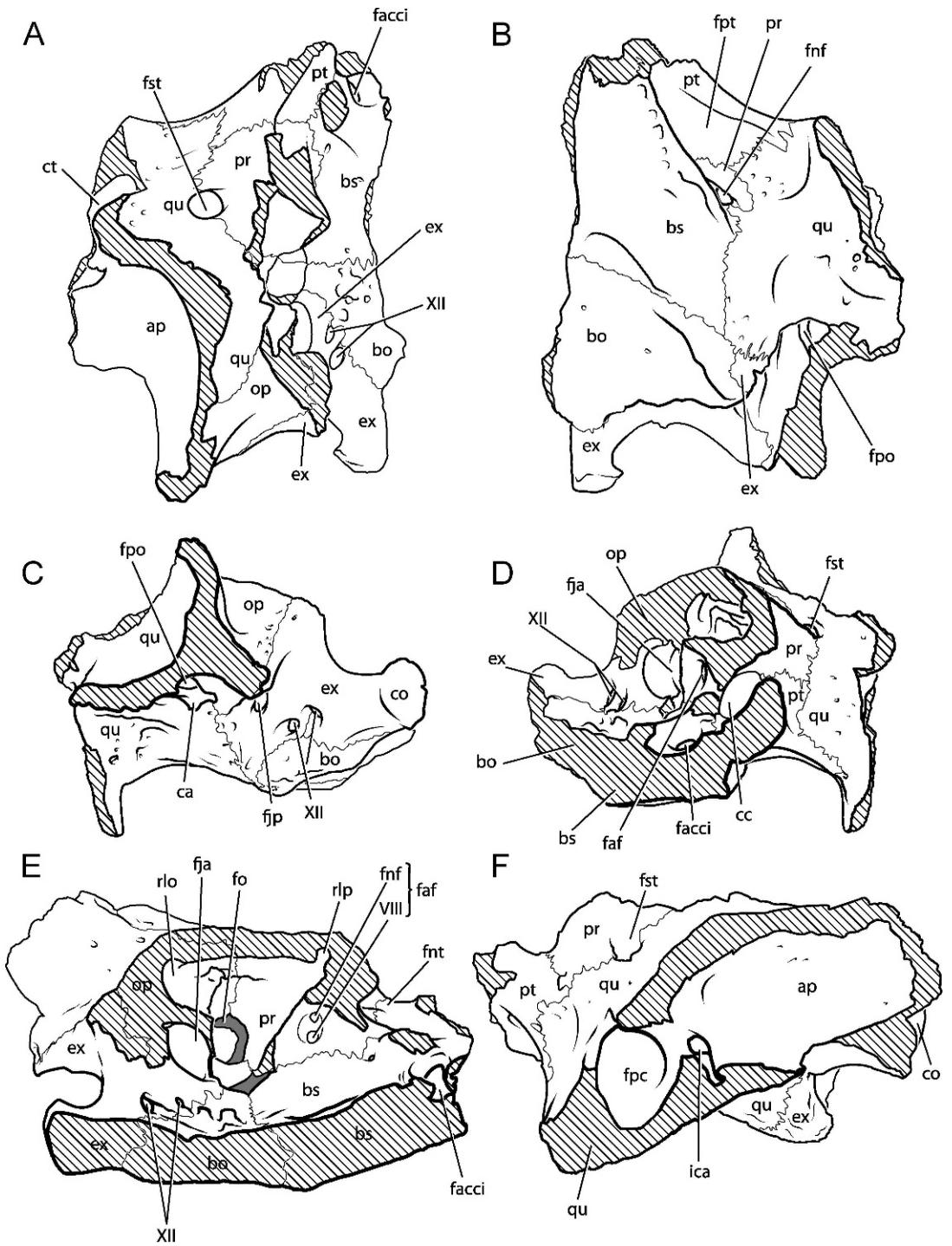
Fig. 6.   *Kinkonychelys* sp. FMNH PR 2446, partial braincase. A, Dorsal; B, ventral; C, posterior; D, anterior; E, medial; F, lateral. Key to Fig. 5. [C. Facella, J. Sharkey, del.]
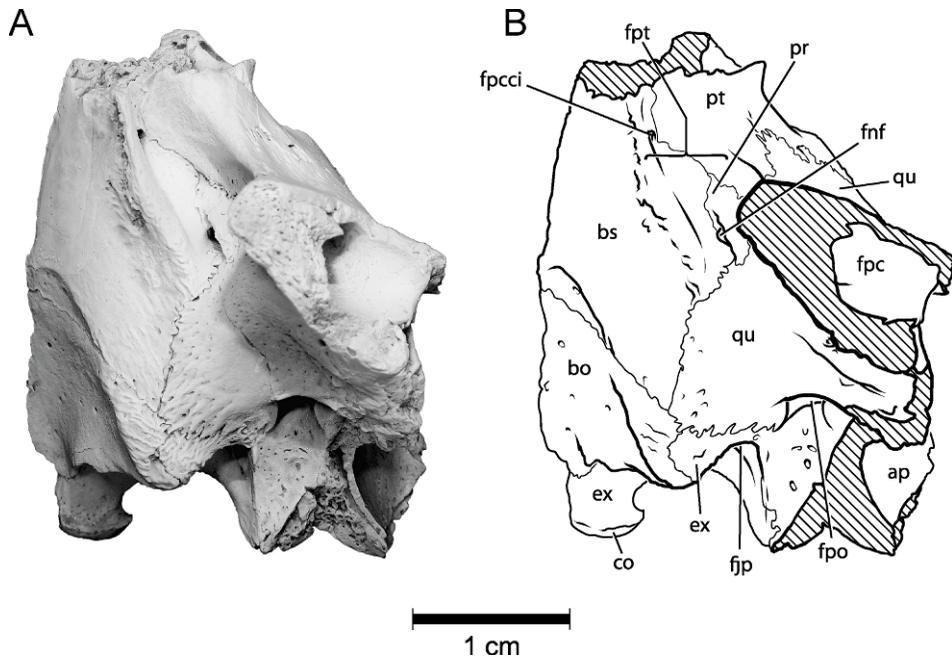
Fig. 7. *Kinkonychelys* sp. FMNH PR 2446, partial braincase in ventrolateral view to show structures in fossa pterygoidea. Anterior toward top of page. A, photograph; B, line drawing. [J. Sharkey, del.]

stapediotemporale (see Prootic) faces dorsally, as in other Kurmademydini. There is a large and well-defined fossa pterygoidea (see Pterygoid) very similar to that in *Kinkonychelys* (UA 9748). The condylus mandibularis in FMNH PR 2446 is broken off, but its position can be determined as farther anteriorly in comparison to that in *Kinkonychelys* and more like that in *Kurmademys*. The fenestra postotica in FMNH PR 2446 is formed laterally, ventrally, and dorsolaterally by the quadrate, with the medial and dorsomedial walls formed by the opisthotic. The fenestra postotica in FMNH PR 2446 is more ovoid and equidimensional, rather than more horizontal as in *Kurmademys* and *Kinkonychelys*. There is also a distinct ridge separating the lateral head vein and stapedial artery in the roof of the fenestra.

PTERYGOID

PRESERVATION: The posteriormost portion of the left pterygoid is preserved in FMNH PR 2446.

CONTACTS: The pterygoid fragment contacts the basisphenoid posteromedially, the prootic posterodorsally, and the quadrate posterolaterally. Viewed in the roof of the fossa pterygoidea, the pterygoid contacts the basisphenoid anteriorly, the prootic medially, and the quadrate posteriorly.

STRUCTURES: The fossa pterygoidea (fig. 7) in FMNH PR 2446 is formed by the pterygoid anterolaterally, the basisphenoid medially, the quadrate posterolaterally, and, in a small part of the roof dorsally, the prootic. Other than the exposure of the prootic, the fossa pterygoidea structure and contacts in FMNH PR 2446 are very similar to those in UA 9748. The prootic exposure has contacts with the other three bones: the pterygoid anterolaterally, the basisphenoid medially, and the quadrate posterolaterally. The foramen posterius canalis carotici interni lies at the anteriormost edge of the fossa pterygoidea, as in UA 9748. There is no indication of a foramen nervi vidiani or foramen caroticum laterale in the fossa pterygoidea. Most of the foramen lies in the basisphenoid.

The anteriormost end of the fossa pterygoidea is broken off, so the complete wall of the fossa is not preserved. In the pterygoid part of the break, anterodorsal to the foramen posterius canalis carotici interni, is the upper half of a small foramen, presumed to be the foramen nervi vidiani, which is in this position in the
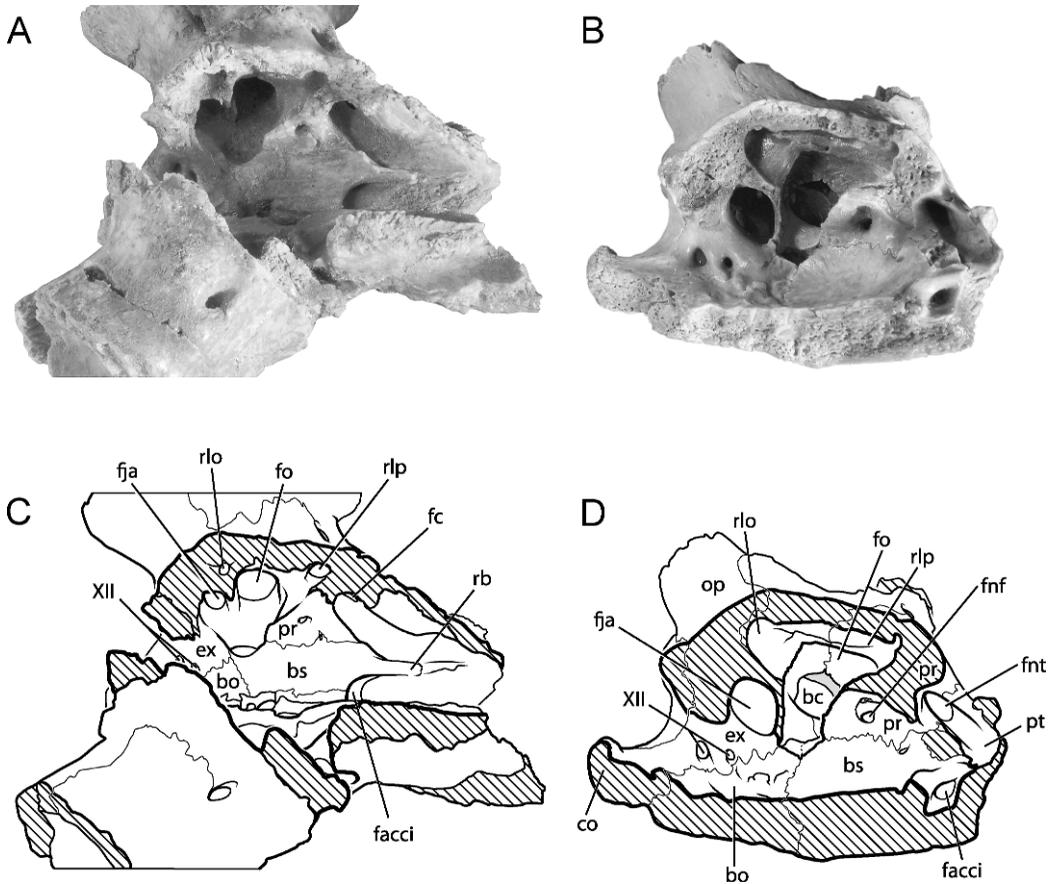
Fig. 8.   Medial views of cavum cranii in two skulls of *Kinkonychelys*. A, C, *Kinkonychelys rogersi*, n. gen. et sp., UA 9748, holotype; B, D, *Kinkonychelys* sp., FMNH PR 2446. Anterior to the right. [I. Kayama, F. Ippolito, del.]

pterygoid of *Kurmademys* (Gaffney et al., 2006: fig. 63).

The ventral margin of the foramen nervi trigemini is preserved and formed by the pterygoid anteriorly and prootic posteriorly. The sulcus cavernosus and canalis cavernosus are also preserved. There is no indication of the foramen caroticum laterale on the dorsal surface of the pterygoid.

EXOCCIPITAL

PRESERVATION: All of the left exoccipital is present except for most of the dorsal process forming the foramen magnum.

CONTACTS: The preserved contacts of the exoccipital in FMNH PR 2446 are with the opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally.

STRUCTURES: In FMNH PR 2446 the condylus occipitalis is formed by the exoccipitals only, without contribution from the basioccipital. Although only one exoccipital is preserved, the formation of the condylus occipitalis by the exoccipitals only can still be determined because the limit of the basioccipital is visible anterior to the base of the exoccipital. This condition also occurs in UA 9748 but not in *Kurmademys*. The foramen nervi hypoglossi in FMNH PR 2446 is paired on both sides and not recessed. The foramen jugulare posterius is formed mostly by the exoccipital, but its lateral wall is formed by the opisthotic.

BASIOCCIPITAL

PRESERVATION: The left half of the basioccipital is preserved. The posterior end of the

bone is a sutural surface indicating that it did not enter into the condylus occipitalis.

CONTACTS: The contacts in FMNH PR 2446 are with the basisphenoid anteriorly, the quadrate laterally, and the exoccipitals posterodorsally.

STRUCTURES: The basioccipital in FMNH PR 2446 is slightly longer than in UA 9748. It does not enter the condylus occipitalis. The tuberculum basioccipitale is slightly more pronounced than in UA 9748.

PROOTIC

PRESERVATION: Most of the prootic is present in FMNH PR 2446, but its dorsomedial portion is broken away.

CONTACTS: These contacts remain in FMNH PR 2446: the quadrate laterally, the pterygoid ventrally, the basisphenoid ventromedially, and the opisthotic posteriorly (at least internally, the external surface is damaged).

STRUCTURES: The prootic in FMNH PR 2446 forms the usual structures: the foramen nervi trigemini with the pterygoid and parietal, and the foramen stapediotemporale with the quadrate laterally. As in UA 9748, this foramen faces dorsally, not anteriorly. In the roof of the fossa pterygoidea, the prootic is exposed and forms the anterolateral margin of the foramen nervi facialis, rather than the whole structure as in other Kurmademydini. The basisphenoid forms the medial edge of the foramen nervi facialis with a small spur of the quadrate extending into the foramen posteriorly. Although this condition is unique for FMNH PR 2446, it could be interpreted as similar to that seen in UA 9748, in which the pterygoid and basisphenoid, with a small spur from the quadrate, form the foramen. Both taxa have the basisphenoid and quadrate in the foramen, with the pterygoid covering the remaining exposed part of the prootic in UA 9748.

OPISTHOTIC

PRESERVATION: Much of the left opisthotic remains in FMNH PR 2446, but it lacks its anterior and posterior ends.

CONTACTS: The remaining contacts of the opisthotic of FMNH PR 2446 are with the prootic anteriorly, the quadrate anterolaterally, and the exoccipital posteromedially.

STRUCTURES: The opisthotic forms the wall between the more medial foramen jugulare posterius and the more lateral fenestra postotica.

BASISPHENOID

PRESERVATION: The left half of the basisphenoid is present; it is broken just anterior to the dorsum sellae anteriorly, but its posterolateral portions remain.

CONTACTS ON VENTRAL SURFACE: The basisphenoid contacts are with a small part of the pterygoid anterolaterally, the basioccipital posteriorly, the prootic laterally, and the quadrate laterally.

STRUCTURES ON VENTRAL SURFACE: The foramen posterius canalis carotici interni lies at the anterior end of the fossa pterygoidea, under the overhang formed by the basisphenoid, as seen in UA 9748. The foramen is formed mostly by the basisphenoid with a small part formed by the pterygoid dorsally. The medial half of the fossa pterygoidea is formed by the basisphenoid and it has an overhang for most of its length, very similar to that seen in UA 9748.

CONTACTS ON DORSAL SURFACE: These are the usual bothremydid contacts: the pterygoid anterolaterally, the prootic laterally, and the basioccipital posteriorly.

STRUCTURES ON DORSAL SURFACE: Because FMNH PR 2446 is broken close to the dorsum sellae, very little of the sella turcica and none of the rostrum basisphenoidale remain. The foramen anterius canalis carotici interni is present at the posterolateral corner of what remains of the sella turcica, as in *Kinkonychelys rogersi* and *Kurmademys*. The processus clinoideus is broken off, but the foramen nervi abducentis (VI) remains.

DISCUSSION

This specimen is a bothremydid because it has the diagnostic characters of an exoccipital-quadrate contact and a fully enclosed incisura columellae auris. It belongs to the tribe Kurmademydini because it has a deep fossa pterygoidea, a small part of the prootic is exposed on the ventral surface at the junction of basisphenoid, pterygoid, and quadrate (not in UA 9748), a foramen stapediotemporale that faces dorsally, a deep fossa precolumellaris, and a large, wide antrum postoticum. It agrees with UA 9748 in the form of the fossa pterygoidea, which is unique. The fossa has the

medial basisphenoid margin overlapping the fossa covering the foramen posterius canalis carotici interni in ventral view. The anterior end of the fossa is deep, not shallow as in *Kurmademys*, and the foramen nervi facialis has at least the basisphenoid and quadrate in its margin rather than being formed entirely by the prootic. FMNH PR 2446 also agrees with UA 9748 in having the condylus occipitalis formed only by the exoccipitals, but this is a character that has evolved a number of times in turtles, not just in pleurodires.

As can be seen in table 1, UA 9748 (*Kinkonychelys rogersi*) and FMNH PR 2446 (*Kinkonychelys* sp.) differ in the following characters:

(1) UA 9748 has a condylus mandibularis that is relatively more posterior than in FMNH PR 2446.
(2) The foramen jugulare posterius has only the exoccipital in its margin in UA 9748, but the opisthotic also enters it in FMNH PR 2446.
(3) The prootic is exposed ventrally in FMNH PR 2446, but it is covered in UA 9748.
(4) Related to (3), the foramen nervi facialis in FMNH PR 2446 has the prootic in its margin and not the pterygoid, but in UA 9748 it is the pterygoid but not the prootic in the foramen margin.

The overhanging medial edge of the fossa pterygoidea in both specimens and their general similarity argue for close relationship. But the above-listed characters make it likely that FMNH PR 2446 represents a different taxon than UA 9748. We recognize this affinity by placing both in the same genus but in different species. UA 9748 is a nearly complete skull and can be appropriately employed to diagnose *Kinkonychelys rogersi*, but the incompleteness of FMNH PR 2446 precludes the naming of a new species, so we recognize it as *Kinkonychelys* sp. It will be difficult to assign new material to this taxon unless it has a well-preserved braincase.

RELATIONSHIPS AND BIOGEOGRAPHY OF *KINKONYCHELYS*

In order to determine the relationships of *Kinkonychelys*, it was entered into the charac-ter matrix of Gaffney et al. (2006) and a new analysis was conducted. The results are shown in figure 9. The single cladogram contains 47 taxa and 175 characters, all characters are unweighted, the consistency index is 0.69, and the retention index is 0.81. The phylogenetic relationships of *Kinkonychelys* are strongly resolved with the Indian taxa *Sankuchemys* and *Kurmademys*, both of about the same age as *Kinkonychelys*. In fact, the phylogenetic resolution for the tribe Kurmademydini is (*Sankuchemys* (*Kinkonychelys*+*Kurmademys*)), indicating that *Kinkonychelys* is embedded within the tribe Kurmademydini, not simply a sister taxon to it. There are interesting biogeo-graphic implications for these relationships.

Raxworthy (2003: 946) recently stated that, "Currently, there are no reptile groups in Madagascar that have well-supported phylog-enies supporting a sister relationship with either the Seychelles or India." As such, the extant Malagasy reptilian fauna shows no evidence of its former connections with the Indian subcontinent and the Seychelles block, the last major landmasses connected to Madagascar. The Indian subcontinent and Seychelles blocks are thought to have separat-ed, as a unit, from Madagascar approximately 88 Ma (Storey et al., 1995, 1997; Torsvik et al., 2000; Reeves and de Wit, 2000; Raval and Veeraswampy, 2003). Separation began in the north, approximately 118 Ma, and spread southward over the next 30 million years, as the Indo-Madagascar landmass passed over the Marion mantle plume (Seward et al., 2004). The Indian subcontinent and Seychelles blocks, in turn, separated from each other approximately 65 Ma, roughly contemporane-ous with the intrusion of the Deccan basalts, or shortly thereafter (Ernst and Buchan, 1997; Pande et al., 2001; Chand and Subrahmanyam, 2003). There is growing consensus that the Indian subcontinent did not contact mainland Asia until at or near the Paleocene/Eocene boundary, roughly 55 Ma (e.g., Rowley, 1996; Clyde et al., 2003; Aitchison et al., 2007; Ali and Aitchison, 2008; Garzanti, 2008).

In this plate tectonic context, the phylo-genetic hypothesis that *Kinkonychelys* is embed-ded within the Indian bothremydid tribe Kurmademydini as the sister taxon of *Kurmademys* (*Sankuchemys* (*Kinkonychelys*,
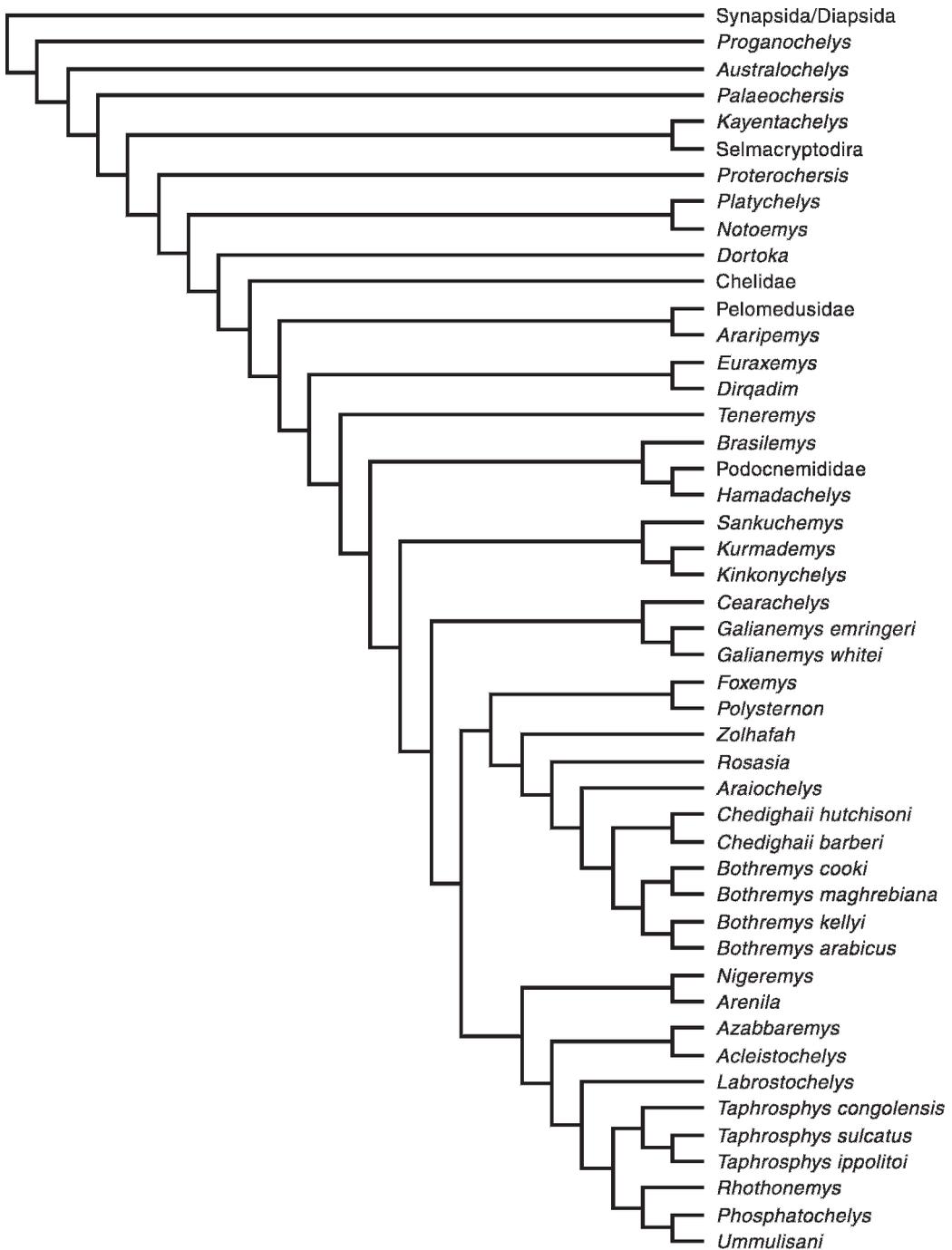
Fig. 9. Cladogram of bothremydids showing position of *Kinkonychelys* resulting from a PAUP analysis when entered into the character list of Gaffney et al. (2006).

Kurmademys)) indicates an even closer phylogenetic relationship than documented for other clades of Late Cretaceous vertebrates from Madagascar and the Indian subcontinent. Among gondwanatherian mammals, the Malagasy form *Lavanify* is more closely related to the Indian form *Bharratherium* (the senior synonym of *Dhakshina* Wilson et al., 2007) than it is to the South American forms *Gondwanatherium* and *Sudamerica* (*Gondwanatherium* (*Sudamerica* (*Bharratherium*, *Lavanify*))) (Krause et al., 1997, Wilson et al., 2007; Prasad et al., 2007). Similarly, among abelisaurid theropod dinosaurs, the Malagasy form *Majungasaurus* is phylogenetically closer to the Indian forms *Indosaurus* and *Rajasaurus* than it is to the South America genus *Carnotaurus* (*Carnotaurus* (*Indosaurus*, *Rajasaurus*, *Majungasaurus*)) (Carrano and Sampson, 2008). As such, *Kinkonychelys* provides additional evidence of a close relationship among the latest Cretaceous terrestrial/freshwater vertebrate faunas of Madagascar and the Indian subcontinent but is the first taxon known from the Late Cretaceous of Madagascar that resides entirely *within* a clade previously known only from the Indian subcontinent.

ACKNOWLEDGMENTS

REFERENCES

Aitchison, J.C., J.R. Ali, and A.M. Davis. 2007. When and where did India and Asia collide? Journal of Geophysical Research 112: B05423.

Ali, J.R., and J.C. Aitchison. 2008. Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian subcontinent from the Middle Jurassic through latest Eocene (166-35 Ma). Earth-Science Reviews 88: 145–166.

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

Bonnaterre, A. 1789. Erpétologie. *In* Tableau encyclopédique et méthodique des trois règnes de la nature. Paris: Panckouke, 28+70 pp.

Carrano, M.T., and S.D. Sampson. 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). Journal of Systematic Palaeontology 6(2): 183–236.

Chand, S., and C. Subrahmanyam. 2003. Rifting between India and Madagascar – mechanism and isostasy. Earth and Planetary Science Letters 210: 317–332.

Clyde, W.C., I.H. Khan, and P.D. Gingerich. 2003. Stratigraphic response and mammalian dispersal during initial India-Asia collision: evidence from the Ghazj Formation, Baluchistan, Pakistan. Geology 31: 1097–1100.

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

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

Depéret, C. 1896. Note sur les dinosauriens sauropodes et théropodes du Cretacé supérieur de Madagascar. Bulletin de la Société Geologique de France 3e série 24: 176–194.

Ernst, R.E., and K.L. Buchan. 1997. Giant radiating dyke swarms: their use in identifying pre-Mesozoic large igneous provinces and mantles plumes. *In* J.J. Mahoney and M.F. Coffin (editors), Large igneous provinces – continental, oceanic, and planetary flood volcanism. AGU Geophysical Monograph 100: 297–334.

Gaffney, E.S. 1972. An illustrated glossary of turtle skull nomenclature. American Museum Novitates 2486: 1–33.

Gaffney, E.S. 1979. Comparative cranial morphology of Recent and fossil turtles. Bulletin of the American Museum of Natural History 164(2): 1–376.

Gaffney, E.S. 1988. A cladogram of the pleurodiran turtles. Acta Zoologica Cracoviensia 31(15): 487–492.

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

Gaffney, E.S., and C.A. Forster. 2003. Side-necked turtle lower jaws (Podocnemididae, Bothremydidae) from the Late Cretaceous Maevarano Formation of Madagascar. American Museum Novitates 3397: 1–13.

Gaffney, E.S., J.H. Hutchison, F.A. Jenkins, Jr., and L.J. Meeker. 1987. Modern turtle origins: the oldest known cryptodire. Science 237: 289–291.

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

Gaffney, E.S., T.H. Rich, P. Vickers-Rich, A. Constantine, R. Vacca, and L. Kool. 2007. *Chubutemys*, a new eucryptodiran turtle from the Early Cretaceous of Argentina, and the relationships of the Meiolaniidea. American Museum Novitates 3599: 1–35.

Gaffney, E.S., A. Sahni, H. Schleich, S.D. Singh, and R. Srivastava. 2003. *Sankuchemys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of India. American Museum Novitates 3405: 1–10.

Gaffney, E.S., H. Tong, and P.A. Meylan. 2006. Evolution of the side-necked turtles: the Families Bothremydidae, Euraxemydidae, and Araripemydidae. Bulletin of the American Museum of Natural History 300: 1–698.

Garzanti, E. 2007. Comment on "When and where did India and Asia collide?" by Jonathan C. Aitchison, Jason R. Ali, and Aileen M. Davis. Journal of Geophysical Research 113: B04411, doi:10.1029/2007JB005276.

Grandidier, A. 1867. Liste des reptiles nouveaux découverts, en 1866, sur la côte sud-ouest de Madagascar. Revue Magazine Zoologique de Paris 19(2): 232–234.

Hewitt, J. 1931. Descriptions of some African tortoises. Annals of the Natal Museum 6: 461–506.

Iverson, J.B. 1992. A revised checklist with distribution maps of the turtles of the world. Privately printed, Richmond, Indiana. 363 pp.

Krause, D.W., P.M. O'Connor, K. Curry Rogers, S.D. Sampson, G.A. Buckley, and R.R. Rogers. 2006. Late Cretaceous terrestrial vertebrates from Madagascar: implications for Latin American biogeography. Annals of the Missouri Botanical Garden 93: 178–208.

Krause, D.W., G.V.R. Prasad, W. von Koenigswald, A. Sahni, and F.E. Grine. 1997. Cosmopolitanism among Late Cretaceous Gondwanan mammals. Nature 390: 504–507.

Lacépède, B.G.E. 1788. Histoire naturelle des quadrupèdes ovipaires et des serpens. Vol. 1. Paris: Imprimerie du Roi, 668 pp.

Lapparent de Broin, F. de. 2000. African chelonians from the Jurassic to the present: phases of development and preliminary catalogue of the fossil record. Palaeontologia Africana 36: 43–82.

Linnaeus, C. 1758. Systema Naturae. 10th ed. Vol. 1. Stockholm: Salvius, 824 pp.

Noonan, B. 2000. Does the phylogeny of pelomedusoid turtles reflect vicariance due to continental drift? Journal of Biogeography 27: 1245–1249.

Noonan, B.P., and P.T. Chippindale. 2006. Vicariant origin of Malagasy reptiles supports Late Cretaceous Antarctic landbridge. American Naturalist 168: 730–741.

Pande, K., H.C. Sheth, and R. Bhutani. 2001. ^{40}Ar–^{39}Ar age of the St. Mary's Islands volcanics, southern India: record of India-Madagascar break-up on the Indian subcontinent. Earth and Planetary Science Letters 193: 39–46.

Prasad, G.V.R., O. Verma, A. Sahni, D.W. Krause, A. Khosla, and V. Parmar. 2007. A new Late Cretaceous gondwanatherian mammal from central India. Proceedings of the Indian National Science Academy 73(1): 17–24.

Raval, U., and K. Veeraswamy. 2003. India-Madagascar separation: breakup along a preexisting mobile belt and chipping of the craton. Gondwana Research 6: 467–485.

Raxworthy, C.J. 2003. Introduction to the reptiles. *In* S.M. Goodman and J.P. Benstead (editors), The natural history of Madagascar. Chicago: University of Chicago Press, 934–949.

Reeves, C., and M. de Wit. 2000. Making ends meet in Gondwana: retracing the transforms of the Indian Ocean and reconnecting continental shear zones. Terra Nova 12: 272–280.

Rogers, R.R. 2005. Fine-grained debris flows and extraordinary vertebrate burials in the Late Cretaceous of Madagascar. Geology 33: 297–300.

Rogers, R.R., J.H. Hartman, and D.W. Krause. 2000. Stratigraphic analysis of Upper Cretaceous rocks in the Mahajanga Basin, northwestern Madagascar: implications for ancient and modern faunas. Journal of Geology 108: 275–301.

Rogers, R.R., and D.W. Krause. 2007. Tracking an ancient killer. Scientific American 296: 42–51.

Rogers, R.R., D.W. Krause, K. Curry Rogers, A.H. Rasoamiaramanana, and L. Rahantarisoa. 2007. Paleoenvironment and paleoecology of *Majunga-*

saurus crenatissimus (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir 8: 21–31.

Romano, P.S.R., and S.A.K. Azevado. 2006. Are extant podocnemidid turtles relicts of a widespread Cretaceous ancestor? South American Journal of Herpetology 1(3): 175–184.

Rowley, D.B. 1996. Age of initiation of collision between India and Asia: a review of stratigraphic data. Earth and Planetary Science Letters 145: 1–13.

Samonds, K.E., I.S. Zalmout, M.T. Irwin, D.W. Krause, R.R. Rogers, and L.L. Raharivony. In press. *Eotheroides lambondrano*, new middle Eocene seacow (Mammalia, Sirenia) from the Mahajanga Basin, northwestern Madagascar. Journal of Vertebrate Paleontology

Seward, D., D. Grujic, and G. Schreurs. 2004. An insight into the breakup of Gondwana: identifying events through low-temperature thermochronology from the basement rocks of Madagascar. Tectonics 23: TC3007.

Storey, M., J.J. Mahoney, A.D. Saunders, R.A. Duncan, S.P. Kelley, and M.F. Coffin. 1995. Timing of hot spot-related volcanism and the breakup of Madagascar and India. Science 267: 852–855.

Storey, M., J.J. Mahoney, and A.D. Saunders. 1997. Cretaceous basalts in Madagascar and the transition between plume and continental lithosphere mantle sources. Geophysical Monograph 100: 95–122.

Torsvik, T.H., R.D. Tucker, L.D. Ashwal, L.M. Carter, B. Jamtveit, K.T. Vidyadharan, and P. Venkataramana. 2000. Late Cretaceous India-Madagascar fit and timing of breakup related magmatism. Terra Nova 12: 220–224.

Vargas-Ramírez, M., O.V. Castaño-Mora, and U. Fritz. 2008. Molecular phylogeny and divergence times of ancient South American and Malagasy river turtles (Testudines: Pleurodira: Podocnemididae). Organisms, Diversity, and Evolution 8: 388–398.

Wilson, G.P., D.C. Das Sarma, and S. Anantharaman. 2007. Late Cretaceous sudamericid gondwanatherians from India with paleobiogeographic considerations of Gondwanan mammals. Journal of Vertebrate Paleontology 27: 521–531.

Complete lists of all issues of the *Novitates* and the *Bulletin* are available at World Wide Web site http://library.amnh.org/pubs. Inquire about ordering printed copies via e-mail from scipubs@amnh.org or via standard mail from: American Museum of Natural History, Library—Scientific Publications, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009.