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Side-Necked Turtle Lower Jaws (Podocnemididae, Bothremydidae) from the Late Cretaceous Maevarano Formation of Madagascar

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ABSTRACT

Two lower jaws from the upper part (early Maastrichtian) of the late Cretaceous Maevarano Formation in the Mahajanga Basin, northwestern Madagascar, are identified as belonging to side-necked turtles (Pleurodira). A nearly complete lower jaw is identified as cf. *Erymnochelys* because of its close resemblance to the living Malagasy *Erymnochelys madagascariensis*. Both uniquely possess the combination of a posteriorly directed processus retroarticularis and a nearly identical triturating surface that is narrow anteriorly with a horizontal labial ridge and a dorsally rising lingual ridge. A second specimen, consisting of an incomplete symphyseal region, is questionably identified as Bothremydidae on the basis of a thick wedge-shaped symphysis with partial or complete pits on the rami. The cf. *Erymnochelys* specimen is the oldest record of *Erymnochelys* or a taxon very similar to it, and it indicates the persistence of a Mesozoic element in the extant Malagasy turtle fauna. The possible bothremydid jaw suggests a more cosmopolitan element now extinct.

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INTRODUCTION

In 1896, Charles Depéret reported numerous indeterminate turtle carapace and plastron fragments collected in northwestern Madagascar from sediments that are now known as the Maevarano Formation. Seventy-eight years later, in 1974, a team of French paleontologists returned to northwestern Madagascar to conduct fieldwork in the Maevarano Formation near the village of Berivotra, the same general area where Déperet's material was collected (Russell et al., 1976). Russell et al. (1976) collected material they identified as a species of pleurodire, an identification based on numerous carapace fragments, vertebrae, a cranial fragment, and a limb bone. Ravoavy (1987), in a summary of known fossils from the Maevarano Formation, was more specific and reported turtles of the family Pelomedusidae, but Ravoavy did not speculate on the number of taxa present.

Recently, Lapparent de Broin (2000) summarized all known fossil turtles from Madagascar, listing two occurrences of Cretaceous pleurodires on the island, the only pre-Holocene turtle record from the island: (1) Berivotra (Mahajanga area) of "Senonian age", and (2) Betsioky (near the Menarandroy River in southwestern Madagascar) of "Cenomanian age". The first locality refers again to the Maevarano Formation and to the specimens previously collected and reported by Russell et al. (1976). However, Lapparent de Broin was more specific and refers the Maevarano turtle material to "Bothremydidae indet., form B" (Antunes and Broin, 1988). Antunes and Broin (1988: 180) reported "Bothremydidae indéterminé, forme B" as consisting of a "portion de crâne avec les carré, opisthotique et prootique partiels, montrant une structure de la région otique caractéristique des bothremydidés et conforme à celle de *Bothremys* et *Rosasia* . . .". Although noted in various lists (Broin, 1988; Lapparent de Broin and Werner, 1998), none of this material has been described or figured, leaving the justification for the identifications unknown.

At the Betsioky locality, Lapparent de Broin identified "Bothremydidae indet., form A (? *Bothremys*)" based on information

from Antunes and Broin (1988) and Lapparent de Broin and Werner (1998). In Antunes and Broin (1988: 179) the Betsioky material was referred to as consisting of a "portion de carapace sans les parties antérieure et postérieure, conforme à *Bothremys* . . .". We are unaware of characters in the carapace unique to the Bothremydidae, despite assertions to the contrary (Lapparent de Broin and Werner, 1998).

Although turtle remains have been known from the Maevarano Formation in the Berivotra region for more than one hundred years, their identifications remain largely undetermined, and none have been figured or described to date. A series of recent expeditions to the Maevarano Formation by the State University of New York at Stony Brook and the Université d'Antananarivo, beginning in 1993, have recovered a diverse vertebrate assemblage that includes birds, crocodylians, dinosaurs, freshwater fishes, mammals, snakes, frogs, and turtles (e.g., Krause et al., 1999). This additional turtle material includes partial and fragmentary carapaces and plastra, cervical vertebrae, girdle and limb elements, and fragmentary cranial material. At least two, and probably more, pleurodire taxa are represented in this material. Despite a virtual pavement of carapace and plastron fragments at several sites in the Maevarano Formation, more complete specimens remain elusive. In this paper we describe two new, distinct turtle taxa based on lower jaw material.

Both specimens described here were collected in 1996 from the Maevarano Formation near the village of Berivotra, Mahajanga Basin, northwestern Madagascar (see fig. 2 in Krause et al., 1999). Although the age of the Maevarano Formation was reported as either Cenomanian (e.g., Antunes and Broin, 1988) or Campanian (e.g., Russell et al., 1976), recent stratigraphic work confirmed that the formation is younger than previously surmised (Rogers et al., 2000). Both specimens described here are from the highly fossiliferous upper members of the Maevarano Formation—the Anembalemba and Miadana Members—which are regarded as early Maastrichtian, and possibly late Maastrichtian in age (Krause et al., 1999; Rogers et al., 2000).

A review of turtle lower jaw anatomy explaining and illustrating the terms used here can be found in Gaffney (1979). Pleurodire jaws are not well represented in the literature, but Fuchs (1931) provided good descriptions of *Podocnemis*. The taxonomy of pleurodires used here, recognizing Bothremydidae, Podocnemididae, and Pelomedusidae, has been developed in recent years. Antunes and Broin (1988) and Broin (1988) revived Bothremydidae, provided a new diagnosis, and added taxa, such as *Rosasia*, based on skulls and shells. Recent papers on fossil pleurodires, such as Meylan (1996), Lapparent de Broin and Werner (1998), and Tong et al. (1998), use the Antunes and Broin (1988) terminology, in which Bothremydidae, Podocnemididae, and Pelomedusidae (restricted to *Pelusios* and *Pelomedusa*) are contained in the Pelomedusoides (which equals Pelomedusidae in the classic sense). Bothremydids are now recognized as a more widespread and diverse group than previously considered.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York
FMNH	Field Museum of Natural History, Chicago
MNHN	Museum National d'Histoire Naturelle, Paris
UA	Université d'Antananarivo, Antananarivo, Madagascar

ANATOMICAL ABBREVIATIONS

ang	angular
art	articular
cor	coronoid
dent	dentary
f. aur	foramen nervi auriculotemporalis
f. dfm	foramen dentofacialis majus
f. pct	foramen posterius chorda tympani
fm	fossa meckelii
pra	prearticular
sa	surangular
scm	sulcus cartilagineus meckelii

SYSTEMATICS

ORDER TESTUDINES LINNAEUS, 1758

SUBORDER PLEURODIRA COPE, 1864

HYPERFAMILY PELOMEDUSOIDES COPE, 1868a

FAMILY PODOCNEMIDIDAE COPE, 1868b

cf. *Erymnochelys*

SPECIMEN: FMNH PR 2231; a nearly complete lower jaw, lacking the anteriormost tip

and most of both prearticulars (figs. 1, 2). Collected by C.A. Forster.

LOCALITY: MAD 93–35, Berivotra region, Mahajanga Basin, northwestern Madagascar.

HORIZON AND AGE: Anembalemba Member, Maevarano Formation, Maastrichtian.

DESCRIPTION

DENTARY

The dentaries of FMNH PR 2231 are fused completely on the midline as in all other podocnemidids and bothremydids (figs. 1, 2). Although there is a crack on the midline, there is no sign of a suture anywhere on the symphysis as seen in *Pelomedusa* and *Emydura*. The symphysis is relatively long as in *Erymnochelys*, *Peltocephalus*, *Podocnemis*, and bothremydids, but shorter than in most pelomedusids. *Peltocephalus* differs from all other living podocnemidids and from bothremydids in having a high, protuberant symphyseal projection; this projection is also absent in FMNH PR 2231. The symphyseal tip of FMNH PR 2231 is broken, but the preserved portion indicates it was probably not pointed as in the living *Erymnochelys* (fig. 3).

The triturating surface in FMNH PR 2231 is relatively narrow at the symphysis (figs. 1A, 2A), as in *Erymnochelys*, in contrast to the wider surface seen in *Peltocephalus* and *Podocnemis*. There is no midline ridge as in some Recent *Podocnemis* species; rather, the midline is flat as in *Erymnochelys* and *Peltocephalus*. The lingual ridge at the symphysis forms the upper margin for a concavity that makes up most of the symphyseal region. The concavity is broadly triangular with its apex pointing anteriorly. This morphology is similar to that of *Erymnochelys*, although the concavity in FMNH PR 2231 is somewhat wider and the curved apex less acute. This region is also similar to that in the bothremydids *Cearachelys* (Gaffney et al., 2001a) and *Kurmademys* (Gaffney et al., 2001b). The left and right dentaries meet at a more obtuse angle in FMNH PR 2231 than in *Erymnochelys*, *Peltocephalus*, or *Podocnemis*, and are more similar to bothremydids in this feature. In bothremydids similar to FMNH PR 2231 (i.e., *Cearachelys* and *Kurmademys*), the inner margin of the triturating surface is slightly S-shaped, while in

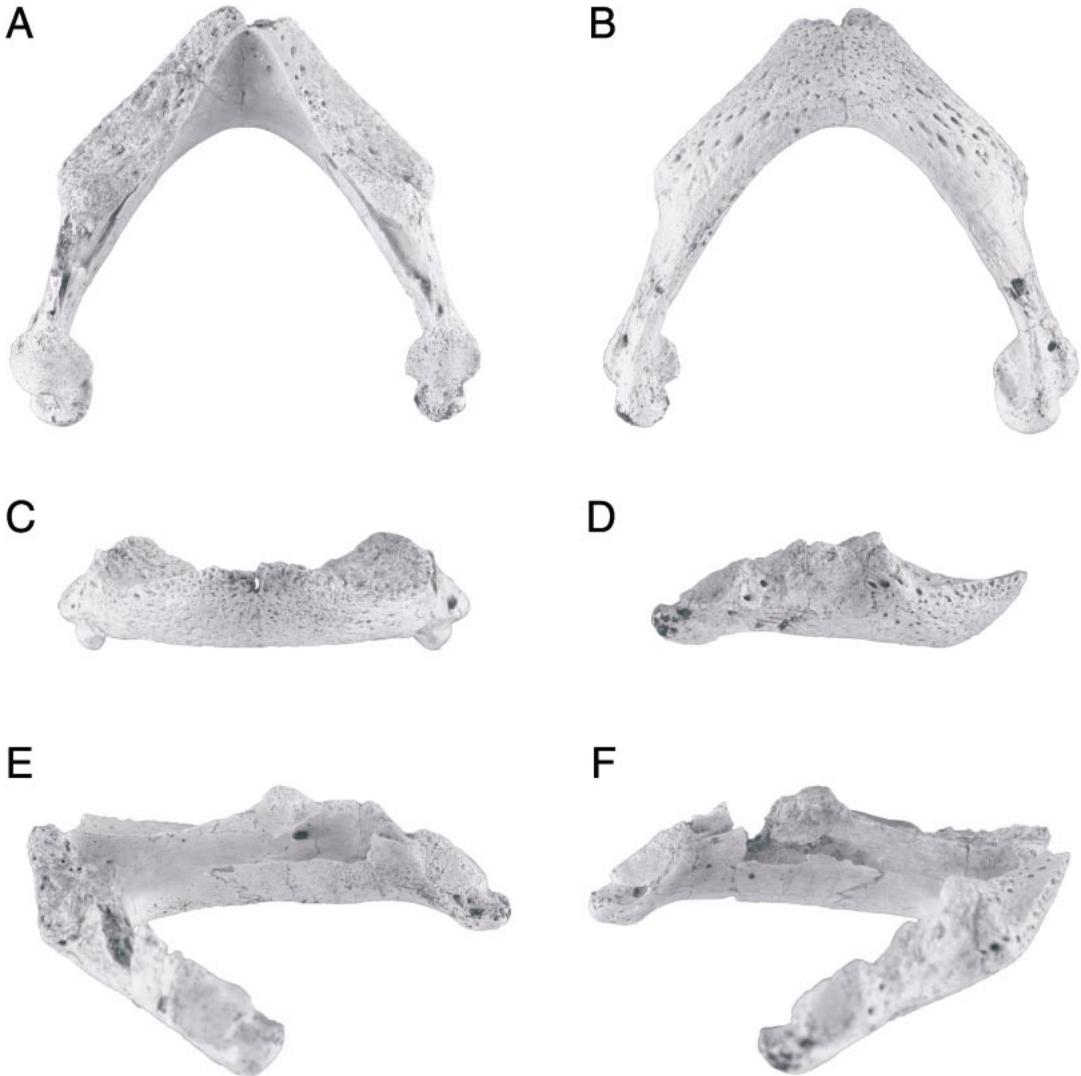


Fig. 1. Photographs of the lower jaw of cf. *Erymnochelys*, FMNH PR 2231. **A**, Dorsal view; **B**, ventral view; **C**, anterior view; **D**, right lateral view; **E**, medial view of right jaw; and **F**, medial view of left jaw. Scale bar equals 1 cm.

FMNH PR 2231 and the living podocnemidids this margin is nearly straight.

The triturating surface on the dentary closely resembles that in *Erymnochelys*. In both taxa, the triturating surface widens posteriorly, contrasting with the condition in *Podocnemis* and *Peltocephalus* where the margins of this surface remain roughly parallel. The triturating surface itself, between the lingual and labial ridges, is a broadly curved plane that faces anterolaterally in FMNH PR 2231 and *Erymnochelys*; in *Podocnemis* and

Peltocephalus it faces more dorsally. This triturating surface shape seen in FMNH PR 2231 also occurs in the bothremydids *Cearachelys* and *Kurmademys*, although these differ in having a shallow depression on the surface. Nonetheless, this morphology may be primitive within the Pelomedusoides at some level. However, *Hamadachelys*, the presumed sister taxon to Podocnemididae (Tong and Buffetaut, 1996) has parallel triturating ridges and lacks this morphology.

The labial ridge rises steadily posteriorly

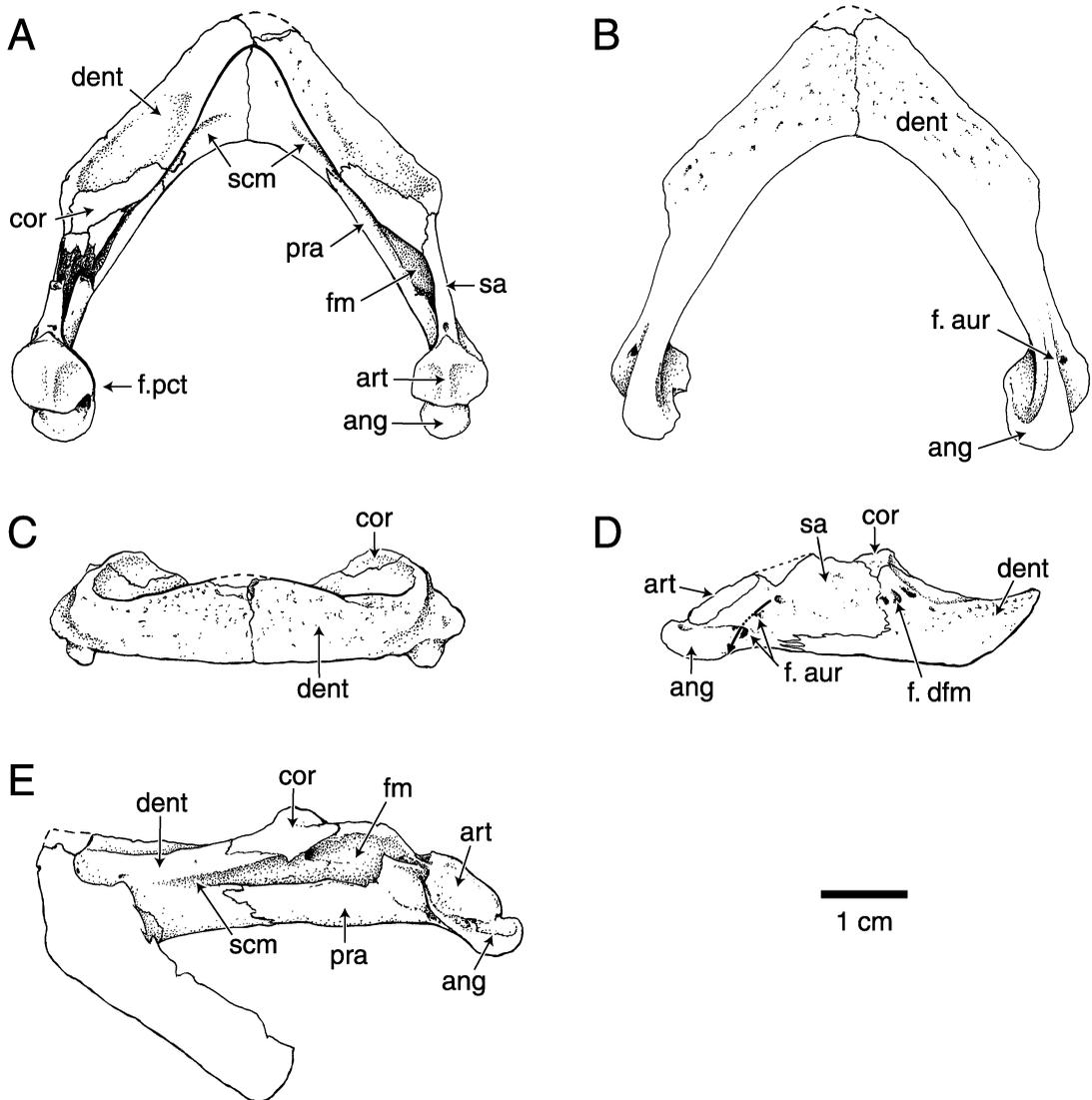


Fig. 2. Drawings of the lower jaw of cf. *Erymnochelys*, FMNH PR 2231. **A**, Dorsal view; **B**, ventral view; **C**, anterior view; **D**, right lateral view; and **E**, medial view of right jaw. Scale bar equals 1 cm.

in *Podocnemis* and *Peltocephalus* but remains low in FMNH PR 2231 and *Erymnochelys* until it reaches the region of the processus coronoideus, where it rises sharply. The labial ridge in FMNH PR 2231 is relatively blunt and resembles that in *Cearachelys* and *Kurmademys*; this ridge also is sharp in living podocnemidids. The lingual ridge in FMNH PR 2231 and *Erymnochelys* is slightly lower than the labial ridge at the symphysis. As it extends posteriorly, the lingual ridge rises dorsally to exceed the labial ridge

in height. As it rises, the lingual ridge meets the processus coronoideus medially.

The contacts of the dentary of FMNH PR 2231 with the postdentary elements are almost completely preserved; these contacts vary little among Pelomedusoides (figs. 1D–F, 2D, E). A splenial does not seem to be present, but the medial jaw surfaces are not complete. On the medial surface the dentary contacts the coronoid posterodorsally, the prearticular (which is incomplete) posteriorly, and the angular posteroventrally. On its

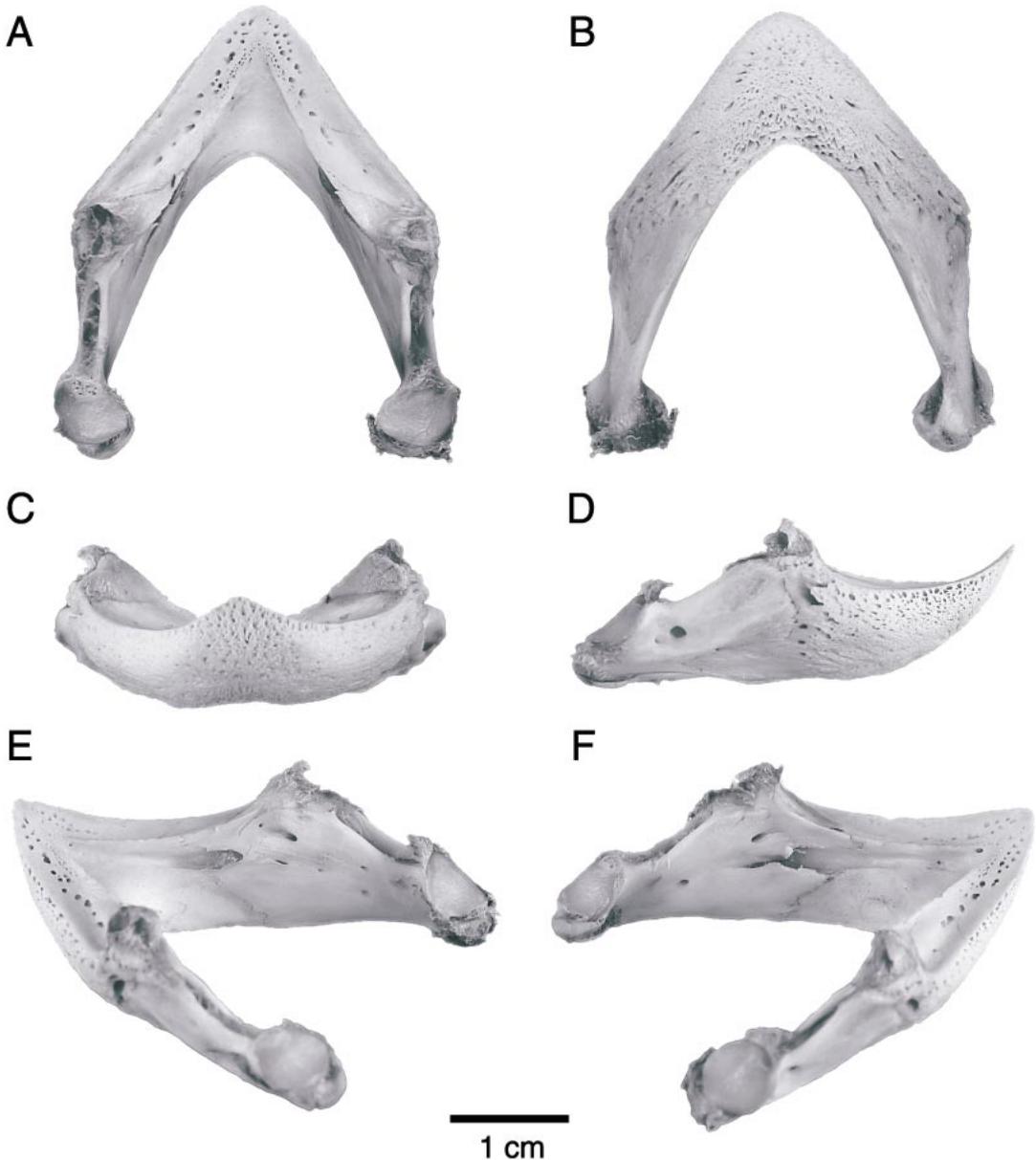


Fig. 3. Photographs of the lower jaw of the extant Malagasy turtle *Erymnochelys madagascariensis* (Bavarian State Natural History Collection, Munich, no. 843/20, Mahajanga, Madagascar, collector Prof. Voeltzkow 1907). **A**, Dorsal view (see Gaffney and Zangerl, 1968: fig. 22C and E for comparable views of *Bothremys*); **B**, ventral view (see Gaffney and Zangerl, 1968: fig. 22A for comparable view of *Bothremys*); **C**, anterior view; **D**, right lateral view; **E**, medial view of right jaw; and **F**, medial view of left jaw. Scale bar equals 1 cm.

lateral surface the dentary contacts the coronoid posterodorsally, the surangular posteriorly, and the angular posteroventrally.

On its medial surface the dentary forms

the sulcus cartilaginis meckelii as in other turtles. The sulcus in FMNH PR 2231 is not as prominent or as well defined anteriorly as it is in *Erymnochelys* and other podocnemi-

dids, but it is more similar to bothremydids. Living podocnemidids also have the sulcus cartilagineus meckelii continuing anteriorly as a distinct groove on the medial surface of the dentary. FMNH PR 2231 is particularly distinct from *Erymnochelys* in this regard as the latter taxon has a distinct trough extending from the sulcus nearly to the symphysis; this trough is absent in FMNH PR 2231.

ANGULAR

The angular is preserved on both sides in FMNH PR 2231, although its sutures, as in many recent podocnemidids, are unclear (figs. 1D–F, 2D, E). There is a dentary-angular suture preserved, however. The angular is a long, thin bone that begins anteriorly on the medial surface and bends posteroventrally to end below the articular bone. The lower, angular margin of the foramen intermandibularis caudalis is present on both sides, although the prearticular margin of the foramen is missing. The posterior contacts between the angular and the surangular and articular are fused as is often the case in other podocnemidids and turtles in general.

SURANGULAR

The surangular is preserved on both sides of FMNH PR 2231 (figs. 1D, 2D), although the left element is slightly eroded. The surangular is a large element lying on the external surface at the posterior end of the jaw. It contacts the coronoid anterodorsally, the dentary anteriorly and ventrally, the angular posteroventrally (this suture is fused), and the articular posteriorly (also fused). The surangular forms the lateral wall of the fossa meckelii, which is open medially in FMNH PR 2231 and best preserved on the right side (figs. 1E, F, 2E). Although the size and shape of the fossa meckelii of FMNH PR 2231 are very similar to those in the living podocnemidids, this morphology varies little within Pelomedusoides and is of limited systematic value.

A complex of foramina and canals formed on the posteroventral surangular—the foramen nervi auriculotemporalis (Gaffney, 1979: 216)—is well preserved on both sides of FMNH PR 2231 (figs. 1D, 2D). This complex is composed of two external foramina

that are connected by a short canal that communicates with a larger internal space. This space joins the fossa meckelii via a short canal. All Pelomedusoides have this complex, although the precise morphology of the external foramina varies throughout the group. Fuchs (1931) provided a description of these structures in *Podocnemis expansa*.

CORONOID

The coronoid in FMNH PR 2231 is defined by sutures on both rami (figs. 1A, 1D–F, 2A, D, E). It forms a low but distinct processus coronoideus similar in morphology to that in *Erymnochelys*. The anterior contact of the coronoid with the dentary lies in the posteromedial part of the triturating surface so that the coronoid forms the posteromedial part of the surface, as in *Erymnochelys* and the other podocnemidids.

ARTICULAR

The articular is preserved on both sides of FMNH PR 2231, although no sutures are discernable due to fusion to adjacent elements (figs. 1A, D–F, 2A, D, E). The area articularis mandibularis is roughly hemispherical as is characteristic of pleurodires (although not unique), as opposed to the median longitudinal ridge usually found in cryptodires (Gaffney, 1979: 217). A low ridge is present in FMNH PR 2231. The area articularis mandibularis is slightly flatter in FMNH PR 2231 and *Erymnochelys* than in *Podocnemis* and *Peltocephalus*.

FMNH PR 2231 has a well-developed, posteriorly directed processus retroarticularis. Chelids and pelomedusids lack such a process, while bothremydids have a large process, and most podocnemidids have a ventrally directed process. An exception is *Erymnochelys*, which has a large, posteriorly directed processus retroarticularis very similar to that in FMNH PR 2231. Podocnemidids have been described as having a processus retroarticularis (Gaffney et al., 1998: 5; also termed the processus subarticularis by Fuchs, 1931) despite its ventral position, because it provides the insertion for the depressor mandibulae muscle. As far as can be determined, *Erymnochelys* is the only living

podocnemidid with a posteriorly directed processus retroarticularis.

At the base of the processus retroarticularis in FMNH PR 2231, on the medial edge of the area articularis mandibularis, is a large foramen posterius chorda tympani. *Erymnochelys* also has this foramen in the same position. The foramen is not ossified in *Peltocephalus* and *Podocnemis* in this position. In the bothremydids (i.e., *Cearachelys* and *Kurmademys*) which have a posteriorly directed processus retroarticularis, there is also a foramen posterius chorda tympani on the medial side of the base of the processus retroarticularis. This is also where this foramen is usually located, when present, in cryptodires.

PREARTICULAR

The prearticular in FMNH PR 2231 is largely missing, although it is slightly better preserved on the left side (figs. 1E, F, 2E). It forms the thin medial wall of the fossa meckelii and the posterior margin for the foramen intermandibularis medialis. The portions of the prearticular preserved in FMNH PR 2231 are consistent with the morphology of this element in *Erymnochelys*.

DISCUSSION

The lower jaw FMNH PR 2231 is most similar to the lower jaw in the living podocnemidid *Erymnochelys madagascariensis* (fig. 3), a monotypic genus endemic to Madagascar (see table 1). They both share this unique combination of characters: nearly identical triturating surface that is narrow anteriorly and broader posteriorly with a horizontal labial ridge and a dorsally rising lingual ridge, posteriorly directed processus retroarticularis, completely ossified foramen posterius chorda tympani, and low symphyseal projection. The primitive bothremydids, *Kurmademys* and *Cearachelys*, have lower jaws similar to FMNH PR2231 in some features of the triturating surface and in the processus retroarticularis. However, the bothremydids have an S-shaped lingual ridge and a labial ridge that rises posteriorly. They also have a deeper trough between the lingual and labial ridges, and wider jaws compared to the midline length.

FMNH PR 2231 differs from the living

Erymnochelys madagascariensis in having a shallower sulcus cartilagineus meckelii, a wider angle between the jaw rami, a less acute symphyseal tip, and a blunter labial ridge. Nonetheless, these are relatively slight differences, and the jaws are very similar. If found in the recent Malagasy fauna, FMNH PR 2231 would probably be identified as *Erymnochelys madagascariensis*. However, morphology of these lower jaws is not greatly different from podocnemidids like *Neochelys* (Eocene of Europe; Broin, 1977), and these features could be more generally distributed among Podocnemididae. Therefore, we do not think that the lower jaw alone is sufficient to positively identify this specimen as *Erymnochelys*. The question of identification of FMNH PR 2231 rests on the specific characters in common with *Erymnochelys*, namely the processus retroarticularis and morphology of the triturating surface, rather than on more general characters for the Podocnemididae. At present, we are unaware of lower jaw characters unique to all Podocnemididae. Nonetheless, FMNH PR 2231 is the oldest *Erymnochelys*-like specimen described, even if one includes the undescribed material of Lapparent de Broin (2000).

The fossil record of Africa, however, presents a number of specimens from the Oligocene to the Pliocene that were identified as belonging to *Erymnochelys* (or a closely related taxon) by Lapparent de Broin (2000: 68). However, none of these specimens includes described skull or jaw material of any sort, so comparisons with FMNH PR 2231 are impossible at this time.

ORDER TESTUDINES LINNAEUS, 1758

SUBORDER PLEURODIRA COPE, 1864

HYPERFAMILY PELOMEDUSOIDES COPE, 1868a

FAMILY BOTHREMYDIDAE BAUR, 1891

Bothremydidae gen. et sp. indet.

SPECIMEN: UA 8708; a dentary fragment consisting of a portion of the right ramus and symphyseal region. Collected by P. Dodson.

LOCALITY: MAD 93-79, Berivotra region, Mahajanga Basin, northwestern Madagascar.

HORIZON AND AGE: Either the uppermost Anembalemba or basal Miadana Member, Maevarano Formation, Maastrichtian.

TABLE 1
 Comparison of Lower Jaws in Sundry and Diverse Pelomedusoides

	FMNH PR 2231	<i>Erymnochelys</i>	<i>Podocnemis</i>	<i>Peltocephalus</i>	Bothremydids	Pelomedusids
Dentaries fused at symphysis	yes	yes	yes	yes	yes	yes
Symphyseal length	long	long	long	long	long	usually short
Symphyseal projection	no	no	no	yes	no	yes and no
Width of triturating surface at symphysis	narrower	narrower	wider	wider	narrow and wide	narrow and wide
Angle of lower jaw rami at symphysis	wider	narrower	narrower	narrower	wider	narrower and wider
Inner margin of triturating surface	straighter	straighter	straighter	straighter	S-shaped	variable
Triturating surface widens posteriorly	yes	yes	no	no	yes	yes and no
Labial ridge relatively horizontal in lateral view	yes	yes	no	no	no	no
Labial ridge	blunt	sharp	sharp	sharp	blunt	sharp
Accessory ridge	absent	absent	present	absent	absent	absent
Lingual ridge much higher than labial posteriorly	yes	yes	yes	no	yes	yes
Processus retroarticularis	present posterior	present posterior	present ventral	present ventral	present posterior	absent
Foramen posterius chorda tympani in base of processus retroarticularis	yes	yes	no	no	yes	no

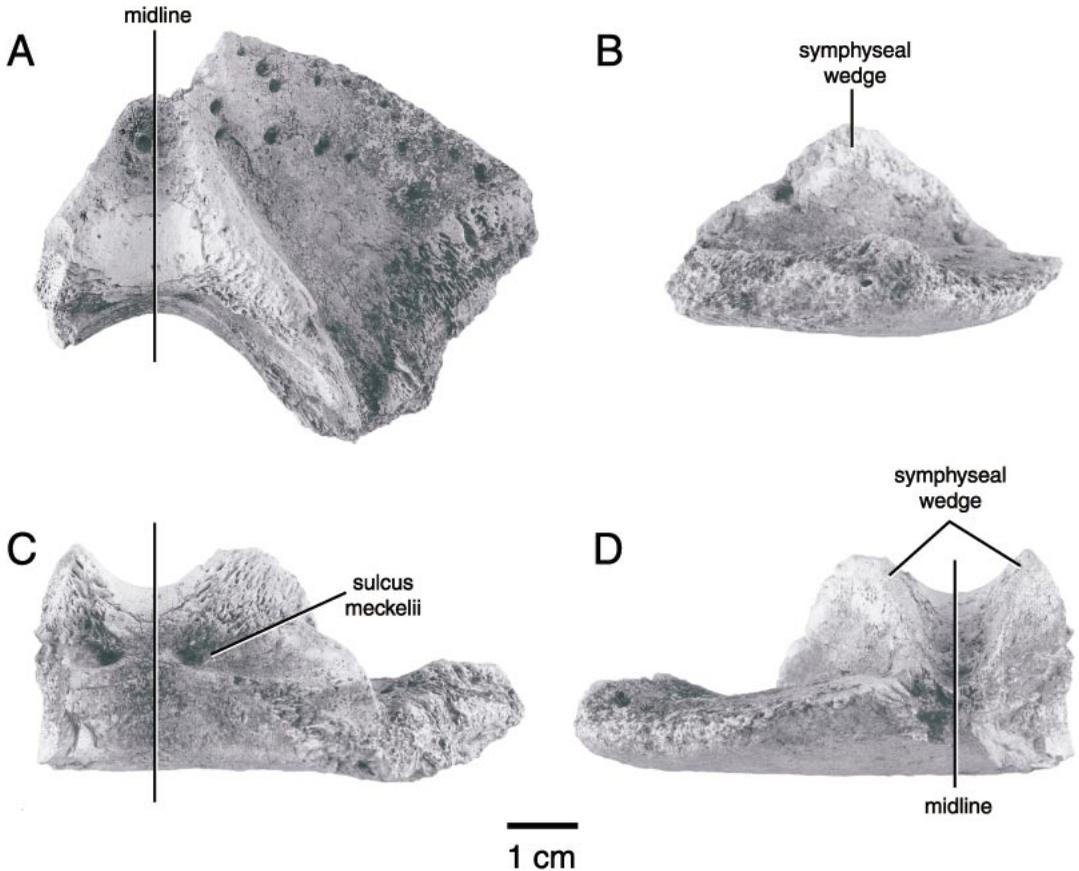


Fig. 4. Photographs of the partial dentary of a possible bothremydid, UA 8708, in: **A**, dorsal view; **B**, right lateral view; **C**, anterior view; and **D**, posterior view. Scale bar equals 3 cms.

DESCRIPTION

UA 8708 preserves the symphysis and partial right ramus of a large, broad, and heavy dentary (figs. 4 and 5). The symphysis itself is broken anteriorly, although only a small section is missing. In cross section the symphysis is thin anteriorly, about 0.5 cm., and thickens markedly posteriorly to 2.8 cm. The symphyseal area is wedge-shaped in dorsal view with its apex pointing anteriorly, and it bears a deep trough along the midline. This trough is bound laterally by a sharp vertical ridge oriented anteromedially to posterolaterally. The vertical ridge drops off sharply laterally to meet the medial margin of the nearly flat, broad triturating surface. A roughened, eroded area is present near the lateral margin of the triturating surface. The ventral surface of the dentary fragment,

while nearly flat, is gently curved and convex ventrally. On the posterior surface of the jaw near the midline, separated by 0.6 cm, are the well-defined anterior margins of the deep, paired sulci meckelii.

The morphology of this unusual jaw fragment is unique, but it has similarities to dentaries in the Bothremyidae. Three lower jaws are available that have features comparable to UA 8708: the type of *Bothremys cooki* (Late Cretaceous, New Jersey), AMNH 2521; *Bothremys alabamiae* (Late Cretaceous, Alabama), FMNH PR 247; and an undescribed bothremydid (Paleocene?, Morocco), AMNH 29989. These jaws all have the unusual *Bothremys* character (Gaffney and Zangerl, 1968) of two large pits on either side of a thickened symphysis. In *Bothremys alabamiae* the symphysis is only slightly

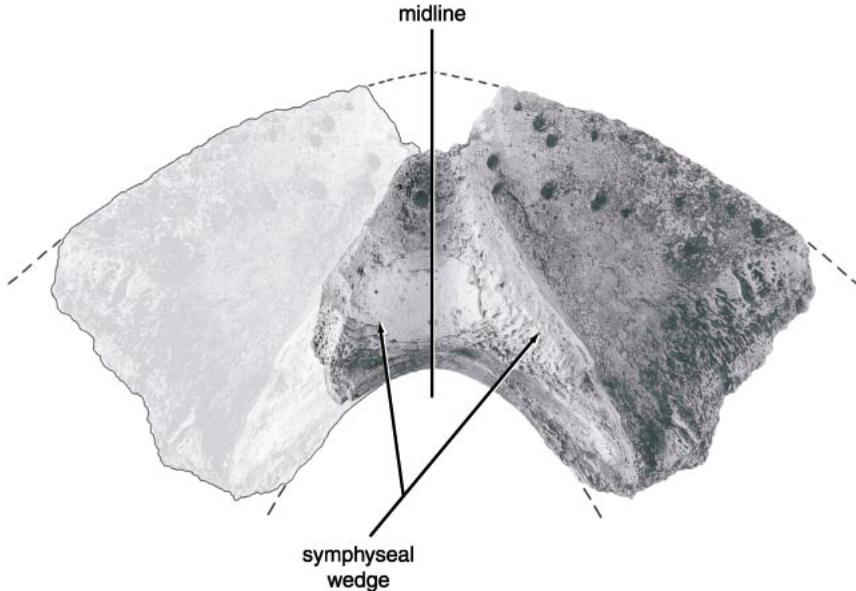


Fig. 5. Partial dentary of possible bothremydid, UA 8708. Left ramus restored by reversing right ramus.

thickened, while in *Bothremys cooki* and the undescribed Moroccan bothremydid it is more thickened posteriorly. However, the symphysis in UA 8708 is nearly twice as thick as in these two latter specimens. In *Bothremys alabamiae* there is a shallow symphyseal trough, while in *Bothremys cooki* the trough is also shallow despite a thickened symphysis. In the Moroccan bothremydid the trough is much deeper and bounded by high lateral walls, exceeding the depth of the symphysis in UA 8708. In size, UA 8708 is closest to *Bothremys cooki*.

The large pits flanking the symphysis of the *Bothremys* jaws are not evident in UA 8708, but a comparable morphology can nevertheless be interpreted. In *Bothremys*, the pits have a flat area immediately anteromedial to them. This area is nearly identical in UA 8708. The posteromedial pit wall forms the lateral side of the symphyseal wedge in *Bothremys*; this area is eroded posteriorly in UA 8708. The base of the lateral pit wall could be represented by the roughened, eroded area near the lateral jaw margin in UA 8708. In UA 8708, a depression on the posterolateral floor of the triturating surface at the posterior end of the symphyseal wedge may represent a ventral remnant of the pit.

DISCUSSION

UA 8708 is by no means identical or even closely comparable to the three bothremydid jaws discussed above, as it has features found in no other turtle jaw. The very thick symphyseal wedge occurs in no other turtle, and the large flat area just posterolateral to it, although comparable to the pits in some bothremydid, is also unique. It is likely that UA 8708 is a new genus of Bothremydidae related to the *Bothremys* Group of Lapparent de Broin and Werner (1998), and Gaffney et al. (2001a, 2001b). Because of its fragmentary nature, we decline to name this taxon at this time.

CONCLUSIONS

The published records of *Erymnochelys* in Africa largely consist of plastra with gular scales meeting on the midline, a feature restricted to *Erymnochelys* among living Pelomedusoides but found among a number of fossil forms (see Hirayama, 1992 for discussion). The numerous records of "*Erymnochelys*" using "aff.", "cf.", "sp. X", and such like in Lapparent de Broin (2000), extending in time from Oligocene to Pliocene, are without reference to specific specimens

or description. These records may consist only of fragments not identifiable to genus by other workers, implying a much denser record of this genus than may actually exist in terms of taxa diagnosable by morphology. The documented records of *Erymnochelys* are shells and a cervical vertebra, described by Hirayama (1992). The characters used by him are diagnostic for *Erymnochelys* when only living taxa are considered but are more widely spread among fossils (Zangerl, 1948; Williams, 1954; Hirayama, 1992). Whether these characters circumscribe a clade containing *Erymnochelys* has not yet been tested with better material. However, Witmer (1990) has reported an undescribed Miocene skull and shell from Kenya, morphologically similar to *Erymnochelys*, so it should be possible to test these ideas at some time.

Krause et al. (1999) found no evidence that any of the Late Cretaceous vertebrates from the Maevarano Formation were closely related to any higher vertebrate taxa living on Madagascar today. This record of cf. *Erymnochelys* represents the first Cretaceous taxon that is a possible candidate for such a relationship. However, the biogeographic significance of a possible close relative of *Erymnochelys* in the late Cretaceous of Madagascar is restricted to the confirmation of this group as a long-lived part of the Malagasy fauna. Further biogeographic conclusions based on podocnemidid distribution await some resolution of the conflicting available phylogenies (e.g., Gaffney, 1988; Gaffney and Meylan, 1988; Noonan, 2000) and description of known but undescribed specimens.

The probable presence of a bothremydid in the Late Cretaceous of Madagascar further widens the distribution pattern of this extinct group. The Cretaceous bothremydids known from India (Gaffney et al., 2001b) and South America (Gaffney et al., 2001a) have more generalized lower jaws, which are distinct from the Madagascar jaw, and most closely resemble pitted bothremydids from North America (Gaffney and Zangerl, 1968) and northern Africa (Lapparent de Broin and Werner, 1998).

The cf. *Erymnochelys* shows the antiquity of one element of the Madagascar turtle fau-

na while the bothremydid suggests another cosmopolitan element.

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