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

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ABSTRACT

Associated skull and shell material from the late Cretaceous (probably Maastrichtian) of Fox Amphoux, southern France, is the new pleurodire taxon *Foxemys mechinorum. Foxemys* is a member of the pelomedusoid family Bothremydidae because it has these synapomorphies of that group: quadrate-basisphenoid covers prootic ventrally, stapedial canal opens anteriorly, precolumellar fossa absent, and eustachian tube separated from incisura columellae auris. A PAUP analysis of 23 characters and four bothremydid taxa has resulted in one cladogram showing *Foxemys* as the sister taxon to *Taphrosphys, Bothremys,* and *Rosasia.* Only one character, an open incisura columellae auris in *Foxemys* (closed in the three others), is the basis for this relationship, however, and it is considered to be weakly supported. The skull and shell of *Foxemys* are most similar to *Polysternon provinciale* from the Campanian of Villevayrac, France. The skull of *Foxemys* is similar to *Polysternon* in being wedge-shaped with a posteriorly expanded triturating surface. These genera differ from each other in that *Polysternon* has its mandibular condyles well anterior to the occipital condyle while in *Foxemys* these structures are nearly lined up transversely.

INTRODUCTION

Turtles have been known from the late Cretaceous of southern France since the last century. Matheron was the first, in 1869, followed by Portis, in 1882, to study turtle remains from the Campanian Fuveau basin of southern France (Matheron, 1869; Portis,

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1882). More important work was done by Nopcsa (1931), who described in detail Matheron's and Portis's material, and de Broin (1977), who reviewed the same collection. Since then, turtle remains have been mentioned from several late Cretaceous localities in southern France (Amiot et al., 1983), but no detailed studies have been made. Two pleurodiran turtles, *Polysternon provinciale* (Matheron, 1869) and *Elochelys perfecta* (Nopcsa, 1931), and one cryptodiran turtle, *Solemys gaudryi* (Matheron, 1869; de Broin and Murelaga, 1996), have been reported from these localities. Recently, renewed field research on the late Cretaceous vertebrate faunas of southern France has resulted in the discovery of new turtle remains. *Polysternon provinciale* and an undetermined cryptodiran turtle have been found at the Montseret and Villeveyrac localities, both Campanian in age (Tong et al., 1993; Buffetaut et al., 1996). We describe here new turtle material from probably Maastrichtian beds at Fox Amphoux (Var, southern France) as a new genus and species of pleurodiran turtle. Turtles have been known from Fox Amphoux for some time (de Broin et al., 1980), but no description has yet appeared. The phylogenetic relationships of this new turtle will be discussed in the present paper.

Vertebrate remains have been known from the continental late Cretaceous of the Fox Amphoux basin, in the northern part of Department Var (Provence, southern France), since the middle of the 19th century (see Buffetaut et al., 1996). Several fossiliferous localities are known in the vicinity of the village of Fox Amphoux (see map in Lapparent, 1947). Systematic excavations were first carried out at one of them, known as Métisson, by Lapparent in 1939 (Lapparent, 1947), and were resumed in the late 1970s (de Broin et al., 1980). The turtle remains from Métisson were briefly mentioned by de Broin et al. (1980), who reported the occurrence of a pelomedusid and an indeterminate cryptodiran. The material described in the present paper comes from a different locality in the same area, known as Bastide Neuve, which has been excavated in recent years by Patrick and Annie Méchin with the assistance of staff of the Musée des Dinosaures (Espéraza).

The Fox Amphoux vertebrates come from sandstones and clays similar to what is known in the Aix-en-Provence basin, farther west, as the lower part of the Rognacian. This local stage is probably a nonmarine equivalent of the Maastrichtian on the basis of magnetostratigraphy (Westphal and Durand, 1990). The Fox Amphoux vertebrate assemblage is thus probably of early Maastrichtian age (Buffetaut and Le Loeuff, 1991). This is in agreement with the composition of its fauna, in which the dominant dinosaurs are titanosaurids and the ornithopod *Rhabdodon.* As shown by Le Loeuff et al. (1994), such assemblages characterize the early part of the Maastrichtian in southern France, whereas late Maastrichtian assemblages are dominated by hadrosaurid dinosaurs, which have not been reported from Fox Amphoux.

Besides turtles, the Fox Amphoux vertebrate assemblage includes hybodont sharks, a *Lepisosteus*-like actinopterygian, alligatorid and crocodylid crocodilians, theropods (including a dromaeosaurid and a possible abelisaurid), titanosaurid sauropods, ornithopods (*Rhabdodon*), ankylosaurs, and large flightless birds.

Acknowledgments

The authors thank Patrick and Annie Méchin for collecting the specimens and presenting part of them to the Musée des Dinosaures d'Espéraza. Fieldwork at Fox Amphoux was partly supported by the Musée des Dinosaures, where some of the preparation of the specimens was done, and the Institut National des Sciences de l'Univers (Paris). We also thank Claude Abrial for the photographs. Frank Ippolito did the computer work and translated the art into digital files. Judy Galkin helped with manuscript work.

We greatly appreciate the generosity of our colleagues, Peter Meylan, Ed Hooks, and Roger Wood, for reviewing the paper. We value the time they took to improve our paper.

Anatomical Abbreviations

ang	angular
ap	antrum postoticum
art	articular
bo	basioccipital

bs basisphenoid
cor coronoid
ct cavum tympani
den dentary
ex exoccipital
fdm foramen dentrofaciale majus
fjp foramen jugulare posterius
fm foramen magnum
fnh foramen nervi hypoglossi
fpc fossa precolumellae
fpp foramen palatinum posterius
fr frontal
ica incisura columellae auris
ju jugal
mx maxilla
op opisthotic
pa parietal
pal palatine
ptp processus coronoideus
pf prefrontal
pm premaxilla
pmc pterygoid muscle chamber
po postorbital
pt pterygoid
ptp processus trochlearis pterygoidei
qj quadratojugal
qu quadrate
scm sulcus cartilaginis meckelii
so supraoccipital
sq squamosal
sur surangular
vo vomer

Institutional Abbreviations

MD Musée des Dinosaures, Espéraza, France
PAM Patrick and Annie Méchin, private collection, Vitroll, France

SYSTEMATICS

ORDER TESTUDINES LINNAEUS, 1758

SUBORDER PLEURODIRA COPE, 1864

HYPERFAMILY PELOMEDUSOIDES COPE, 1868

FAMILY BOTHREMYDIDAE BAUR, 1891

Foxemys, new genus

DIAGNOSIS: Bothremydid pleurodire (sensu Meylan, 1996) with the following bothremydid synapomorphies: quadrate-basisphenoid covers prootic ventrally, stapedial canal opens anteriorly, eustachian tube separated from incisura columellae auris; skull similar to *Polysternon provinciale* in being wedge-shaped with a posteriorly expanded triturating surface, moderately developed temporal emargination, and ventrally opening concavities formed by pterygoid and basisphenoid (also in *Rosasia*); differs from *Polysternon provinciale* in having an anteriorly wider triturating surface, a deeper pterygoid–basisphenoid concavity, and a more anterior condylus occipitalis; differs from *Bothremys, Taphrosphys,* and *Rosasia* in having a slitlike but open incisura columellae auris; differs from *Bothremys* and *Rosasia* in having a flat triturating surface; shell similar to *Polysternon* but lacking the nuchal emargination and having a relatively large intergular scute and a rounded anal notch.

TYPE SPECIES: *Foxemys mechinorum,* n. gen., n. sp.

DISTRIBUTION: Maastrichtian (late Cretaceous) of southern France.

ETYMOLOGY: From the name of the locality, Fox Amphoux in southern France.

Foxemys mechinorum, new genus, new species

ETYMOLOGY: In honor of the discoverers of the material, Patrick and Annie Méchin.

HOLOTYPE: MD t 10, a dorsoventrally crushed skull with right half of carapace and complete plastron (figs. 1, 2). The skull was found inside the shell.

HYPODIGM: An almost complete skull (PAM 511A, figs. 3–6); an incomplete lower jaw (PAM 511B, figs. 7, 8); an almost complete and well-preserved shell in which the plastron is complete and only the posterior part of the carapace is missing (lacking right 6th to 8th costal and part of 7th and 8th left costal bones, 8th to 11th right peripheral and 11th left peripheral bones, suprapygal and pygal bones; PAM 548, figs. 9, 10); a partial shell consisting of the anterior third of the carapace in poor condition and a complete plastron (MD t 09, fig. 11), one right scapula-precoracoid (MD t 11), and several isolated plates.

TYPE LOCALITY: Fox Amphoux, southern France.

TYPE HORIZON: Maastrichtian, late Cretaceous.

DIAGNOSIS: Same as for genus.

DISCUSSION: In addition to *Foxemys,* two pleurodires are known from late Cretaceous localities in southern France. *Polysternon*

Fig. 1. *Foxemys mechinorum,* n. gen., n. sp. Skull and carapace (holotype MD t 10) in dorsal view.

provinciale (Matheron, 1869) is known from a large series of shells and a skull, while *Elochelys perfecta* (Nopsca, 1931) is known only from a few shells. *Elochelys* differs from *Foxemys* in its smaller size (carapace length 20–25 cm), the apparent lack of a suprapygal bone, and an intergular scute that completely separates the humeral scutes (Nopsca, 1931; de Broin, 1977). The shell of *Foxemys* is similar to that of *Polysternon*

Fig. 2. *Foxemys mechinorum,* n. gen., n. sp. Skull and plastron (holotype MD t 10) in ventral view.

provinciale, although there are significant differences (table 1). The recently described skull of *Polysternon provinciale* (Buffetaut et al., 1996) is also similar to the skull of *Foxemys,* but again there are significant differences (table 1), particularly in the relative positions of the mandibular condyles and the occipital condyles.

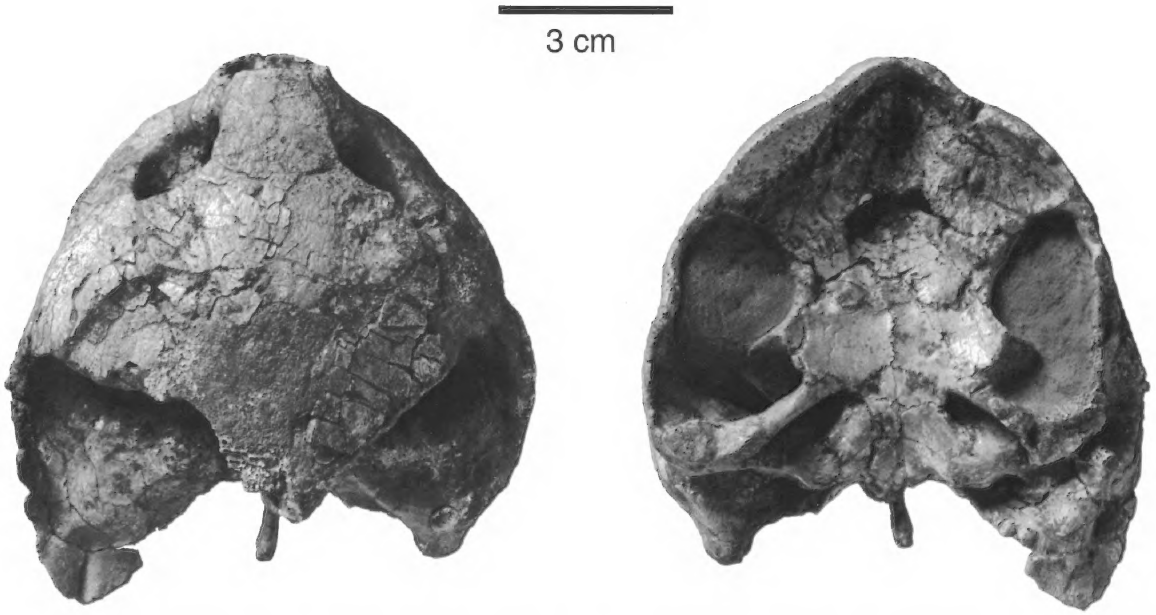

Fig. 3. Skull of *Foxemys mechinorum,* n. gen., n. sp. (PAM 511A) in dorsal (**A**) and ventral (**B**) views. Scale bar: 5 cm.

According to the description of *Polysternon atlanticum* (de Broin and Muregala, 1996), this species from the late Cretaceous of northern Spain differs from *Foxemys* in being much smaller and in having a narrow first vertebral scute.

Skull Morphology

PRESERVATION: The description is based on the most complete skull, PAM 511A (figs. 3–6), which is morphologically identical with the holotype skull, MD t 10 (figs. 1, 2), but larger (table 2). PAM 511A is an almost

TABLE 1
Comparisons of Characters Between *Foxemys* and *Polysternon*

	Foxemys	*Polysternon*
Carapace shape	long oval	short oval
Nuchal emargination	absent	present
Carapace posterior emargination	present	absent
Anterior margin of plastron	straight	rounded
Lateral margins of posterior lobe of plastron	rounded	not much rounded
Anal notch	wide	narrow
Mesoplastra	included in the bridge	not exclusively in the bridge
Midline length of humerals	short	long
Intergular	large, one-third to one-half of entoplastron length	small, one-third of entoplastron length
Triturating surface	wide	narrow
Pterygoid–basisphenoid depression	deep	shallow
Condylus mandibularis	close to level of condylus occipitalis	far anterior to condylus occipitalis

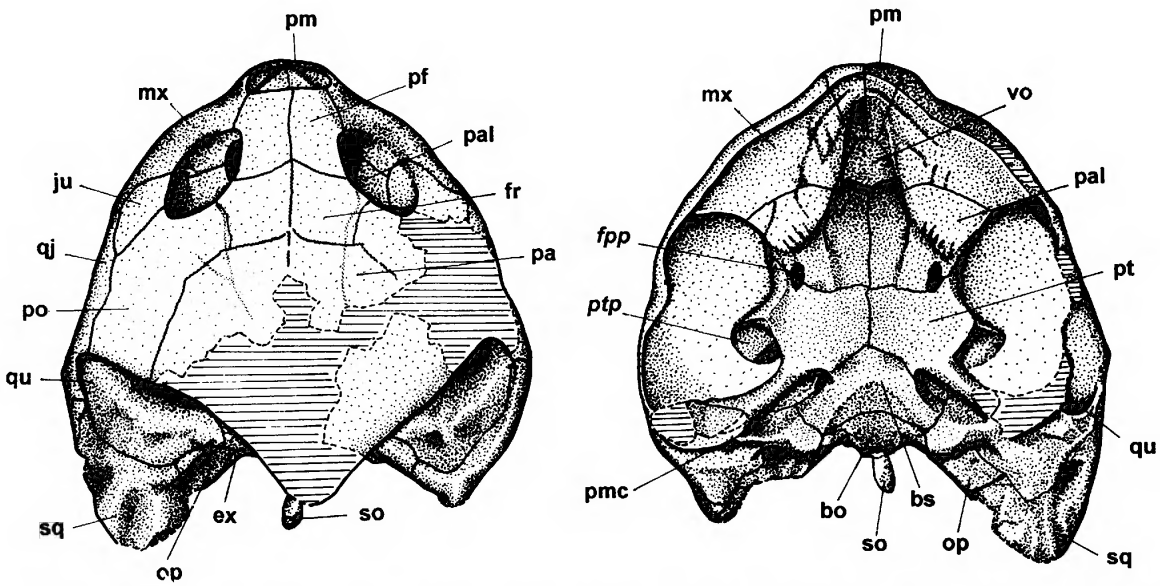

Fig. 4. Skull of *Foxemys mechinorum,* n. gen., n. sp. (PAM 511A) in dorsal (**A**) and ventral (**B**) views.

complete skull without deformation, but the posterior half of the roof is in poor condition. Both parietals are damaged and a large part of the right postorbital, jugal, and quadratojugal are missing. The lateral processes on both sides are incomplete. The occipital condyle is not preserved. The ventral part of the left quadrate is damaged so that the left cavum tympani is incomplete and the left mandibular condyle of the quadrate is not preserved. The right side of the mandibular condyle is not complete. One incomplete lower jaw (PAM 511B) has been found with the skull, but it was not in articulation.

GROSS ASPECT: In dorsal view, the skull has a roughly triangular shape with a prominent "pinched" snout. The apertura narium externa is anterodorsally directed. The orbits have a roughly oval shape with their posterior part narrowed and are dorsolaterally directed. The interorbital space is wide and flat, and thus there is no longitudinal groove like that found in the living *Podocnemis.* The temporal emargination is relatively large, wide, and asymmetric. The crista supraoccipitalis has been restored; it seems to be short but the exact length cannot be determined. In lateral view, the skull is high and slopes anteriorly. The cheek emargination is clearly present but small. On the right side, where it is well preserved, the cheek emargination is roughly triangular in shape (about 2 cm long and 0.6 cm high).

SCALES: Some of the skull roof scales are preserved (fig. 4). In dorsal view, the interparietal and parietal scales are present. The interparietal is anteroposteriorly elongated, being triangular in shape. Its anterior limit is not visible and its posterior portion is not preserved, so we cannot determine if it completely separates the parietals. In lateral view, the subocular as well as the masseteric scales are present.

DERMAL ROOFING ELEMENTS: In dorsal view (figs. 3–6), both prefrontals are complete. Their anterior edge does not completely cover the apertura narium externa dorsally, so that the latter is visible in dorsal view. The prefrontal is rectangular and flat. It contacts the maxilla anterolaterally and forms the upper edge of the apertura narium externa and the anteromedial margin of the orbit. The prefrontals join in the midline for their total length, although their contact with the frontals is slightly convex anteriorly. The frontals are complete and form the posteromedial margin of the orbit. The frontal is slightly shorter than the prefrontal and contacts the postorbital laterally by a short suture and the parietal posteriorly by a transverse suture.

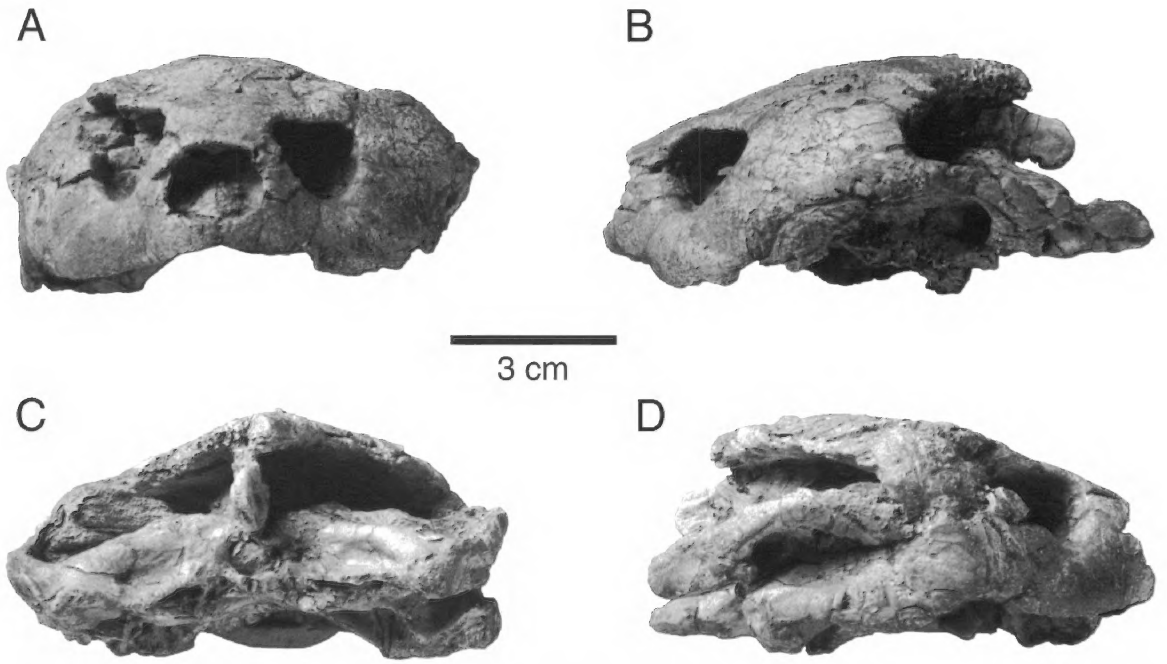

Fig. 5. Skull of *Foxemys mechinorum,* n. gen., n. sp. (PAM 511A) in anterior (**A**), posterior (**B**), left lateral (**C**), and right lateral (**D**) views. Scale bar: 5 cm.

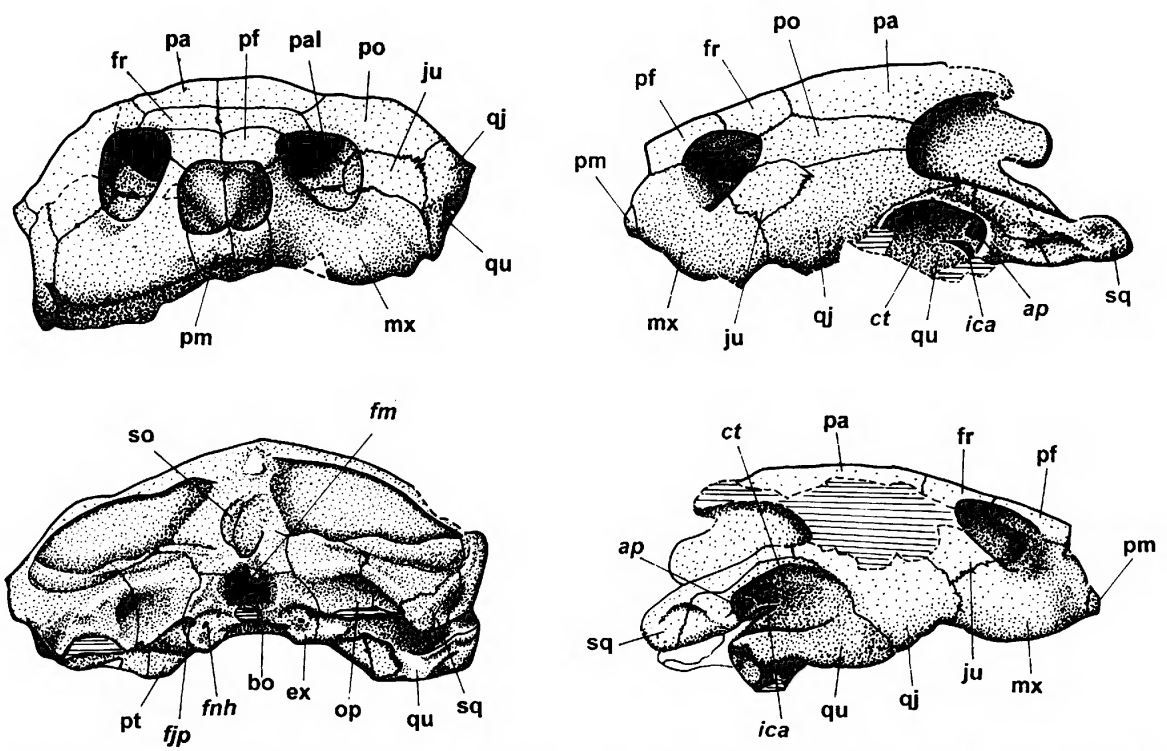

Fig. 6. Skull of *Foxemys mechinorum,* n. gen., n. sp. (PAM 511A) in anterior (**A**), posterior (**B**), left lateral (**C**), and right lateral (**D**) views.

TABLE 2
Measurements of the Skull (in centimeters)

	MD t 10 (holotype)	PAM 511A
Length[a]	6.3	10.0
Width[b]	6.1	9.5

[a] Greatest preserved length from snout to posterior end of the left lateral process.

[b] Greatest width at the level of midcavum tympani.

The parietals are damaged and restored on both sides. They are large elements forming two-thirds of the medial margin of the temporal emargination and contact the postorbitals laterally. The posterior end of the parietal is broken off and has been restored during preparation. Its contact with the supraoccipital is not preserved in dorsal view, and the contact between parietal and supraoccipital in lateral view under the skull roof is not visible.

The left postorbital is complete, whereas the right one is missing. The postorbital is very large and has an anteroposteriorly elongated shape. The postorbital forms the posterior margin of the orbit and reaches the temporal emargination posteriorly between the parietal and quadratojugal, resulting in no contact between the two latter elements. The jugal is complete on the left side but slightly damaged on the right side. It forms the posterolateral corner of the orbit. The jugal is much smaller than the postorbital and contacts the maxilla anteriorly, the quadratojugal posterolaterally, and the postorbital posteromedially. The medial process of the jugal contacts the palatine on the posterolateral wall of the orbit. The jugal does not reach the cheek emargination. The quadratojugal is damaged at its upper part on the right side and at its lower part on the left side. It is moderately large and elongated. The quadratojugal has a long longitudinal suture with the postorbital medially. The quadratojugal contacts the jugal anteromedially, the maxilla anteriorly (below the jugal in lateral view), the quadrate posterolaterally, and the squamosal posteriorly by a very short suture above the cavum tympani.

The quadratojugal forms the posterior half of the cheek emargination and a small lateral part of the temporal emargination. The squamosal is not complete on either side—the left one, which is better preserved, has a roughly triangular shape in dorsal view and is much larger than the opisthotic. The squamosal is larger than that of living pelomedusoides, which have a small squamosal that is transversly elongated in dorsal view. The squamosal forms a large and wide process posterior to the quadrate and lateral to the processus paroccipitalis of the opisthotic. The anteroposteriorly directed ridge of the opisthotic is distinct, as in living pelomedusoides. The lateral surface of the squamosal bears an anteroposteriorly elongated concavity, which is not present in *Podocnemis* or *Erymnochelys.*

PALATAL ELEMENTS: In ventral view (figs. 3, 4), the premaxilla, maxilla, and palatine form the triturating surface, which is large and strongly expanded posteriorly, with two weak additional ridges displayed at the anterior part near the lingual margin. Unlike *Bothremys,* there is no pit on the triturating surface and the jugal does not take part in the triturating surface. The labial ridge is high, strong, almost vertical, and has no break in the middle; the lingual margin slopes down to the sulcus palatinus. The sulcus palatinus is narrow and deep, with the anterior portions of the lateral margin parallel to each other, then enlarged posteriorly.

Both premaxillae are well preserved. They are triangular in ventral view and contact the maxilla laterally and the vomer posteriorly. The foramen prepalatinum is placed in the premaxilla as in most pelomedusoides, except for *Bothremys,* in which this foramen is placed on the premaxilla—vomer suture. Both maxillae in *Foxemys* are well preserved and form the anterior and lower margins of the orbit and the lateral margin of the apertura narium externa as in other pelomedusoides. The maxillae contact the prefrontal dorsally, the premaxilla anteroventrally and ventromedially, the jugal posterodorsally, and the quadratojugal posterolaterally. The horizontal part of the maxilla contacts the vomer medially and the palatine posteromedially. The vomer is large, nearly oval, and covers the apertura narium interna ventrally. The apertura is roughly triangular in shape and is oriented posteriorly. The palatines are

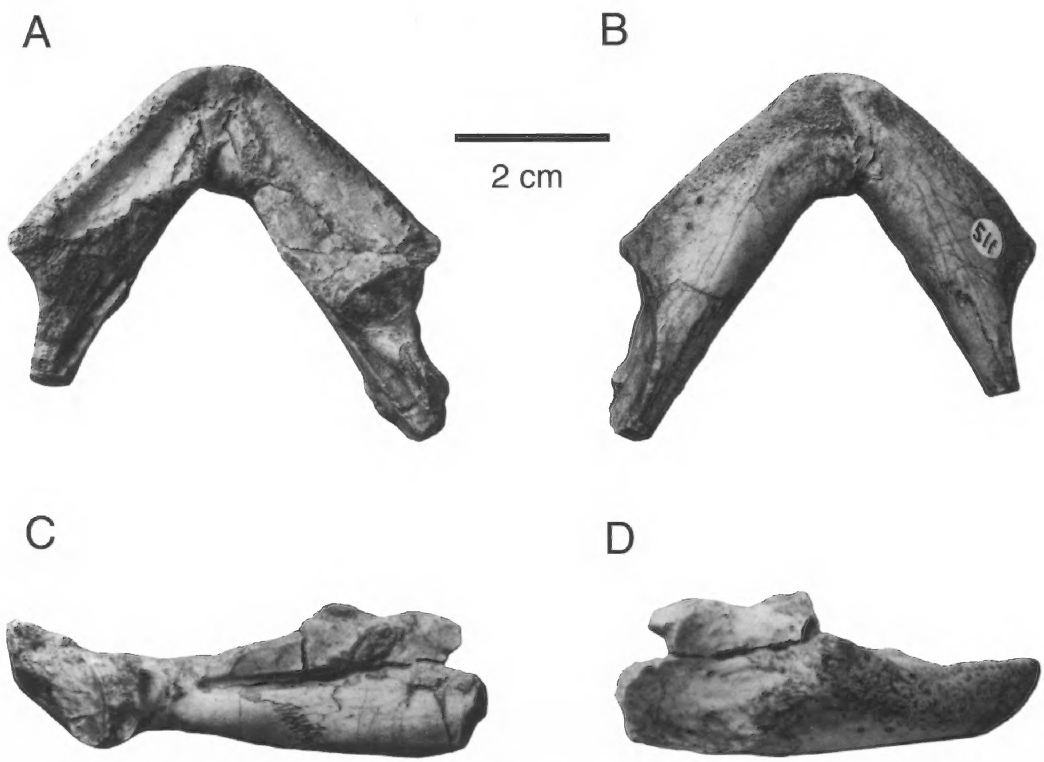

Fig. 7. Lower jaw of *Foxemys mechinorum,* n. gen., n. sp. (PAM 511B) in dorsal (**A**), ventral (**B**), internal (**C**), and external (**D**) views. Scale bar: 5 cm.

complete, form the posterior part of the triturating surface, and contact the pterygoids posteriorly by a transverse suture. The paired foramen palatinum posterius is large and is placed on this suture near the lateral border of the palate.

PALATOQUADRATE ELEMENTS: The pterygoids are complete. They are short, wide, and slightly concave in the middle. The processus trochlearis pterygoidei, directed laterally, is moderate in size and slightly higher than the main part of the pterygoid. The posterolateral ramus of the pterygoid forms (along with the quadrate) a very strong vertical anterior wall of the enlarged pterygoid muscle chamber; it is even higher than the processus trochlearis pterygoidei of *Podocnemis.* Posteriorly, the pterygoid contacts the basisphenoid by an anteriorly curved suture. The large pterygoid muscle concavity, which is a long, deep, anteromedially directed groove, is formed by the pterygoid anteriorly, the quadrate posterolaterally, and the basisphenoid posteromedially. Its anterior wall is vertical and very strong as mentioned above, whereas its posterior wall is much lower than the anterior one. The foramen posterius canalis carotici interni, which is moderate in size and oval in shape, is at the anterior end of the pterygoid muscle chamber on the pterygoid–basisphenoid suture. Unlike the podocnemidids, the pterygoid does not project a posterolaterally developed flange to cover the pterygoid muscle chamber, and the prootic is not visible in ventral view.

Both quadrates are damaged, but the right one is better preserved. In lateral view, the quadrate forms a large and broadly oval cavum tympani. The incisura columellae auris is a narrow fissure that is oriented anterodorsally. Its anterior end is filled by the stapes, which are preserved in part internally. The incisura is narrowed posteriorly but not completely closed. Although the incisura is not completely enclosed by bone it appears that the eustachian tube is excluded from it because the incisura is so narrow. The antrum postoticum is moderately large, similar

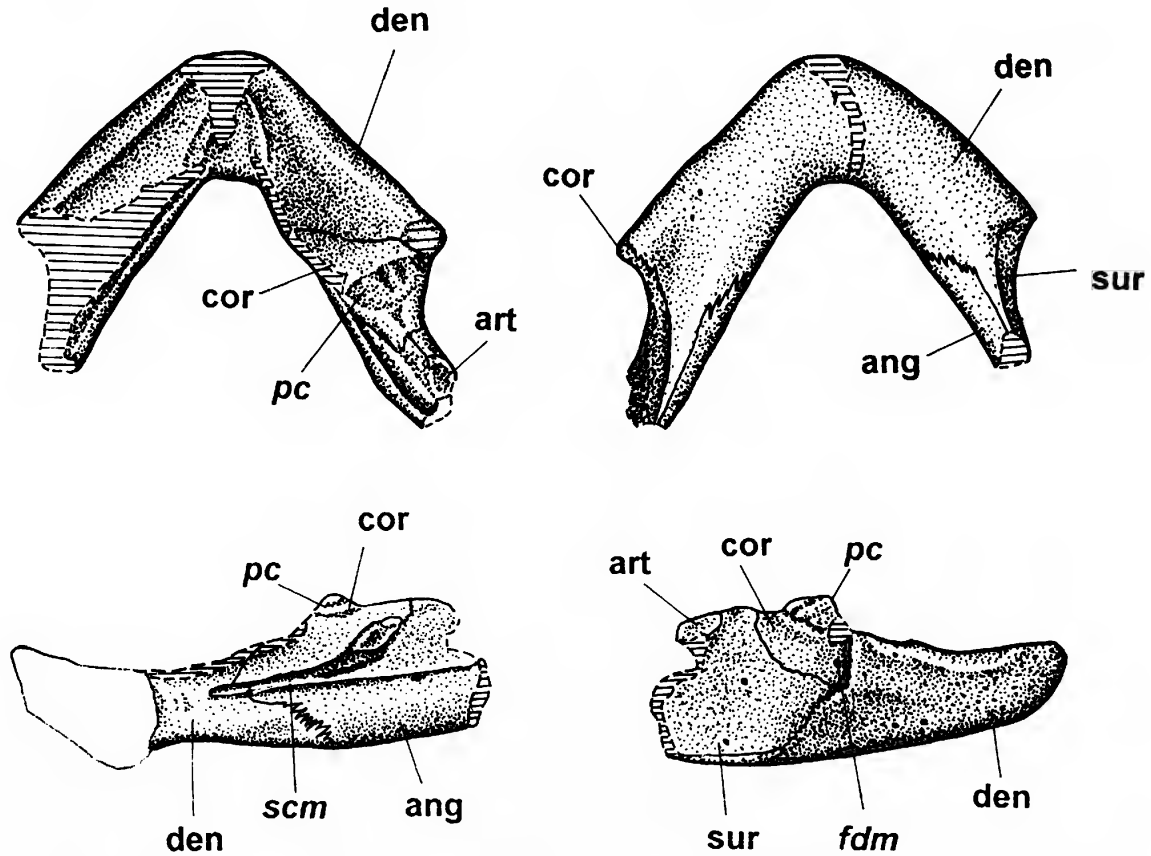

Fig. 8. Lower jaw of *Foxemys mechinorum,* n. gen., n. sp. (PAM 511B) in dorsal (**A**), ventral (**B**), internal (**C**), and external (**D**) views.

to *Podocnemis,* and there is no precolumellar fossa. Ventrally, the quadrate forms the mandibular condyle, which has the typical concave facet of pelomedusoides. Ventromedially, a medial process of the quadrate meets the basisphenoid and basioccipital. The quadrate and basisphenoid form a strong plate on each side of the basioccipital, just behind the pterygoid muscle chamber, as in *Podocnemis.*

BRAINCASE ELEMENTS: The basisphenoid is complete and is broad and roughly triangular in shape. The basioccipital is concave in ventral view, with the concavity extending anteriorly to the basisphenoid. The basisphenoid–basioccipital suture is slightly convex anteriorly. The basioccipital of *Foxemys* is relatively shorter than in *Podocnemis,* but is longer than in *Bothremys.* The occipital condyle is broken off, but its preserved base indicates that it is posterior to the mandibular condyle of the quadrate, as in *Bothremys.* The occipital condyle is formed only by the exoccipitals. The basioccipital stops anterior to the condyle. The exoccipitals are complete and form the lateral margin of the foramen magnum, which is wider than high. The ventral part of the exoccipital in posterior view is only slightly concave, in comparison to *Podocnemis* and *Erymnochelys* in which it is much more concave. Two foramina nervi hypoglossi are present on each side of the occipital condyle, both in the exoccipital.

The supraoccipital forms the upper margin of the foramen magnum. The crista supraoccipitalis has been restored, its total length is not known. Both prootics are complete and exposed anteriorly. They contact the quadrate ventrally and laterally and the supraoccipital medially and posteriorly. There is no contact between the prootic and the opisthotic. The foramen stapedio-temporale rests on the

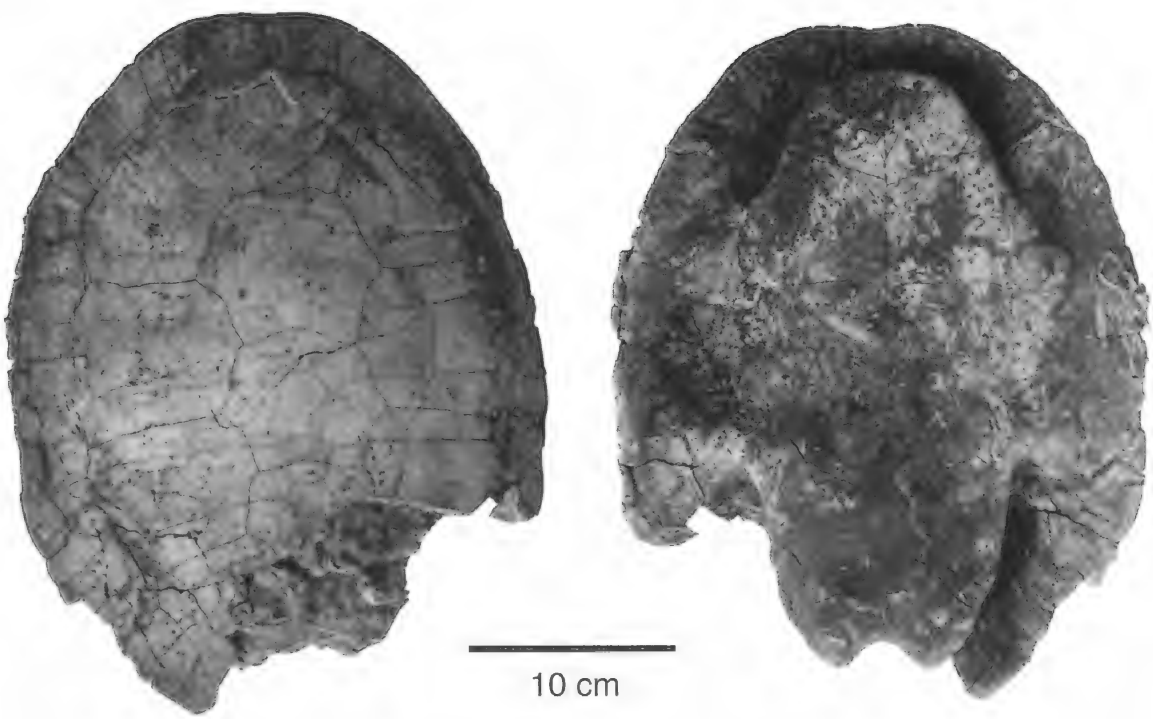

Fig. 9. Carapace (left) and plastron (right) of *Foxemys mechinorum,* n. gen., n. sp. (PAM 548).

prootic–quadrate suture anteriorly. Both opisthotics are broken posteriorly. They form, with the squamosal, a flange posteromedial to the quadrate. An elongated concavity lies under the flange. This structure is different from that of *Erymnochelys* in which the opisthotic forms a flange without a concavity beneath. In posterior view, the fenestra postotica is separated from the incisura columellae auris by bone, but it is continuous with the foramen jugulare posterius.

LOWER JAW: One lower jaw (PAM 511B, figs. 7, 8, consisting of right and left ramus) was found together with a skull (PAM 511A), but it was not in articulation with the latter. This lower jaw seems to be too small to be from the same individual as the skull. The posterior part of both rami are missing in the lower jaw.

The lower jaw in *Foxemys* is closer to that of *Erymnochelys* than to that of *Podocnemis* in general appearance. In comparison to *Erymnochelys,* however, the triturating surface is very wide, particularly posteriorly. The triturating surface is concave in the middle. It is bordered by a lateral ridge that is moderately sharp anteriorly and becomes lower and rounder posteriorly. Unlike *Erymnochelys,* there is no symphyseal hook on the lower jaw. The medial edge of both sides is damaged. The lingual ridge is as high as the labial ridge anteriorly, but posteriorly it is slightly higher, as in *Erymnochelys.* The concavity in the middle of the triturating surface runs along the labial ridge, so the triturating surface on its posterior part slopes mainly toward the lateral side. One additional crest, which is short and roughly parallel to the lingual ridge, is present near the symphysis and does not reach the anterior margin of the triturating surface. The right dentary is tightly fused to its counterpart, and the symphysis is low and moderate in length. The triturating surface of the lower jaw is smooth, whereas the upper part of the lateral surface of the dentary is full of small nutrient foramina.

Both dentaries are damaged, but the right one is more complete. The dentary forms the main part of the triturating surface and contacts the coronoid posterodorsally, the angular posteromedially, and the surangular posterolaterally. Unlike *Erymnochelys,* in which the dentary sends a process posteroventrally on the lateral surface, the dentary

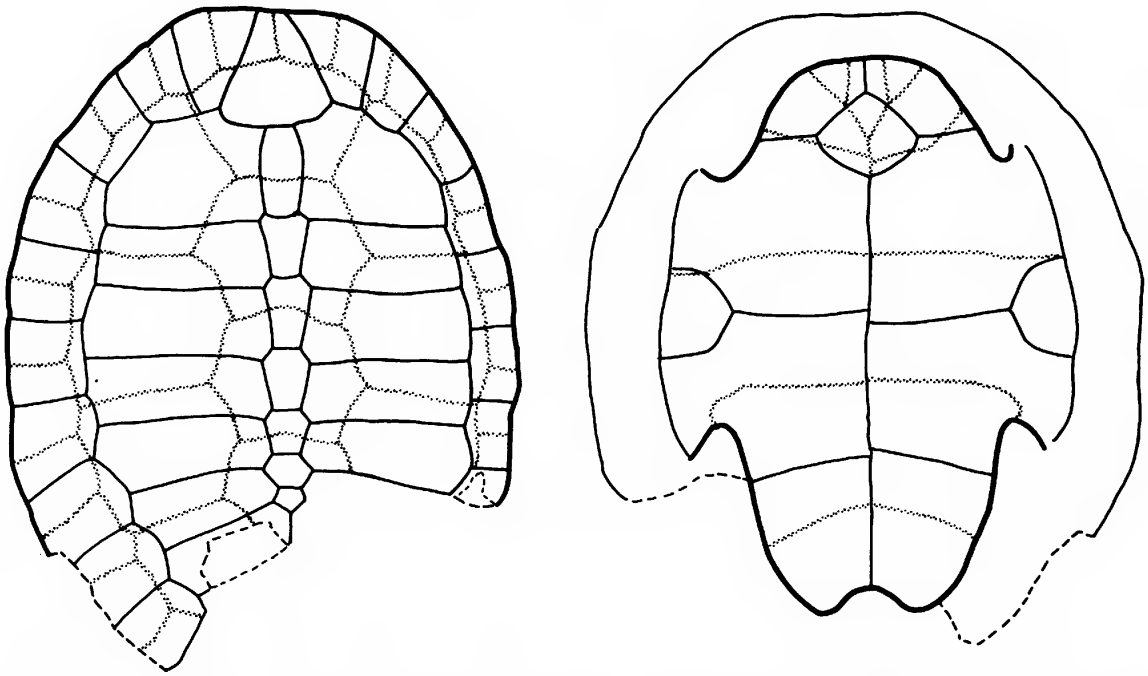

Fig. 10. Carapace (left) and plastron (right) of *Foxemys mechinorum,* n. gen., n. sp. (PAM 548).

of *Foxemys* sends a process between the angular and surangular, as in *Podocnemis* (although the general morphology of the lower jaw is very different in these two forms). The triturating surface is bound posteriorly by a very strong processus coronoideus. On the lateral surface of the coronoid, lateral to the processus coronoideus and posterior to the triturating surface, there is a posteriorly directed foramen, the foramen dentofaciale majus. This foramen in *Erymnochelys* and *Podocnemis* is under the processus coronoideus (as in *Foxemys*), but it is in the dentary, not in the coronoid, as in *Foxemys.*

The inner surface of each ramus exposes the sulcus cartilaginis meckelii and fossa meckelii, which are most visible on the right ramus. The sulcus cartilaginis meckelii is large and extends anteriorly. The prearticular is not preserved, so the fossa meckelii is also exposed on the inner surface. The ostium inferius inframaxillaris is present on the lateral wall of the sulcus cartilaginis meckelii, just anterior to the fossa meckelii. The coronoid has a small rough surface on the anterodorsal border of the fossa meckelii, which is the prearticular contact. The part of the angular bordering the sulcus cartilaginis meckelii posteroventrally is missing its posterior end. Both surangulars are incomplete, but the right one is better preserved. The surangular is very large compared to that in *Erymnochelys.* In *Foxemys* the surangular contacts the dentary on the lower margin of the lower jaw. The surangular and the coronoid form a large depression for the attachment of the musculus adductor mandibulae externus superficialis (Gaffney, 1979), which occupies the whole posterior of the lateral face of the lower jaw. This depression in *Erymnochelys* is restricted to the dorsolateral face of the lower jaw. A small part of the right articular is preserved, the lateral part of the area articularis mandibularis.

Postcranial Morphology

SHELL: Three shells are available: MD t 90, MD t 010, and PAM 548 (table 3). The most complete shell is PAM 548 (figs. 9, 10), which is well preserved without crushing. MD t 09 is well-preserved plastron (fig. 11).

The carapace is low in lateral view. The surface of the carapace and plastron is covered by a "pelomedusian" ornamentation that consists of fine forking and irregular vas-

TABLE 3
Measurements of Carapace in *Foxemys mechinorum*, n. gen., n. sp. (in centimeters)

	MD t 10	PAM 548
Length	47	40*
Width	32*	34

* Estimated.

cular grooves. In dorsal view, the outline of the carapace is oval in shape without a nuchal emargination, so that the anterior margin of the carapace is straight. A wide posterior emargination on the carapace is preserved on MD t 10 (holotype). The axillary buttress is strong and sutured to the lateral part of the first costal bone. The inguinal buttress reaches the lateral margin of the fifth costal and the eighth peripheral bones.

The nuchal bone is trapezoidal. In PAM 548, its anterior margin is very short and strongly expanded posteriorly. The greatest width of the nuchal in PAM 548 is more than four times that of its anterior margin, whereas in MD t 10, already noted as the holotype, its greatest width is less than two times that of its anterior margin. Seven neural bones are present. The first one is the largest and is rectangular in shape. The second to the fourth neurals are hexagonal with short anterolateral edges, all being longer than wide. The fifth and sixth neural bones are also hexagonal, but are much shorter than the anterior ones. The seventh neural is very small and is pentagonal in shape, with its posterior margin pointing posteriorly. All eight pairs of costal bones are preserved. The first to sixth costals of each side are separated from each other by neural bones, whereas the posterior part of the seventh and the eighth pairs of costals meet in the midline. Eleven peripheral bones are present. The first one is subtriangular in shape with a very short posterior margin. The suprapygal and pygal bones are preserved in MD t 10, but are incomplete. The suprapygal is roughly triangular in shape. The pygal bone has a wide notch on its posterior margin.

There is no cervical scute. The first to fourth vertebral scutes are all slightly wider than long and their width decreases from the second to the fourth scute. The fifth vertebral is not preserved (PAM 548) or is in bad condition (MD t 10). The first vertebral scute is restricted to the first peripheral bones in MD t 10, whereas in PAM 548 the first vertebral scute extends onto the second peripheral bone. Four pleural scutes are present that extend onto peripheral bones. Twelve marginal scutes are present, all restricted to peripheral bones.

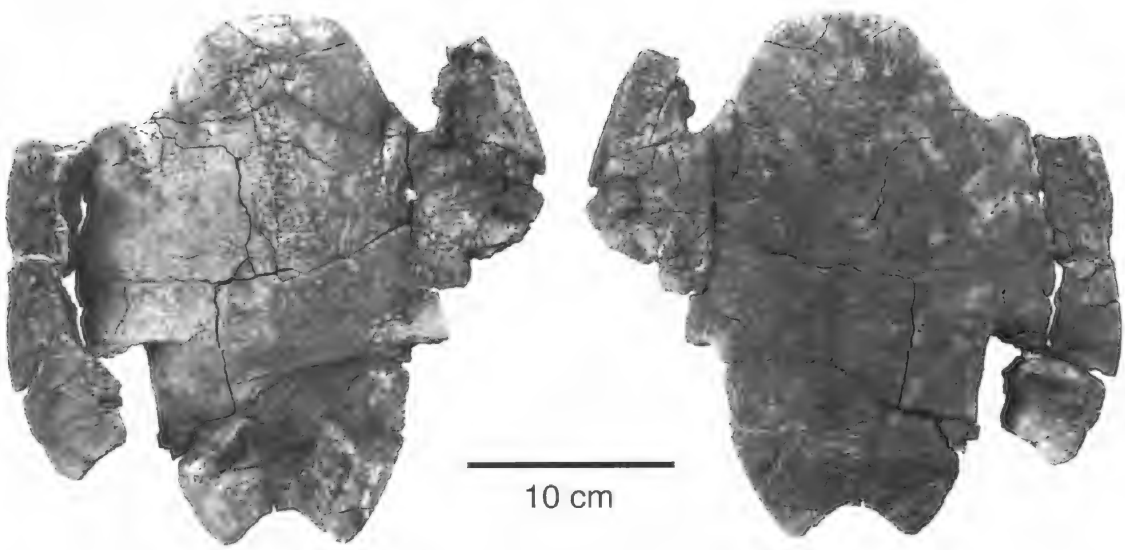

Fig. 11. *Foxemys mechinorum*, n. gen., n. sp. (MD t 09); plastron in dorsal (left) and ventral (right) view.

TABLE 4
Measurements of Plastron in *Foxemys mechinorum*, n. gen., n. sp. (in centimeters)

	MD t 10	PAM 548	MD t 09
Maximum length	34.5	34.0	26.0
Anterior lobe length	9.0	6.8	5.5
Anterior lobe width	20.0	16.0	13.0
Posterior lobe length	12.0	11.8	10.0
Posterior lobe width	19.8	16.0	13.0
Bridge length	13.5	15.4	10.5
Anal notch length	2.5	1.6	1.7
Anal notch width	6.5	5.1	5.5
Epiplastra length (max.)	5.8	4.4	3.4
Epiplastra midline length	2.9	2.2	1.3
Entoplastron length	5.9	5.3	4.0
Hyoplastra length	7.6	8.0	5.7
Hypoplastra length	8.3	8.9	6.3
Xiphiplastra length (max.)	9.7	9.9	8.4
Mesoplastra length (max.)	5.0	5.3	3.9
Gulars length	2.5	2.8	1.6
Intergulars length	4.2	4.9	3.3
Humerals length	1.8	1.4	1.1
Pectorals length	5.9	5.6	4.0
Abdominal length	9.0	7.4	6.0
Femorals length	7.0	7.8	4.9
Anals length (max.)	6.0	6.8	6.7

There are three well preserved plastra (table 4). The plastron of MD t 10 and MD t 09 are prepared on both ventral and dorsal sides. The plastron consists of 11 bones. The anterior lobe is short with an almost straight anterior margin. The bridge is longer than the posterior lobe, which is longer than the anterior lobe. The posterior lobe has almost straight lateral margins. A broad but shallow anal notch is present that is about three times wider than deep.

The epiplastra meet in the midline in a moderately long epiplastral symphysis. Its length is about one-third to one-half that of the entoplastron. The large and diamond-shaped entoplastron is wider than long, and its posterior tip reaches the level of the bridge. The length of the entoplastron is slightly longer than the distance between the posterior end of the entoplastron and the pectoroabdominal sulcus. The hyoplastra and the hypoplastra have a similar midline length.

A pair of mesoplastra are present on the bridge. They are roughly semicircular in shape and longer than wide. Two scars are

TABLE 5
Bothremydid Character Distributions

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1 Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 Pelomedusidae	1	0	0	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0
3 Araripemydidae	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
4 Podocnemididae	1	0	0	1	0	0	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0
5 *Bothremys*	?	1	1	1	1	1	0	2	2	1	1	1	1	1	1	1	0	2	1	1	0	1	1
6 *Rosasia*	?	1	1	?	1	?	0	?	?	1	1	0	1	1	1	1	1	2	1	0	0	?	1
7 *Taphrosphys*	0	0	1	1	1	1	0	2	2	1	1	1	1	1	?	1	0	?	1	1	1	0	0
8 *Foxemys*	0	0	1	1	1	?	0	2	1	1	1	1	1	1	1	0	1	2	0	0	0	1	0

TABLE 6
Characters Used in Table 5

1. Postorbital
   0: long
   1: short
2. Deep depressions in palate
   0: absent
   1: present
3. QU-BS covers prootic
   0: no
   1: yes
4. QU-BO contact
   0: no
   1: yes
5. Stapedial canal
   0: opens dorsally
   1: opens anteriorly
6. BO excluded from occipital condyle
   0: no
   1: yes
7. PT flange extends past QU
   0: no
   1: yes
8. Precolumellar fossa
   0: moderate
   1: deep
   2: absent
9. Antrum postoticum
   0: large
   1: moderate
   2: very small or absent
10. Eustacian tube
    0: in incisura columellae auris
    1: separated from incisura columellae auris
11. Neural series complete
    0: yes
    1: no
12. Pectoral scales contact entoplastron
    0: no
    1: yes
13. Cervical scale
    0: present
    1: absent
14. Mesoplastra
    0: meet medially
    1: lateral, small
    2: absent
15. PAL contribution to triturating surface
    0: narrow or absent
    1: substantial

TABLE 6—(*Continued*)

16. Incisura columellae auris closed
    0: open
    1: closed
17. PT-BS depression
    0: absent
    1: present
18. Triturating surface
    0: narrow
    1: wide posteriorly
    2: very wide posteriorly
19. Incisura columellae auris bony canal
    0: no bony canal
    1: well-developed bony canal
20. Foramen posterius canalis carotici interni
    0: formed by BS or PT-BS
    1: formed by PT-QU
21. Maxilla deep
    0: no
    1: yes
22. SO-QU contact
    0: absent
    1: present
23. Jugal exposed on triturating surface
    0: not strongly
    1: strongly

visible on the dorsal surface of the xiphiplastra. The anterior one, the articulation of the pubis, is an anteromedially oriented elongate oval, with its anterior tip pointed. The posterior one, the articulation of the ischium, is elongated and roughly triangular in shape. Its anterior margin is tranverse and its posterior tip is placed anteriorly to the anterior margin of the anal notch.

Thirteen plastral scutes are present. Gular scutes are large and triangular in shape. They reach but do not cut the anterior margin of the entoplastron. In specimens PAM 548 and MD t 09, the intergular scute is large, separating the gulars widely and reaching half the length of the entoplastron. The humeral scutes have a very short midline length, because the humeropectoral sulcus cuts the entoplastron near its posterior tip and then cuts the epihyoplastral suture at about half the length of the latter. The shell in MD t 10 has a smaller intergular scute that reaches only the anterior third of the entoplastron and is entirely anterior to the epihyoplastral suture.

The pectoral scutes cover the anterior two-thirds of the hyoplastra. The pectoroabdominal sulcus is straight and does not reach or barely reaches the anterior margin of the mesoplastra. The abdominal scutes are the largest plastral scutes. They cover the posterior third of the hyoplastra and the anterior half of the hypoplastra and mesoplastra. The abdominofemoral sulcus is straight, with the lateral end curved posteriorly. The femoral scutes cover the posterior half of the hypoplastra and the anterior part of the xiphiplastra. The femoroanal sulcus is curved anteriorly. The anal scutes are included inside the xiphiplastra.

OTHER POSTCRANIA: The right scapulocoracoid is nearly complete in MD t 11, with only the distal end of the scapula being damaged. It is similar to that of *Podocnemis*. The scapula is roughly cylindrical. The coracoid is shorter than the scapula and flat but not broad medially, joining at an angle of about 75°.

A slightly deformed pelvis is preserved in MD t 10. The ilium, ischium, and pubis contribute equally to the acetabulum. The ilium extends from the acetabulum dorsally and is sutured to the 7th and 8th costal bones. The ischium descends from the acetabulum posteroventrally to the xiphiplastron, to which it is strongly sutured. The pubis extends anteroventrally to contact the xiphiplastron. It has a medial process extending horizontally toward the midline that is not in contact with the plastron.

No vertebrae are visible.

Relationships

Foxemys is clearly a pleurodire because it has the following derived characters: processus trochlearis pterygoidei present, medial process of quadrate present, and foramen palatinum posterius behind orbit (Gaffney and Meylan, 1988). It is a member of Pelomedusoides (= Pelomedusidae sensu lato) because of the following characters: nasal bones absent, prefrontals meeting in midline, and splenial absent (Gaffney and Meylan, 1988). The Pelomedusoides (de Broin, 1988) contains four families: Araripemydidae (early Cretaceous of South America), Pelomedusidae (Cretaceous to Recent of Africa), Podocnemididae (Eocene of Europe, Cretaceous to Recent of South America, Cretaceous to Plio-Pleistocene of southern Asia, Cretaceous to Miocene of Africa, and Holocene of Madagascar), and Bothremydidae (Cretaceous to Eocene of Africa, Cretaceous to Miocene of North and South America, Cretaceous to Paleocene of Europe).

A PAUP analysis of 23 characters resulted in one cladogram (fig. 12) with a length of 32 steps, a consistency index of 0.78, and a retention index of 0.80. Most of the characters resolving relationships among the higher taxa, Araripemyidae, Pelomedusidae, Podocnemididae, and Bothremydidae, are from Meylan (1996). We have added characters that are relevant to resolution within the Bothremydidae and deleted redundant characters resolving taxa within the other families. As work on the Bothremydidae proceeds, we assume that more characters will become apparent that could easily change this cladogram. Although we found only one cladogram, the taxa within the Bothremydidae largely collapse when cladograms one step longer are included. Thus, the full resolution of taxa within the Bothremydidae cannot be considered well supported. However, placement of those taxa, including *Foxemys,* within the Bothremydidae is well supported.

In this analysis, the characters uniting the Bothremydidae are: 3) quadrate-basisphenoid covers prootic ventrally, 5) anteriorly opening stapedial canal, 8) precolumellar fossa absent, and 10) eustachian tube separated from incisura columellae auris. These are all found in *Foxemys*. The primitive conditions can be seen in the other pleurodire taxa, including chelids (Gaffney, 1979).

Within the Bothremydidae, *Foxemys* is the sister group of the three other described skull taxa because it lacks characters 9) small or absent antrum postoticum, and 19) a well-developed bony canal for the stapes, present in *Taphrosphys, Bothremys,* and *Rosasia. Foxemys* has a moderately developed antrum postoticum and an open groove for the stapes, primitive conditions for this family. *Bothremys* (Gaffney and Zangerl, 1968) and *Rosasia* (Antunes and de Broin, 1988) are united by 2) deep palatal depressions formed by the jugal, maxilla, and palatine, and 23)

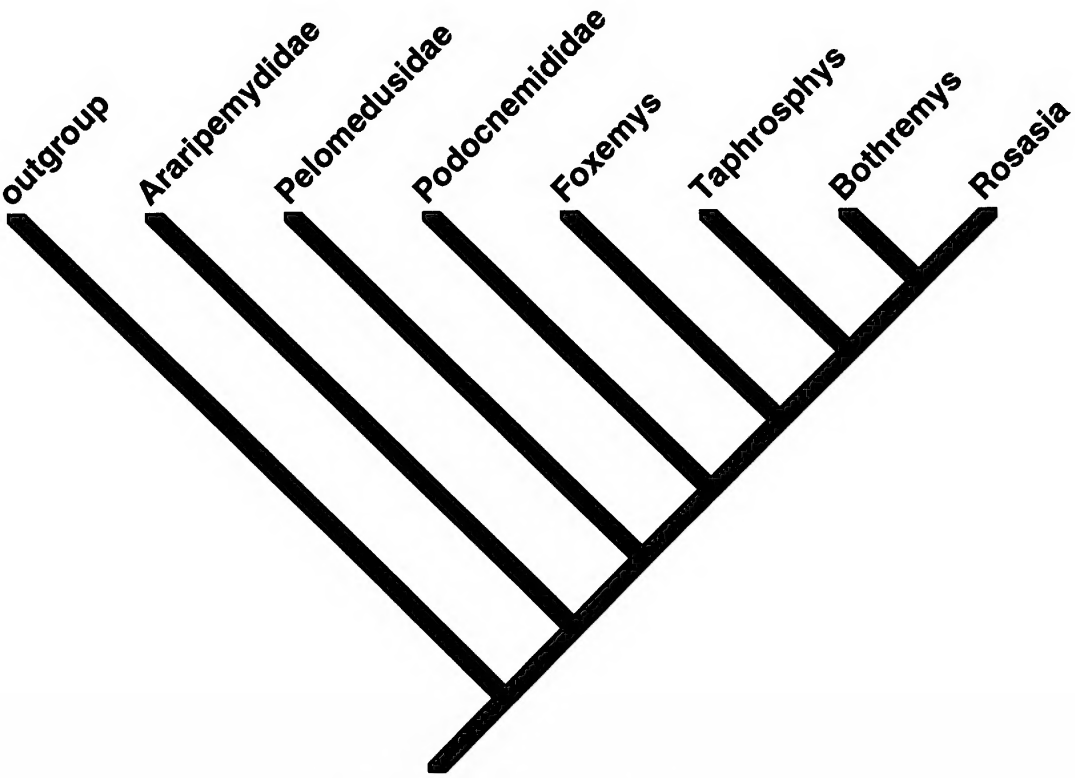

Fig. 12. Cladogram of Bothremydidae.

strong contribution of jugal to triturating surface (possibly linked to the first character).

There is a character contradiction both *Foxemys* and *Rosasia* have a relatively well-developed, ventrally open concavity formed at least by the pterygoid and basisphenoid (char. 17). *Taphrosphys* and *Bothremys* are flat in this area. This concavity is the attachment area for at least part of the pterygoideus muscle (Gaffney, 1979). Our preferred cladogram requires independent loss of the concavity twice (*Taphrosphys, Bothremys*) or independent origin of it twice (*Foxemys, Rosasia*). We consider the palatal features uniting *Rosasia* and *Bothremys* to be particularly strong.

REFERENCES

Amiot M., M. Bilotte, F. de Broin, F. Colombo, J. P. Durand, M. Feist, M. Floquet, M. Gayet, B. Lange-Badré, A. Masriera, M. Massieux, J. Medus, Y. Tambareau, J. Ullastre, and J. Villatte
1983. Le Sénonien supérieur continental de la France méridionale et de l'Espagne septentrionale: état des connaissances biostratigraphiques. Géol. Méditerr., T.X., 3–4: 245–268.

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

Buffetaut, E., and J. Le Loeuff
1991. Late Cretaceous dinosaur faunas of Europe: some correlation problems. Cretaceous Res. 12: 159–176.

Buffetaut, E., J. Le Loeuff, M. Martin, J.-C. Rage, X. Valentin, and H. Tong
1996. An early Campanian vertebrate fauna from the Villeveyrac Basin (Hérault, Southern France). N. Jhrb. Geol. Paläontol. Montsh. 1: 1–16.

de Broin, F.
1977. Contribution à l'étude des Chéloniens.

Chéloniens continentaux du Crétacé et du Tertiaire de France. Mém. Mus. Natl. Hist. Nat. Ser. C Geol. 38: 1–366.

1988. Les tortues et le Gondwana. Examen des rapports entre le fractionnement du Gondwana et la dispersion géographique des tortues pleurodires à partir du Crétacé. Stud. Paleocheloniol. 2: 103–142.

de Broin, F., E. Buffetaut, H. Cappetta, P. Kerrourio, J. C. Koeniguer, D. Russell, S. Secretan, D. Sigogneau-Russell, P. Taquet, and S. Wenz

1980. Nouvelles découvertes de vertébrés maastrichtiens dans le gisement de Fox Amphoux (Var). 8e Réunion Annuelle des Sciences de la Terre, Marseille 1980. Paris Soc. Géol. Fr. Éditeur.

de Broin, F., and X. Muregala

1996. Une nouvelle faune de chéloniens dans le Crétacé supérieur européen. C. R. Acad. Sci. Ser. II A Sci. Terre Planetes 323: 729–735.

Gaffney, E. S.

1979. Comparative cranial morphology of recent and fossil turtles. Bull. Am. Mus. Nat. Hist. 164(2): 65–376.

Gaffney, E. S., and P. A. Meylan

1988. A phylogeny of turtles. *In* M. J. Benton (ed.), The phylogeny and classification of tetrapods: 157–219. Oxford: Clarendon Press.

Gaffney, E. S., and R. Zangerl

1968. A revision of the chelonian genus *Bothremys* (Pleurodira: Pelomedusidae). Fieldiana Geol. 16: 193–239.

Lapparent, A. F. de

1947. Les dinosauriens du Crétacé supérieur du Midi de la France. Mém. Soc. Géol. France 26(56): 1–54.

Le Loeuff, J., E. Buffetaut, and M. Martin

1994. The last stages of dinosaur faunal history in Europe: a succession of Maastrichtian dinosaur assemblages from the Corbières (southern France). Geol. Mag. 131(5): 625–630.

Matheron, P.

1869. Notice sur les reptiles fossiles des dépôt fluvio-lacustres crétacé du bassin à lignites de Fuveau. Mém. Acad. Sci. Belles-Lettres Marseille: 345–379.

Meylan, P. A.

1996. Morphology and relationships of the Early Cretaceous side-necked turtle, *Araripemys barretoi* (Testudines:Pelomedusoides:Araripemydidae) from the Santana Formation of Brazil. J. Vertebr. Paleontol. 16(1): 20–33.

Nopcsa, F.

1931. Sur de nouveaux restes de tortues du Danien du Midi de la France. Bull. Soc. Géol. France 5(1): 223–235.

Portis, A.

1882. Les Chéloniens de la Molasse Vaudoise conservés dan le Musée géologique de Lausanne. Mém. Soc. Paléontol. Suisse 9:78 pp.

Tong, H., E. Buffetaut, J. Le Loeuff, L. J. Cavin, and V. Martin

1993. Découverte de restes de vertébrés dans le Crétacé Supérieur de Montséret (Corbières orientales, Aude). Bull. Soc. Etud. Sci. Aude 93: 161–164.

Westphal, M., and J. P. Durand

1990. Magnétostratigraphie des séries continentales fluviolacustres du Crétacé supérieur dans le synclinal de l'Arc (région d'Aix-en-Provence, France). Bull. Soc. Géol. France 6: 609–620.

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