

**DESCRIPTION OF THE SKULL OF *POLYSTERNON PROVINCIALE* (MATHERON, 1869),
A SIDE-NECKED TURTLE (PELOMEDUSOIDES : BOTHREMYDIDAE)
FROM THE LATE CRETACEOUS OF VILLEVEYRAC, FRANCE**

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Abstract : *Polysternon* is a European side-necked turtle based only on shell material. A skull found from the Late Cretaceous of Villeveyrac, Hérault, France, is referred to this taxon because shells clearly belonging to *Polysternon provinciale* occur in the same beds. The skull of *Polysternon* shows that it is a bothremydid with the quadrate-basisphenoid covering the prootic ventrally, the eustachian tube separated from the stapes, *precolumnellar fossa* absent, *condylus occipitalis* consisting only of exoccipitals and an exoccipital-quadrate contact. *Polysternon* lies in the *Bothremys*-Group because it has triangular, expanded triturating surfaces, extensive exposure of the palatine on the triturating surfaces, and a supraoccipital-quadrate contact. *Polysternon* is most closely related to *Foxemys*. They possess a number of characters in common including an open *incisura columellae auris* and a deep pterygoideus muscle concavity. *Polysternon* differs from *Foxemys* in having a broader midline, palatal depression, a narrower triturating surface with lower labial ridges, and a *condylus occipitalis* that is placed farther posterior.

Key words: pleurodire, *Polysternon*, bothremydid, Late Cretaceous, France

**Description du crâne de *Polysternon provinciale* (Matheron, 1869),
une tortue pleurodire (Pelomedusoides : Bothremydidae)
du Crétacé supérieur de Villeveyrac (France)**

Résumé : *Polysternon* est une tortue pleurodire européenne décrite uniquement sur des restes de carapaces. Un crâne trouvé dans le Crétacé supérieur de Villeveyrac, Hérault, France, est attribué à *Polysternon provinciale*, dont des carapaces ont été trouvées dans les mêmes niveaux. Le crâne de *Polysternon* montre qu'il s'agit d'un bothremydidé d'après les caractères suivants: carré-basisphénoïde couvrant le prootique ventralement, tube d'Eustache séparé du stapes, *precolumnellar fossa* absent, *condylus occipitalis* formé seulement par les exoccipitaux et contact exoccipital-carré. *Polysternon* est placé dans le groupe *Bothremys* à cause de la surface triturante triangulaire et élargie, de la vaste participation du palatin à la surface triturante, et du contact supraoccipital-carré. *Polysternon* est particulièrement proche de *Foxemys* par la possession de nombreux caractères en commun comprenant une *incisura columellae auris* ouverte et une dépression du pterygoïde profonde. *Polysternon* diffère de *Foxemys* par une dépression palatale médiane plus large, une surface triturante plus étroite avec une crête labiale plus basse, et un *condylus occipitalis* placé plus postérieurement.

Mots clés : pleurodire, *Polysternon*, bothremydidé, Crétacé supérieur, France

INTRODUCTION

The genus *Polysternon* was erected by Portis in 1882 on the basis of a posterior portion of shell from the Late Cretaceous of the Fuveau basin, southeastern France. Portis (1882) referred to the genus *Polysternon* the material (two shell fragments including an anterior portion of carapace) from the same basin described as *Pleurosternon provinciale* by Matheron (1869). Unfortunately, Matheron did not figure any specimen. The material described by Portis (1882) is now housed in the Musée Cantonal de Géologie de Lausanne, Switzerland. In 1931, Nopcsa studied four turtle shells from the Late Cretaceous of southern France in the Musée d'Histoire Naturelle de Marseille, and reviewed Matheron's and Portis' material. He recognized *Polysternon* and erected a new genus, *Elochelys*, including two species, *E. major* and *E. perfecta* (Nopcsa, 1931). Later, de Broin (1977) studied the Late Cretaceous and Tertiary continental turtle faunas of France, and synonymized *Elochelys major* Nopcsa, 1931 and *Polysternon provinciale* (Matheron, 1869). All these are based on shell material, the skull was, until very recently, unknown. *Foxemys mechinorum* (Tong *et al.*, 1998) was the first pleurodiran turtle from the Late Cretaceous of southern France described on the basis of both skull and shell material. The turtle skull described here was collected by Mr Guy Costa. It was figured and referred to *Polysternon provinciale* in Buffetaut *et al.* (1996) and Lapparent de Broin and Werner (1998, fig. 4). The identification of this skull as *Polysternon provinciale* is based solely on the occurrence of the skull in the same formation and geographic region as shells of *P. provinciale*. It is possible that further discoveries will alter this provisional identification. Nonetheless, we feel that this course is preferable to naming a new taxon or to not identifying the skull at all. In any case, both skull and shells are bothremydids.

The Villeveyrac quarries are located about 20 km south-west of Montpellier (Hérault, France). The vertebrate fauna comes from the lower series of the Late Cretaceous beds, which are Lower Campanian dark clays. It includes fishes (Ginglymodi and Teleostei), frogs, turtles, lizards, crocodiles and dinosaurs (theropods, iguanodonts and ankylosaurs). Turtle remains are mainly abundant shell fragments; they

include both the pleurodiran bothremydid *Polysternon provinciale* and the cryptodiran *Solemys*. The palaeoecology of the vertebrate-bearing Late Cretaceous beds of Villeveyrac has been reconstructed on the basis of sedimentological and paleontological studies which indicate an estuarine landscape combining freshwater and brackish environments (see Buffetaut *et al.*, 1996).

Although the Bothremydidae was named as early as 1891 by George Baur, the term fell into disuse for most of this century and the few included taxa, particularly *Bothremys* and *Taphrosphys*, were simply included in the Pelomedusidae. Antunes and Broin (1988) and Broin (1988) revived Bothremydidae, provided a new diagnosis and added taxa, such as *Rosasia*, based on skulls. 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 realized to be a more widespread and diverse group than previously considered.

Useful reviews of the literature on bothremydids can be found in Broin (1988) and Antunes and Broin (1988). Previously described bothremydid skulls are as follows: *Bothremys* (Gaffney and Zangerl, 1968; Gaffney, 1977), *Taphrosphys* (Gaffney, 1975), *Rosasia* (Antunes and Broin, 1988), *Foxemys* (Tong *et al.*, 1998), *Zolhafa* (Lapparent de Broin and Werner, 1998), *Arenila* (Lapparent de Broin and Werner, 1998), and *Nigeremys* (Bergounioux and Crouzel, 1968; Lapparent de Broin and Werner, 1998). A general treatment and description of pleurodire skulls, turtle skull morphology and terminology, and a literature review is in Gaffney (1979).

SYSTEMATICS

Order TESTUDINES Linnaeus
 Suborder PLEURODIRA Cope
 Hyperfamily PELOMEDUSOIDES Cope
 Family BOTHREMYDIDAE Baur
 POLYSTERNON Portis 1882
Polysternon provinciale (Matheron, 1869)
 (Fig. 1-2)

Revised Diagnosis: Bothremydid pleurodire with the following bothremydid synapomorphies: quadrate-basisphenoid covers prootic ventrally, eustachian tube separated from stapes, *precolumellar fossa* absent, *condylus occipitalis* consisting only of exoccipitals and exoccipital-quadrate contact; differs from all other bothremydid except *Foxemys* in having an open rather than closed *incisura columellae auris*; skull agrees with *Foxemys* but differs from *Nigeremys* and *Taphrosphys* in being wedge-shaped with a posteriorly expanded triturating surface; agrees with *Arenila* and *Foxemys* in having a relatively deep

pterygoideus muscle concavity; differs from *Foxemys* in having a broader midline, palatal depression, a narrower triturating surface with lower labial ridges, a shallower pterygoideus muscle concavity, a shorter exoccipital midline contact, a wider and longer basioccipital, and a more posterior *condylus occipitalis*; smooth triturating surface as in *Foxemys* but distinct from the pits seen in *Bothremys*, *Rosasia*, and *Zolhafa*: shell similar to *Foxemys* but having a nuchal emargination, a small intergular scale, and an acute anal notch.

Measurements : see Table 1.

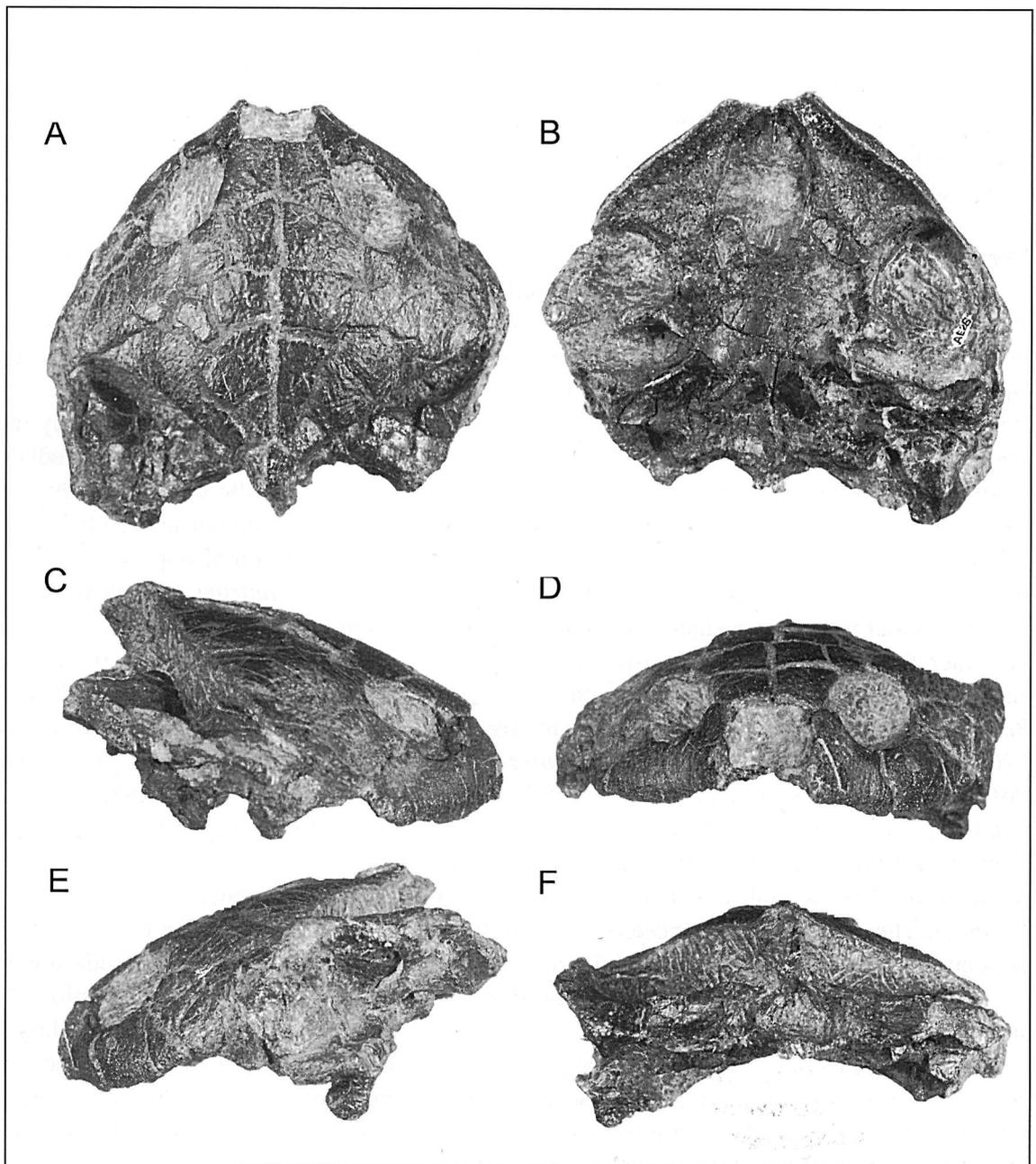


Figure 1
Polysternon provinciale,
 Late Cretaceous,
 Villeveyrac, France.
 Skull,
 A - dorsal view,
 B - ventral view,
 C - right lateral view,
 D - anterior view,
 E - left lateral view,
 F - occipital view.

DESCRIPTION

Material : an isolated and nearly complete skull without lower jaw (AE28, Costa Collection), collected by Guy Costa in one of the Villeveyrac quarries. See Buffetaut *et al.* (1996) for further locality data.

Preservation : The skull is almost complete but slightly crushed dorsoventrally; the right otic region and the middle of the palate are damaged. All the sutures of the skull are opened and confluent with cracks that are all filled with the reddish, ironstone matrix.

General aspect:

The skull is like *Foxemys* in being triangular-shaped in dorsal view, but it is shorter and the trituberculate surface is narrower, separated by a wider midline palatal depression. There are no scale markings visible on the surface of the skull.

Dermal roofing elements:

Polysternon has a well preserved skull roof, except for all the cracks, and, unusually for bothremyids, the complete extent of the roof and temporal emargination is preserved. The prefrontals of *Polysternon* are very similar to those in *Foxemys*. The anterior edges are natural and are transverse with no projection. The contact with the dorsal process of the maxilla is broken on both sides but the right one is better preserved. The internal portion of both prefrontals is covered by matrix. The orbits are slightly closer together in *Foxemys* than in *Polysternon* so in the latter the prefrontals and the frontals are wider and shorter. In common with such forms as *Bothremys* and *Zolhafa* (and in contrast to *Arenila*, *Nigeremys* and *Taphrosphys*), *Foxemys* and *Polysternon* have a broad preorbital part of the skull. The frontals of *Polysternon* are also close in morphology to *Foxemys*. They form the posteromedial part of the orbits. The parietals are also similar to those in *Foxemys*. They have a straight posterior margin trending anterolaterally from the supraoccipital.

The jugals are preserved on both sides of AE28 and are similar to *Foxemys*.

The jugal in *Polysternon* is relatively small and lies in the posteroventral corner of the orbit. The jugal contacts the postorbital dorsally, the quadratojugal posteroventrally, and the maxilla anteroventral-

ly. In ventral view, a small part of the medial process of the jugal is visible contacting the maxilla anteriorly and the palatine medially.

The right quadratojugal in AE28 is mostly missing but the remaining portion shows its contacts with the postorbital, jugal, and maxilla. The left quadratojugal is complete but much of it is broken and disturbed by cracks. As preserved it agrees with *Foxemys* in the jugal, maxilla, and postorbital contacts, and the presence of a shallow cheek emargination which is longer than high. The quadratojugal forms a curved contact with the quadrate anterior to the *cavum tympani* of the quadrate in *Polysternon* as in *Foxemys*. In both *Polysternon* and *Foxemys* the quadratojugal forms the anterolateral corner of the temporal emargination and a process extends posteriorly to contact the squamosal preventing the quadrate from being exposed in the temporal margin.

The right squamosal is missing in AE28 and the left one is damaged by crushing. Its posterior margin is mostly broken, but it could have had a horizontal flange as in *Foxemys*. Sutures limiting the squamosal are hard to make out in AE28 but some can be seen. On the lateral surface, above the *cavum tympani*, the quadratojugal-squamosal and quadrate-squamosal sutures are visible but ventrally the quadrate contact becomes obscure. Posteromedially the squamosal just reaches the opisthotic. On the dorsal surface of AE28 the squamosal-quadrate contact can be seen medially but it disappears in crushed bone more laterally. The *antrum postoticum* is largely crushed and its internal structure is not visible.

The postorbital is complete on both sides of AE28. It is very similar to *Foxemys* but shorter in *Polysternon*. The postorbital-quadratojugal suture looks slightly shorter in *Polysternon*, suggesting that the temporal emargination may be slightly more extensive in *Polysternon* than in *Foxemys*.

Palatal elements

The premaxillae in AE28 are preserved, but not complete, the anterior ends are missing. From the angle of the preserved portion it is likely that the snout of *Polysternon* was slightly more pointed than in *Foxemys*. Only the ventral surface of the premaxilla is visible, the dorsal surface is covered with matrix. The midline suture is visible as well as the two *foramina praepalatina* which are placed in the

Figure 2.

Key to Fig. 1.

Abbreviations :

bo - basioccipital ;

bs - basisphenoid ;

ex - exoccipital ;

fp - fenestra
postotica ;

fjp - foramen jugulare
posterius ;

fnh - foramen nervi
hypoglossi ;

fpcci - foramen
posterius canalis
carotici interni ;

fpp - foramen
palatinum posterius ;

fr - frontal ;

ica - incisura
columellae auris ;

ju - jugal ;

mx - maxilla ;

op - opisthotic ;

pa - parietal ;

pal - palatine ;

pf - prefrontal ;

pm - premaxilla ;

po - postorbital ;

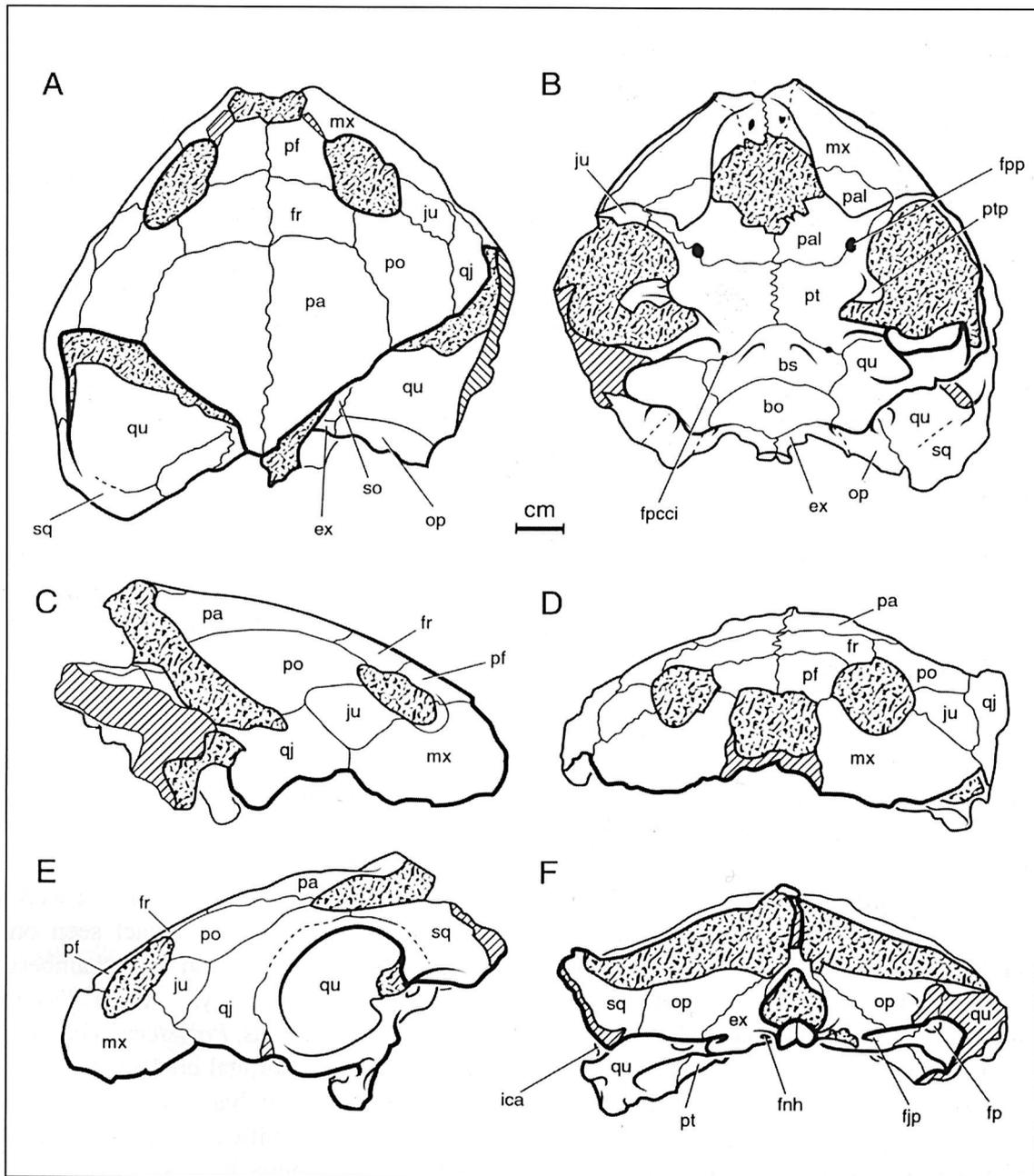
pt - pterygoid ;

qj - quadratojugal ;

qu - quadrate ;

so - supraoccipital ;

sq - squamosal.



premaxillae as in *Foxemys*, but unlike *Bothremys* in which these foramina are placed on the premaxilla/vomer suture.

The triturating surface on the midline at the anterior end of the skull was probably very narrow in *Polysternon*, as in *Foxemys*. Just posterior to the triturating surface the premaxillae and maxillae form a midline depression in *Polysternon* that is much wider and more sharply defined than in *Foxemys*. The vomer in AE28 is missing and the posterior edges of the premaxillae and anterior edges of the

palatines are broken margins.

The maxillae in *Polysternon* form most of the large triturating surfaces. Except for the premaxillary contact, the margins of the maxilla are clearly visible. Only its ventral and lateral surfaces in AE28 are exposed, the dorsal surfaces are covered with matrix. The triturating surface in *Polysternon* is quite similar to *Foxemys*, it is strongly triangular, very narrow anteriorly, and wide posteriorly. The posterior part of the triturating surface is broader in *Foxemys* than in *Polysternon*, resulting in a distinctly narrower

apertura narium interna in *Foxemys* than in *Polysternon*. Anteromedially the triturating surface of *Polysternon* has a low lingual ridge along the edge of the *apertura narium interna* that is sharper and more clearly defined than the very low one in *Foxemys*, and the labial ridge in *Polysternon* is clearly lower than that of *Foxemys*. The actual surface of the triturating area in *Polysternon* is flat, curving out to the labial ridge, but a low concavity can be seen on both sides in the region of the maxilla-palatine suture.

The palatines in *Polysternon* are similar to those in *Foxemys*, differing primarily in the width of the *apertura narium interna*. Each *foramen palatinum posterius* is formed half by the palatine (anteriorly) and half by the pterygoid (posteriorly).

Palatoquadrate elements

The quadrate in AE28 is largely missing on the right side and damaged to some extent on the left. Nonetheless, enough is preserved to show that it has strong similarities to *Foxemys*, in contrast to other bothremydids. The *incisura columellae auris* of *Foxemys* is unusual among bothremydids in being open, with no complete bony bar separating the stapes from the eustachian tube. *Polysternon* as preserved clearly shows an open *incisura columellae auris* on the left quadrate as in *Foxemys*. The dorsal margin of the incisura is broken and obscured by matrix holding some bone fragments, but the ventral margin and the posterior part of the dorsal margin are intact and clearly show smooth bone surfaces with no missing bone that could have closed the incisura. This is in contrast to the figure of *Polysternon* (AE28) in Lapparent de Broin and Werner (1998, fig. 4h) which shows a closed *incisura columellae auris* in this same specimen.

The *incisura columellae auris* of *Polysternon* as preserved is widely open, much wider than in *Foxemys*. But it is apparent that the *condylus mandibularis* of the quadrate has been bent ventrally in this skull. Also the dorsal margin of the incisura is absent, represented by a ridge of matrix and bone fragments. The very base of the incisura seems to be well preserved and is relatively narrow as in *Foxemys* but the original extent of the rest of the incisura was probably narrower than preserved at present. Although the *incisura columellae auris* is open in *Polysternon*, it is interpreted as being very narrow as in *Foxemys*.

Based on comparisons with other pelomedusoides, it is likely that the eustachian tube was not present in the small, narrow incisura, rather, it was separated from the stapes as in all other bothremydids. The pathway of the stapes and more medial and internal parts of the quadrate are not visible. The *cavum tympani* in AE28 is cracked and slightly dislocated but it is well enough preserved to show that there was no *precolumellar fossa*. The *cavum* surface is smooth. This differs from *Foxemys* which has a slight concavity but not a distinct *precolumellar fossa*.

The *antrum postoticum* in *Polysternon* is crushed flat and its original extent is not completely determinable. However, there is enough of its dorsal edge present to show that at least a moderate antrum was present, not the extremely small or absent antrum seen in *Bothremys*. It is also clear that a large *antrum postoticum* of the sort seen in pelomedusids was not present in *Polysternon*. It is most likely that the antrum of *Polysternon* was the same as that in *Foxemys*.

The quadrates are visible on both otic chambers although the left side is more complete. Sutures are not clear but the opisthotic contact can be made out on both sides and part of the squamosal suture is visible on the left side. As in *Bothremys*, *Rosasia*, and *Foxemys*, *Polysternon* has a well developed quadrate-supraoccipital contact seen on the right side of AE28. All of both otic chambers are covered with matrix anteriorly. As in *Foxemys* and the other bothremydids, *Polysternon* has a well developed quadrate-exoccipital contact, but it is more extensive in *Polysternon* than in *Foxemys*.

A significant difference between *Polysternon* and *Foxemys* is the position of the *processus articularis* of the quadrate in relation to the occipital region of the skull. In *Polysternon* the *condylus mandibularis* and *processus articularis* of the quadrate are more anterior with respect to the *condylus occipitalis* in contrast to *Foxemys* where they are more posterior, much closer to the *condylus occipitalis*. Although this area of the quadrate in AE28 has been subjected to some post mortem displacement, it has not been moved very much in relation to the occiput.

The pterygoids in AE28 are both preserved and visible in ventral view. They are similar to the pterygoids in *Foxemys* except for the posterolateral process, the quadrate ramus. In *Foxemys* this process is

directed more posteriorly and in *Polysternon* it is directed more anterolaterally in relation to the position of the *processus articularis*.

The pterygoideus muscle concavity in *Polysternon* is shallower than in *Foxemys* but some of this is due to breakage in AE28. Similarly, the depression is wider in *Polysternon* than in *Foxemys*, presumably related to the more anterior position of the *processus articularis* in *Polysternon*. The *processus trochlearis pterygoidei* is present on both pterygoids. Its anterior surface is visible on the left side and its posterior face on the right side. The processus is at right angles to the skull midline as in *Foxemys* and the other bothremydids.

Braincase elements

The supraoccipital in AE28 is broken near its base so the extent of the *crista supraoccipitalis* is not determinable. The ventral processes are slightly disarticulated and pushed ventrally, reducing the size of the *foramen magnum*. Only a small amount of the supraoccipital is exposed on the skull roof. Although there is a certain amount of damage, the supraoccipital-quadrates contact can be seen on both sides. It is best preserved on the right.

The exoccipitals are preserved on both sides of AE28 with most of their sutures visible. The exoccipitals in *Polysternon* form all of the *condylus occipitalis*, none of the basioccipital even reaches the base of the condylus. The *foramen jugulare posterius* is open laterally on both sides but it is better preserved on the right side, although broken on both. Only one *foramen nervi hypoglossi* is visible, and that is on the left exoccipital, because of crushing in the area of both exoccipitals. The exoccipital-quadrates suture and the exoccipital-opisthotic suture are both visible on both sides of the skull. The exoccipital as preserved is quite similar to that bone in *Foxemys*, except that in *Polysternon* the exoccipitals have a more extensive ventral exposure and present a longer ventral midline suture anterior to the occipital condyle. In *Foxemys*, the exoccipitals are less visible on the ventral side, with a shorter midline suture.

The basioccipital in *Polysternon* is similar to that bone in *Foxemys*. Laterally it has well developed contacts with the quadrates and posteriorly sends only a shallow, pointed process towards the *condylus occipitalis* and does not even reach the base of the

condylus. The basioccipital of *Polysternon* and *Foxemys* show some important differences. In *Polysternon* the basioccipital is as wide as the basisphenoid and nearly as long. In *Foxemys* the basioccipital is narrower and much shorter. The *condylus occipitalis* (broken in *Foxemys* but its bases show its position) is further anterior in *Foxemys* than in *Polysternon* and the basioccipital is curved, concave posteriorly.

The basisphenoid in *Polysternon* is triangular and very similar to that bone in *Foxemys*. The pterygoid and basisphenoid contacts are clear but the lateral limits of the basisphenoid lie in regions of broken bone. Most of the quadrates-basisphenoid contact can be seen or extrapolated through cracks except for the area where the quadrates-ptyerygoid-basisphenoid come together in the center of the pterygoideus muscle concavity. The *foramen posterius canalis carotici interni* is placed at the anterior end of the pterygoideus muscle concavity, on the pterygoid/basisphenoid suture as in *Foxemys*. This is in contrast to that figured for the same specimen in Lapparent de Broin and Werner (1998, fig. 4d) in which this foramen is placed on the pterygoid/quadrates/basisphenoid contact.

The prootic is presumably exposed on the dorsal surface of the otic chambers, but it is entirely covered by matrix on both sides. The opisthotics are preserved on both sides. Dorsally the opisthotic-quadrates suture is visible on both sides. Best preserved on the right otic chamber, the opisthotic does not reach the prootic due to the supraoccipital-quadrates contact. The *fenestra postotica* is not well preserved on either side, but enough is available, particularly on the right, to show that the fenestra is closed laterally and medially as in *Bothremys* and all other bothremydids.

DISCUSSION

The skull described here, AE28, was collected in deposits at Villeveyrac which are Early Campanian in age (Buffetaut *et al.*, 1996). This skull was previously identified as *Polysternon provinciale* by Buffetaut *et al.* (1996) and by Lapparent de Broin and Werner (1998). The basis of this identification is the presence of this skull in the same deposits as shells identified as *Polysternon provinciale* by Buffetaut *et al.* (1996). This shell material, described and figured (*ibid.*), is

very similar to the type of *Polysternon provinciale* (see Broin, 1977, for references and figures). Although this is not an association of a shell and skull of the same individual, we feel that a provisional identification of the skull as *Polysternon* is the most conservative course to adopt for the present.

Identification of a skull as *Polysternon provinciale* finally allows an assessment of the relationships of this genus. The shells of Pelomedusoides (sensu Antunes and Broin, 1988) are notoriously conservative and have provided few characters for higher category systematics in pleurodires, but the skulls have yielded many systematically important characters. *Polysternon* is a bothremydid because it has the quadrate-basisphenoid covering the prootic ventrally, eustachian tube that is separated from the stapes, *pre-columellar fossa* absent, *condylus occipitalis* consisting only of exoccipitals and an exoccipital-quadrate contact. Within the Bothremydidae, *Polysternon* lies in the “*Bothremys* Group” of Lapparent de Broin and Werner (1998) because it has broad, triangular triturating surfaces, extensive exposure of the palatine in the triturating surfaces, and a supraoccipital-quadrate contact.

Among the bothremydids the skull of *Polysternon* is most similar to *Foxemys mechinorum* (Tong *et al.*, 1998) from the Late Campanian/Early Maastrichtian Fox Amphoux locality, southeastern France, and has some derived characters in common with it, indicating a close relationship between them. The triturating surfaces of both are very narrow anteriorly and wide posteriorly. Unique among the described Bothremydidae, both *Foxemys* and *Polysternon* have an open *incisura columellae auris*, interpreted as a derived character within this group. Although some differences can be noticed between these two taxa, especially on the palate and the basioccipital region (see table 2.), *Foxemys* is more advanced as compared to *Polysternon* in having a more developed triturating surface which is much broader posteriorly with a higher labial ridge, and therefore a narrower midline palate depression, and in having a more shortened posterior part of the skull, in which the *condylus occipitalis* is more forwardly placed and the basioccipital is very short.

The general morphology of the shell of *Polysternon provinciale* is very similar to that of *Foxemys mechinorum* (Tong *et al.*, 1998). The shell

of *Polysternon provinciale* has tiny and close-set ridges on the shell surface, a shallow and broad nuchal emargination and the first vertebral scute extending onto the first peripheral bone. The shell of *Foxemys mechinorum* has a nearly smooth surface, without a nuchal emargination, and has a broader first vertebral scute which may extend onto the second peripheral bone. Another species of *Polysternon*, *P. atlanticum*, has been described on the basis of shell fragments only, from the Late Campanian/Early Maastrichtian Laño locality, southern Spain (Lapparent de Broin & Murelaga, 1996). *P. atlanticum* is smaller than *P. provinciale*, with a narrower first vertebral scute cutting the nuchal plate and a smooth shell surface (Lapparent de Broin & Murelaga, 1999).

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Table 1	Measurements of AE28 (in mm)
A. midline length as preserved	72,9
B. maximum width	85,9
C. width between orbits	21,0
D1. width of left orbit	19,7
D2. width of right orbit	18,4
E. width of external nares	14,5
F. width of internal nares	19,0
G. (maximum) height at quadrate	39,8
H. width of skull at middle of orbits	59,8
I. length from anterior margin of prefrontals to posterior margin of parietals	60,8
J1. height of left orbit	14,7
J2. height of right orbit (both measured in plane of orbit, not vertical)	13,2
K. skull height at occipital condyle	27,8
L. anterior width of triturating surface	6,3 (L) 5,9 (R)
M. posterior width of triturating surface	16,5 (L) 17,5 (R)
N. width of palate across foramina palatinum posterius	40,4
O. length from front of skull to posterior edge of condylus articularis	53,6

Table 2 : Comparison of *Polysternon* and *Foxemys*

	<i>Polysternon</i>	<i>Foxemys</i>
Orbits	farther apart	closer together
Midline palatal depression	broader	narrower
Lingual ridge	sharper	weaker
Labial ridge	lower	higher
Posterior width of triturating surface	narrower	wider
Condylus mandibularis of quadrate	far anterior to condylus occipitalis	close to level of condylus occipitalis
Pterygoideus muscle concavity	wider and shallower	deeper and narrower
Exoccipital midline suture on ventral surface	longer	shorter
Basioccipital	wider and longer	narrower and shorter