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EUGENE S. GAFFNEY¹

ABSTRACT

A natural endocast of the skull of *Bothremys*, a pelomedusid pleurodire from the Late Cretaceous (Magothy Formation of Cliffwood Beach, New Jersey) is unusual in preserving the orbital

cavities as well as the brain cavity. The endocast provides new information on the basicranium, as well as the orbital and nasal cavities, and allows comparison with Recent pelomedusids.

INTRODUCTION

The Cretaceous pleurodire, *Bothremys*, is known from a series of shells and two skulls, described and figured in Gaffney and Zangerl (1968, see also references to previous work on this genus). Subsequent to the publication of that paper another specimen referable to *Bothremys* has come to my attention and I have developed a new reconstruction of the palate. The purpose of the present paper is to give the description of the new *Bothremys* specimen. The relationships of *Bothremys* lie with the pelomedusid pleurodires (*ibid.*) and a study of this group is deferred to the future.

The specimen described here is unique and unusual in the manner, as well as the taxon, preserved. The fossil consists of the infilling of a skull by limonitic sandstone forming a natural cast of the internal cranial morphology. Although fossil "brains" are not particularly rare

(see Edinger, 1929, for a review), there are very few reported for turtles. Furthermore, this endocast preserves high quality representations of the orbital and nasal cavities as well as the basicranium. The only natural turtle endocast reported in the literature is that of a presumed sea turtle (Edinger, 1934). In this specimen, from the Cretaceous of Europe, the cavum cranii and adductor chambers are preserved with some indications of the orbits. Artificially made endocasts of turtles are reported by Edinger (1929), Zangerl (1960), and Gaffney and Zangerl (1968).

The new *Bothremys* endocast comes from the Cretaceous coastal plain sediments of New Jersey and is preserved in a manner that seems to be typical of invertebrate fossils from certain lithologic units in this region. Unfortunately, there is little available information on the process of steinkern formation and I am unable to advance

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any useful hypotheses about the taphonomy of the endocast. The rock forming the endocast is a relatively coarse-grained, quartz sandstone with limonitic cement. Limonite formation seems to have been concentrated on the bone surfaces resulting in a very high fidelity image of the bone morphology. Sutures, foramina, and impressions of vessels are all preserved in the endocast. The sandstone has not been analyzed petrographically but it does seem to contain a high percentage of wood and plant fragments. The dorsal surface of the orbital cavities and the cavum cranii shows the impressions of elongated lumps, possibly representing some sort of invertebrate fecal matter.

The *Bothremys* endocast has had an interesting scientific history. It was "found loose on the beach at Cliffwood, New Jersey, by C. J. Adami, Princeton '26, on May 28th, 1926" (label). It was identified as a brain cast of a gavial and a sketch (possibly by W. J. Sinclair) accompanying the specimen shows that the endocast was reversed with the foramen magnum identified as the nasal area and the orbits as pterygoid bullae. Later, the endocast became part of the Princeton Geology Museum "What is a Fossil?" display and remained there for some time. Recently, Dr. Donald Baird, Director of the Museum, reoriented the specimen and discovered that the "bullae" were orbital infillings. He also identified the endocast as *Bothremys*. Dr. Baird also discovered in the files a sketch made some time ago by the late Dr. Tilly Edinger, the foremost student of fossil "brains." In this sketch the major features (carotids, cerebrum, olfactory tract, pituitary) are correctly identified and the specimen is oriented properly. The identification "turtle?" is also on the sketch. As far as I am aware, however, there is no reference to this specimen in Edinger's published works.

ACKNOWLEDGMENTS

I am very grateful to Dr. Donald Baird, Director of the Geology Museum at Princeton University, who brought this specimen to my attention and also provided me with the background material on its history. The photographs are the work of Mr. Chester Tarka and the drawings are by Ms. Lorraine Meeker, both of the Department of Vertebrate Paleontology.

ABBREVIATIONS

INSTITUTIONS

AMNH[H], Department of Herpetology, the American Museum of Natural History
FMNH, Field Museum of Natural History
PU, Princeton University

ANATOMICAL

ang, angular
art, articular
bo, basioccipital
bs, basisphenoid
cor, coronoid
dent, dentary
epi, epipterygoid
ex, exoccipital
fr, frontal
ju, jugal
mx, maxilla
na, nasal
op, opisthotic
pa, parietal
pal, palatine
pf, prefrontal
pm, premaxilla
po, postorbital
pr, prootic
pra, prearticular
pt, pterygoid
qj, quadratojugal
qu, quadrate
so, supraoccipital
sq, squamosal
sur, surangular
vo, vomer

SYSTEMATICS

ORDER TESTUDINES

SUBORDER CASICHELYDIA

INFRAORDER PLEURODIRA

FAMILY PELOMEDUSIDAE

Bothremys sp.

Locality. "Found loose on the beach at Cliffwood, N. J." (label).

Horizon. "Supposedly from the ferruginous sand layer at the top of the Magothy Clay. Slabs of similar matrix with marine Cretaceous shells are found loose on the beach" (label). Late Cretaceous.

Collector. C. J. Adami, May 28, 1926.

The *Bothremys* endocast is conspicuously different from most other natural endocasts in preserving the orbital cavities and portions of the palate as well as the cavum cranii proper. The identification of the endocast as *Bothremys* is first of all based on its identification as a pleurodire. The position of the foramen palatinum posterius and the development of a postorbital wall is diagnostic for pleurodires (Gaffney, 1975) and the endocast has the pleurodiran condition. Among pleurodires (actually, among all turtles that I am familiar with) the extensive enclosure of the orbital cavities by bone and the dorso-lateral orientation of the orbital openings (Gaffney and Zangerl, 1968, fig. 14) are unique to *Bothremys*. This combined with the skull width, internal morphology of the fossa nasalis, and the basicranial structure strongly substantiate the identification of the specimen as *Bothremys*.

The Princeton specimen, however, does show some differences from the other two known *Bothremys* skulls. The Princeton endocast is nearly twice the size of the type specimen of *Bothremys cooki* (AMNH 2521) and about the same size as the Selma skull *B. barberi* (Gaffney and Zangerl, 1968; FMNH PR 247). The width of the cavum cranii at the level of the cerebral expansions is somewhat greater in PU 12951 than in FMNH PR 247 even though the skulls are about the same size. The cavum cranii, then, is very similar in the two New Jersey specimens (AMNH 2521 and PU 12951), which differ from the Selma specimen (FMNH PR 247). This fact seems to refute the contention (Gaffney and Zangerl, 1968, p. 228) that the differences in the endocranium of *B. cooki* and *B. barberi* are due solely to relative skull size. Other comparisons between PU 12951 and FMNH PR 247 are difficult to make because of the poor preservation and fragmentary nature of the latter specimen. A subjective comparison of the orbital cavities (fossa orbitalis) in AMNH 2521 and PU 12951 seems to indicate that the cavities are relatively smaller in the former, which is the smaller skull. Precise measurements were not attempted and the fragile nature of the American Museum's *Bothremys* skull precludes making a complete internal cast for comparison.

The anteroventral and portions of the lateral

walls of the fossa nasalis are represented in the endocast. The morphology is quite consistent with that area of AMNH 2521 and little new information can be obtained. The paired foramina praepalatina lie in the floor of the fossa and are prominent in the endocast. The central part of the endocast forming the fossa nasalis is hollow, presumably due to weathering. Very little of the apertura narium externa is preserved although the anterodorsal margin of it is buried in matrix. The posterior portion of the fossa nasalis, the apertura narium interna, the foramen orbito-nasale, and most of the dorsal surface of the palate are not preserved in the endocast, which has a large, irregular area missing in this region.

The fossa orbitalis in PU 12951 is nearly spherical and broadly connected to the cavum cranii region medially and posteromedially. The orbital openings are obscured by matrix anteromedially but otherwise can be seen to agree with the openings in AMNH 2521. Bone remains deeply buried in the matrix in the area between the apertura narium externa and the orbits. The visible interorbital cross-section shows a thick sheet of bone comparable in depth to FMNH PR 247 and relatively thinner than in AMNH 2521. What appears to be the foramen alveolare superius lies in the area between the fossa nasalis and the fossa orbitalis and can be seen on the left side of the specimen. A foramen supramaxillare was not identified by Gaffney and Zangerl (1968) in *Bothremys*, and the endocast supports this. Albrecht (1976) has reported that the foramen supramaxillare is absent in *Pelusios* and *Pelomedusa* but present in *Podocnemis*. The presence of this foramen in nearly all other turtles leads me to conclude that its absence is derived and is consistent with monophyly of *Bothremys*, *Pelomedusa*, and *Pelusios*. Further comparative work, however, will be required. There is a foramen at the anterolateral margin of the fossa orbitalis that occurs in *Podocnemis*, *Pelomedusa*, and *Pelusios* as well as *Bothremys*. Albrecht (1976) identified this in the living pelomedusids as the foramen alveolare superius. However, the foramen alveolare superius usually opens inside the fossa nasalis and I have found such a foramen in the living pelomedusids and in *Bothremys*. In *Podocnemis* and *Pelomedusa* this foramen com-

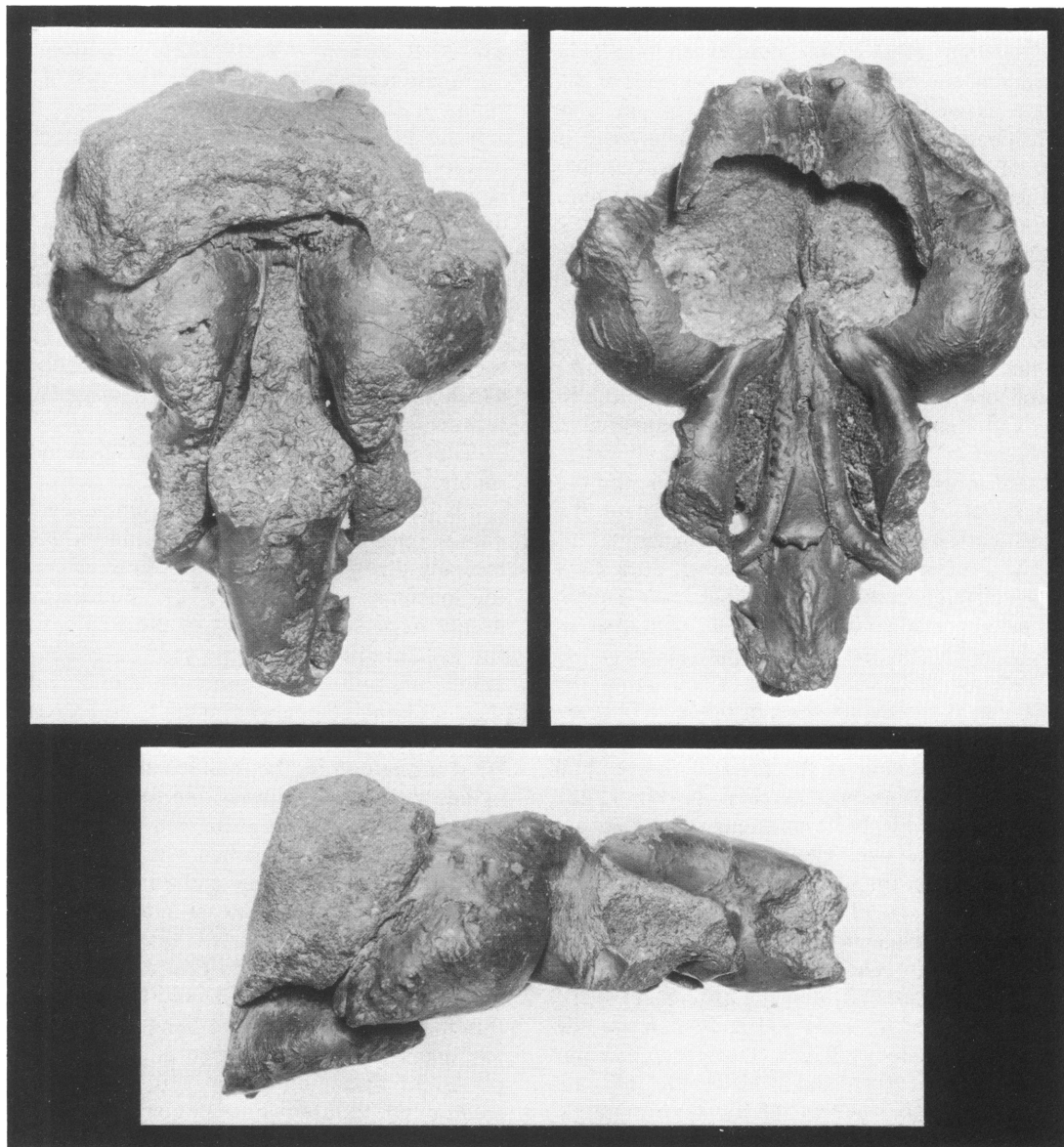


FIG. 1. *Bothremys* sp. (PU 12951, 93 mm. maximum length), Late Cretaceous, Magothy Formation, New Jersey. Dorsal (left), ventral (right), and left lateral (lower) views of natural endocast. See figure 2.



FIG. 3. *Bothremys* sp. (PU 12951), Late Cretaceous, Magothy Formation, New Jersey. Latex cast of basicranium. See figure 2 (right) for identification of structures.

municates with the canalis alveolaris superior (Albrecht, 1976, but again he identified it as the foramen alveolare superius). If Albrecht has, as I suggest here, missed the "true" foramen alveolare superius, then this foramen is unnamed. In any case, it is not the foramen supramaxillare because both the foramen supramaxillare and the "unnamed" foramen are present in *Podocnemis*. The "unnamed" foramen is double in many *Podocnemis* specimens and seems to be double in *Bothremys*. In both taxa it is distinct and prominent in contrast to *Pelusios* in which it is quite small.

Posteromedially, the fossa orbitalis is confluent with a block of matrix that represents the space between the processus inferior parietalis (medially) and the processus trochlearis ptery-

goidei (laterally). Although the region is present in cryptodires, the development of a lateral bony margin is a distinctive pleurodire feature. In living pleurodires portions of the *M. pterygoideus* occupy this region (Schumacher, 1973). Some of the bone making up the processus inferior parietalis persist and are particularly visible as spicules of bone in the ventral view (fig. 2). Posteriorly, this portion of the endocast is confluent with the matrix extending out of the foramen nervi trigemini. The foramen palatinum posterius lies behind the posterior orbital wall as in other pleurodires and is prominent in the endocast.

The dorsal portion of the fossa nasalis is buried in matrix and the roof of most of the cavum cranii is not preserved. The outline of the

sulcus olfactorius and the cerebral expansions can be seen, however. The cerebral expansions are relatively well developed, as in AMNH 2521, in contrast to FMNH PR 247. The cartilaginous extension of the supraoccipital is partly preserved and the cavum cranii roof is preserved posterior to the extension or "rider." The general position of the foramen magnum is apparent but its margins are not preserved nor are indications of the exoccipitals or condyle.

The lateral walls of the cavum cranii show the positions of the foramen nervi trigemini, foramen cavernosum, and (on the right side) the fossa acustico facialis and hiatus acusticus. Ventrally, most of the features of the basicranium are preserved. A latex peel (fig. 3) was made of this area to facilitate comparison with living pelomedusids (figs. 4-7) and the other specimens of *Bothremys* (Gaffney and Zangerl, 1968, fig. 19). The following description is primarily of the latex peel, for ease of comparison with Recent specimens, and with references to the natural endocast in parentheses. The most lateral troughs are the spaces defined by the processus trochlearis pterygoidei laterally, and the processus inferior parietalis - crista pterygoidea medially. The wall formed by the processus inferior parietalis and crista pterygoidei is relatively much thicker in *Bothremys* than in any living pelomedusid. Seemingly, this is related to the apparent crushing adaptations seen in the palate. Medial to this wall is a trough (ridge), the sulcus cavernosus. Some small foramina are visible in the sulcus but I think they are only nutritive in nature. Posteriorly, the sulcus is confluent with the foramen nervi trigemini rather than separated from it by a ridge as in living pelomedusids. The endocast stops roughly at the position of the foramen cavernosum. The rostrum basisphenoidale in *Bothremys* is long and narrow as in *Podocnemis* rather than short and blunt as in *Pelusios*. The outline of the sella turcica of *Bothremys* also resembles *Podocnemis* more than it does *Pelusios*. At present I cannot hypothesize the significance of these similarities but it appears that the rostrum basisphenoidale character

is a synapomorphy between *Bothremys* and *Podocnemis*, as an elongated rostrum does not occur in chelids or living pelomedusids.

As stated by Gaffney and Zangerl (1968), *Bothremys* lacks the hypertrophied canalis caroticus internus of *Podocnemis* and the Princeton endocast substantiates this statement. The foramen anterius canalis carotici interni open into the sella turcica beneath the dorsum sellae overhang, and may be seen in the endocast figures (fig. 1) more clearly than in the latex peel. A paired structure, the processus clinoideus, usually occurs on each side of the dorsum sellae but each one appears to be broken off in the Princeton specimen. The broken base of each processus clinoideus reveals a groove, the foramen nervi abducentis.

Albrecht (1976) and Gaffney (1975) have pointed out the utility of basicranial structures in elucidating pleurodire phylogeny. I hope that this description of the basicranium in one of the oldest known pleurodires will eventually aid phylogenetic work on this group.

RECONSTRUCTION OF THE PALATE IN *BOTHREMYS*

The type skull of *Bothremys cooki* (AMNH 2521) was figured in Gaffney and Zangerl (1968) but this specimen is lacking many of the posterior regions of the skull. Another specimen (FMNH PR 247) identified as *Bothremys barberi* by Gaffney and Zangerl has the otic regions preserved. A reconstruction (fig. 8) of *Bothremys* is presented here using information from both skulls. The AMNH skull is indicated in the figure by the shaded area, whereas the outline and sutures of the FMNH skull are added. The FMNH skull, besides being identified as a separate species, is also about twice the size of the AMNH specimen, so the reconstruction must be considered with these qualifications.

The identification of bones and structures can be readily obtained from the figures in Gaffney and Zangerl (1968) and are not repeated here.

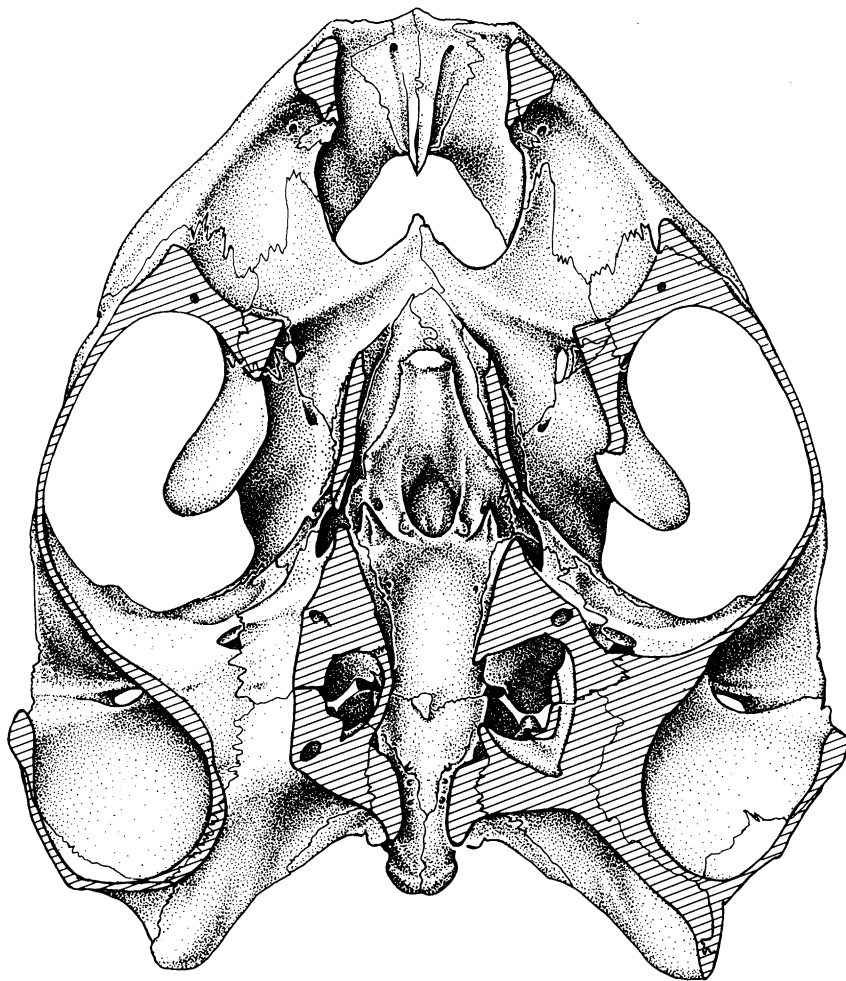


FIG. 4. *Pelusios* sp. (AMNH[H] 10062, 52 mm. in length), Recent, Zaire. Dorsal view of horizontally sectioned skull. Hatching indicates cut surfaces.

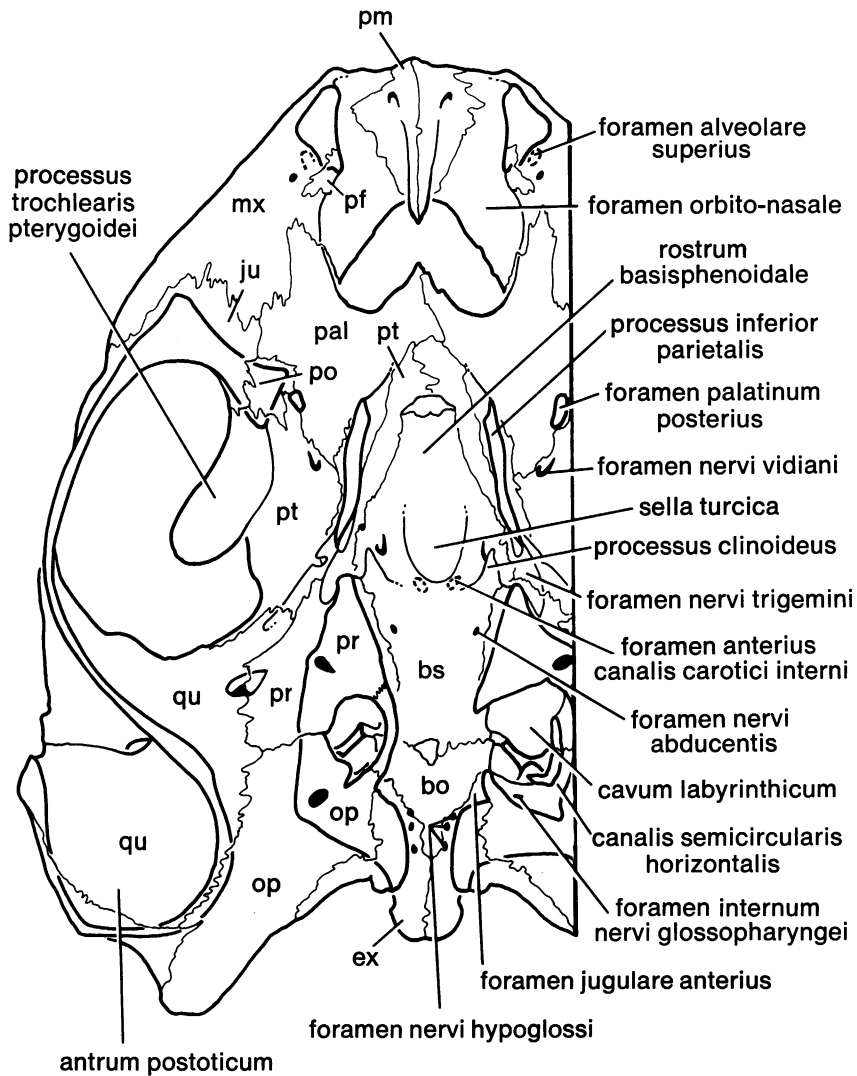


FIG. 5. Key to figure 4.

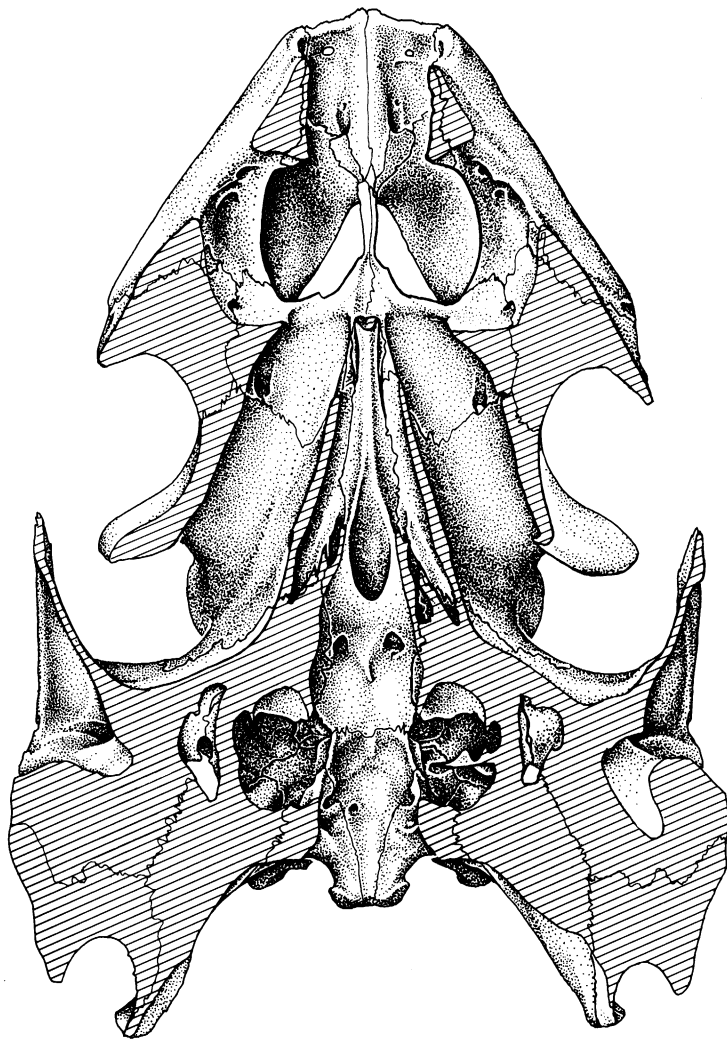


FIG. 6. *Podocnemis expansa* (AMNH[H] 97124, 126 mm. in length), Recent, Bolivia. Dorsal view of horizontally sectioned skull. Hatching indicates cut surfaces.

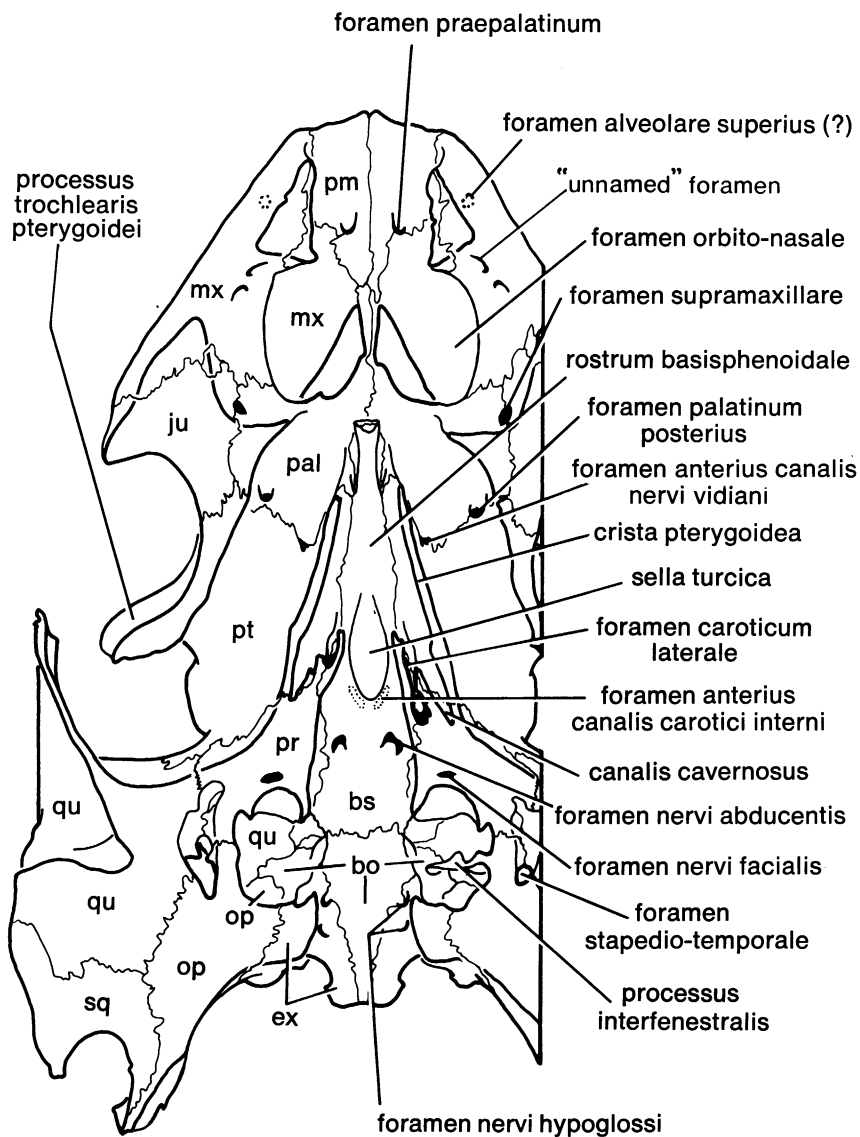


FIG. 7. Key to figure 6.

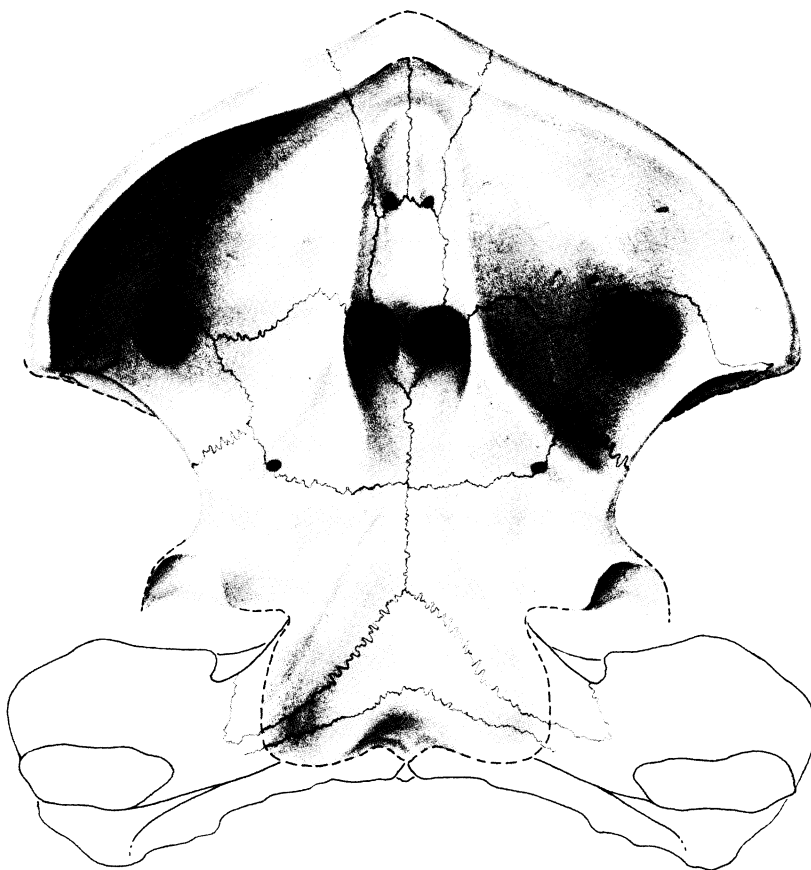


FIG. 8. *Bothremys cooki* (AMNH 2521, skull length as preserved 69 mm.), Late Cretaceous (?), Hornerstown Formation, New Jersey. Palatal views with posterior restored from *Bothremys barberi* (FMNH PR 247), Late Cretaceous, Selma Formation, Alabama. Limits of processus trochlearis pterygoidei hypothetical.

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