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Cranial Morphology of the Baenid Turtles

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ABSTRACT

The family Baenidae is a group of extinct cryptodiran turtles known from more than a dozen well-preserved skulls from the Cretaceous, Paleocene, and Eocene. The baenid skull is characterized by significant generalized features in the skull roof and basicranium that are consistent with their hypothesized relationship as the sister group to the

living cryptodires, the Eucryptodira. The arterial canals of the skull are preserved in enough specimens to conclude that baenids had an arterial pattern characterized by a large and well-developed canalis stapedio-temporalis and a small but persistent canalis caroticus lateralis.

INTRODUCTION

The Baenidae is an important group of Cretaceous to Eocene non-marine turtles that have been considered as the sister group to all living cryptodires (Gaffney, 1975). While information on the systematics of this group has been available (Gaffney, 1972), a more complete study of the cranial morphology has been lacking. The present paper is intended to fill this void, particularly in the description of basicranial regions. A number of important figures of baenid crania have already appeared in Gaffney (1972, 1979b) and Archibald and Hutchison (1979). To eliminate repetition, I assume that the reader has these three papers available and is familiar with the contents of Gaffney (1979b).

PREVIOUS WORK

Gaffney (1972) provided the primary basis for current systematic work on baenids and

included diagnoses, synonymies, lists of specimens, skull and shell figures, and a review of the literature up to 1972. Descriptions were lacking and the present work is an effort to fill this lack for skulls. The relationships of taxa within the Baenidae were also discussed in Gaffney (1972), but in 1975 I dealt with the relationships of baenids to other turtles and the question of the "Amphichelydia," a supposedly ancestral turtle group that was characterized by baenids. Evans and Kemp (1975, 1976) described two skulls, *Mesochelys* and *Dorsetochelys*, and discussed relationships of these taxa to baenids and other turtles. Gaffney (1979a) described *Glyptops* and presented an analysis of relationships involving this genus, *Mesochelys*, *Dorsetochelys*, and baenids. The most important work on taxa within the Baenidae since 1972 is Archibald and Hutchison's paper (1979) on *Palatobaena* which described

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new, well-preserved material of this heretofore poorly known form and proposed a new scheme of its phylogenetic relationships. An important but as yet unpublished work is Archibald (MS), which describes the first skull-shell associations of *Eubaena* and *Stygiochelys* and proposes a baenid phylogeny based on shell features. Gaffney's cranial morphology review (1979b) has whole skull drawings of all the baenid genera (but does not repeat the important palatal stereophotographs from Gaffney, 1972), as well as a series of figures showing more detailed, internal features of baenid skulls. Lower jaws of baenids are dealt with to some extent in Gaffney (1979b) and Archibald and Hutchison (1979) but a detailed study is in preparation. Also under way is a new phylogenetic analysis and classification of the family.

ACKNOWLEDGMENTS

I am grateful to the curators and collection managers of the institutions from which I have borrowed baenid specimens over the years (a complete institutional list is in Gaffney, 1972). Dr. David Archibald, Yale University, very kindly allowed me to use information from his unpublished Ph.D. thesis and with the aid of Dr. Howard Hutchison, University of California, Berkeley, made specimens available to me that I otherwise would not have been aware of.

Ms. Lorraine Meeker drew figures 6 and 13, Mr. Chester Tarka took the photographs in figures 3 and 4, Mrs. Jennifer Emry drew figures 1 and 2, the American Museum Graphic Arts Department did figure 8. I very much appreciate the assistance of these people. I took the remaining photographs.

ABBREVIATIONS

AMNH, American Museum of Natural History
CCM, Carter County Museum
MCZ, Museum of Comparative Zoology, Harvard University
PU, Princeton University
UCMP, University of California at Berkeley, Museum of Paleontology
USNM, National Museum of Natural History
UW, University of Wyoming
YPM, Yale Peabody Museum

MORPHOLOGY

NASAL: Nasals are characteristically retained in baenids and lost in most eucryptodires. In baenids the nasals retain the primitive (for amniotes) posterior contact with the frontals, whereas in those eucryptodires with nasals the prefrontals meet medially and posterior to the nasals.

In most baenids (Gaffney, 1979b, fig. 1) the nasal contacts the maxilla laterally, the frontal posteriorly, and the other nasal medially. The anterior edge is free and forms the dorsal margin of the apertura narium externa. Within the baenids, *Hayemys* is unique in having exceptionally large nasals that are laterally and posteriorly expanded in comparison to other baenid nasals. In *Baena* the nasals are either lost or fused to the frontals. Sutures differentiating nasals are not visible in any of the numerous specimens (including presumed juveniles) of *Baena*, suggesting loss rather than fusion. The anterior margin of the apertura narium externa in *Baena* is thickened with an anterior facing concavity, similar to one seen in *Palatobaena bairdi*. *Chisternon* is unique among baenids in lacking a nasal-maxilla contact, this being caused by an anterior extension of the frontal.

In *Palatobaena* the preorbital part of the skull is highly modified from the general baenid pattern by extreme shortening anteroposteriorly and widening laterally. Nasals are known only in one specimen of *Palatobaena bairdi* (CCM 77-11, figured in Gaffney, 1979b; Archibald and Hutchison, 1979) where they are seen to be widely separated from each other by the extension of the frontals into the apertura narium externa. Although the limits of the nasals are not entirely clear in this specimen they do show a dorsolateral and medial contact with the frontal and ventral contact with the maxilla. The rim of the entire apertura narium externa is recessed in *Palatobaena bairdi*, whereas in *P. gaffneyi* (Archibald and Hutchison, 1979) only the ventral margin is recessed. There are no signs of nasals in this last specimen.

The ventral morphology of the nasal area (Gaffney, 1979b, fig. 3) has paired troughs concave ventrally and separated by a median ridge along which the two nasals meet. The

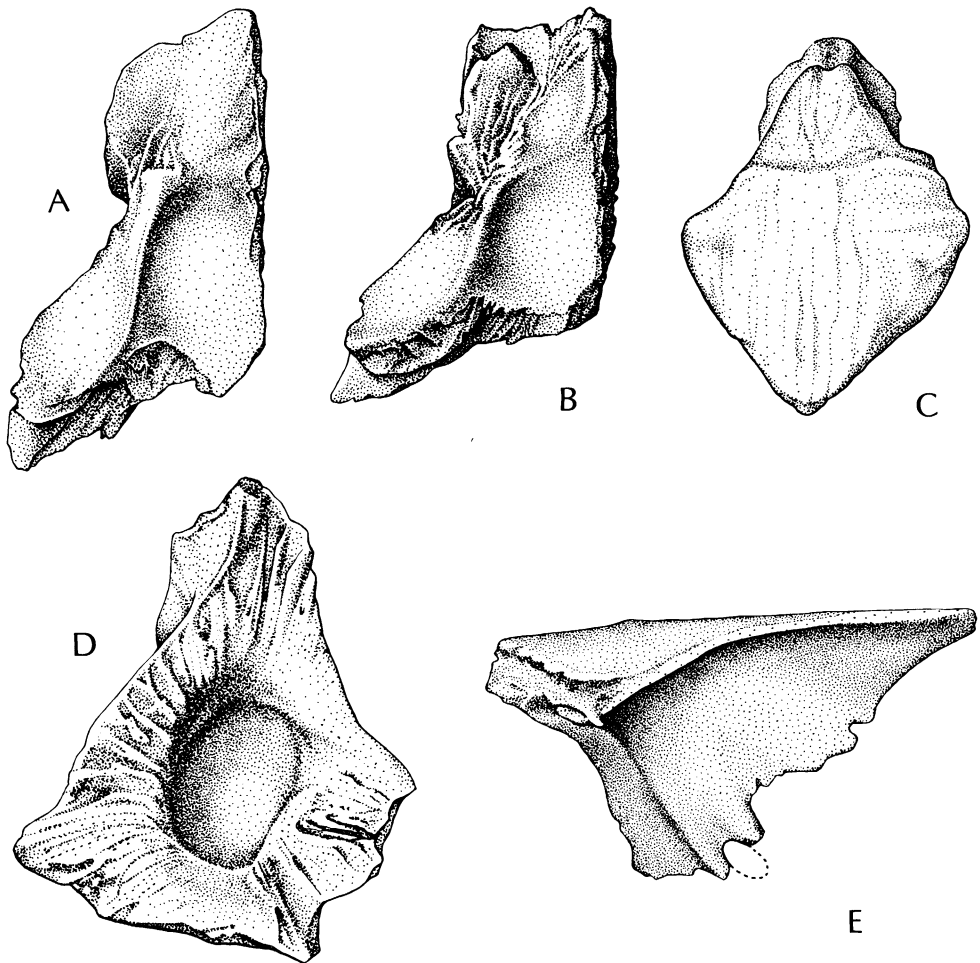


FIG. 1. Disarticulated baenid bones from the Late Cretaceous, Hell Creek Formation, Bug Creek Anthills, McCone County, Montana. A. Ventral view of right frontal (MCZ 3551), a presumed juvenile, 9.6 mm. in length. B. Ventral view of right frontal (MCZ 3554), 22.7 mm. in length. C. Dorsal view of supraoccipital (MCZ 3558), 12.8 mm. in length. D. Ventral view of squamosal (AMNH 8558), 16.6 mm. in length. E. Lateral view of left parietal (MCZ 3526), presumed juvenile, 21.4 mm. in length, anterior is to left, dashed line indicates foramen nervi trigemini.

troughs housed the olfactory bulbs and are an anterior extension of the sulcus olfactorius.

PREFRONTAL: The prefrontal in turtles usually consists of two plates, a horizontal dorsal one and a vertical ventral one. As emphasized by Evans and Kemp (1976) and discussed by Gaffney (1979a) baenids are generally characterized (see Gaffney, 1979b, fig. 1) by a reduction of the dorsal plate in comparison with what is hypothesized as the

primitive chelonian condition, whereas eucryptodires typically have conspicuously large dorsal prefrontal plates that meet in the midline. *Hayemys*, however, does have a moderately large dorsal plate that probably approximates the primitive condition, but at present I interpret this as an autapomorphy for *Hayemys*.

The ventral process of the prefrontal is a broadly curved plate oriented in a roughly vertical plane, extending anterolaterally, and

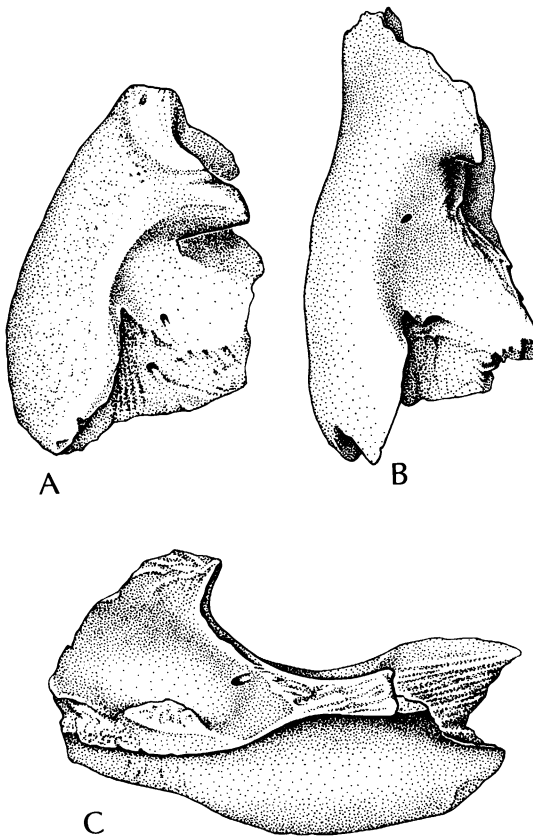


FIG. 2. A. Dorsal view of left maxilla, *Palatobaena bairdi* (AMNH 8550). B. Dorsal view of left maxilla, *Eubaena cephalica* (MCZ 3519). C. Medial view of right maxilla (MCZ 3519, reversed), *Eubaena cephalica*. All are Late Cretaceous, Hell Creek Formation, Bug Creek Anthills, McCone County, Montana.

forming the posterolateral wall of the fossa nasalis and the anterior wall of the fossa orbitalis. The lateral edge of the bone is a long curved contact with the maxilla which continues to the floor of the fossa orbitalis where the prefrontal contacts the palatine, just lateral to the foramen orbito-nasale. The palatine contact continues medial to the foramen orbito-nasale for a short distance until it contacts the vomer. The latter forms the ventromedial limit of the prefrontal. Dorsal to the vomer the prefrontal has a curved edge which defines the fissura ethmoidalis. The fissura

is a mere vertical slit in *Glyptops*, whereas in the Baenidae it is wider but not so wide as in the Testudinidae.

In my earlier paper on baenids I figured *Trinitichelys* as lacking a dorsal exposure of the prefrontal (Gaffney, 1972, fig. 2). Since then I have been convinced by other students of this specimen that a small prefrontal lappet is present and have modified the new reconstruction accordingly (Gaffney, 1979b, fig. 164).

Hay (1904, 1905, 1908) reported the presence of a lacrimal in *Eubaena*, *Baena*, and *Chisternon*. Hay's "lacrimal" is here identified as the prefrontal in view of the following features held in common between the prefrontal of baenids and living cryptodires:

- (1) articulates with the vomer ventromedially
- (2) borders the foramen orbito-nasale ventrolaterally
- (3) meets the palatine between the two above structures
- (4) has a long suture with the maxilla along the anterior border of the fossa orbitalis
- (5) forms the anterior wall of the fossa orbitalis

The only significant distinction between them seems to be the small or absent dorsal plate in baenids. Hay's identification of this element as the lacrimal required further identifications to be consistent with that determination. A reevaluation suggests the following changes in Hay's identification:

nasal	nasal
prefrontal	frontal
lacrimal	prefrontal
frontal plus fused parietal	parietal

Hay's identifications were repeated in Romer's figure of *Chisternon* (1956, fig. 50).

FRONTAL: The frontal of baenids (Gaffney, 1979b, figs. 152-164) is essentially a flat bone situated between the midline and the orbit. Its contacts are usually as follows: anteriorly with the nasal, anterolaterally with the maxilla, anteroventrolaterally with the prefrontal, posterolaterally with the postorbital, poste-

riorly with the parietal, and medially with the other frontal. The dorsal surface is broadly convex. The ventral surface (fig. 1; Gaffney, 1979b, fig. 3; Archibald and Hutchison, 1979, fig. 6) usually has a parasagittal ridge defining a medial sulcus olfactorius. A low transverse ridge generally separates the fossa nasalis from more posterior regions of the cavum cranii.

The frontal broadly enters the orbital margin in most baenids, the exceptions being *Palatobaena*, *Hayemys*, and *Eubaena*. In *Hayemys* the large dorsal plate of the prefrontal forms the principal border for the orbit, and the prefrontal reaches posteriorly to contact the postorbital. The type specimen of *Eubaena cephalica* (YPM 1785) has no frontal exposure in the orbit but this is due to closer approximation of the prefrontal and the anterodorsal margin of the postorbital rather than a large prefrontal. Another specimen (AMNH 4948) of *Eubaena* has a limited frontal exposure in the orbit. In *Palatobaena* the frontal has reduced orbital exposure due to approximation of maxilla and postorbital.

The posterolateral margin of the frontal tends to be extended posteriorly to form "wings" that are particularly apparent in *Eubaena* and *Chisternon*. *Hayemys* is unique among baenids in having a frontal that is proportionally larger than the parietal. The well-developed frontal-maxilla contact seen in most baenids and absent in *Glyptops*, *Mesochelys*, and *Trinitichelys* is hypothesized here as a derived character for the group containing *Plesiobaena*, *Palatobaena*, *Eubaena*, *Stygiuchelys*, *Baena*, and *Chisternon*.

PARIETAL: The parietal (fig. 1) consists essentially of two plates of bone, a horizontal one and a vertical one, meeting at right angles; both are well developed in baenids. The horizontal plate is dorsal and roofs the fossa temporalis and cavum cranii in the posterior region of the skull. It usually contacts the frontal anteriorly, postorbital laterally, and sometimes the squamosal posterolaterally. The posterior limits of the horizontal plate are usually involved in emargination of some sort. On the ventral surface of the horizontal plate lateral to the cavum cranii is a pit for

the attachment of the *M. pterygoideus* muscle. This pit is usually behind the orbit and is demarcated by a ridge anteriorly and a ridge posteriorly (see Gaffney, 1979b, fig. 3; Archibald and Hutchison, 1979, fig. 6). The muscle mass itself parallels and is attached to the lateral surface of the processus inferior parietalis.

The vertical wall is situated parasagittally with the cavum cranii medial to it and the fossa temporalis lateral to it. The anterior part, the processus inferior parietalis (Gaffney, 1979b, fig. 13) is usually longer and articulates with the crista pterygoides of the pterygoid. The foramen nervi trigemini perforates the posteroventral border of the processus. The parietal articulates with the prootic laterally behind the foramen nervi trigemini. The posterior margins of both plates of the parietal contact the supraoccipital ventromedially.

Within the Baenidae, there is some variation in size of the skull roof portion of the parietal. *Hayemys* has a parietal that is relatively smaller than in other baenids and this is interpreted as an autapomorphy due to the absence of this feature in comparable outgroups. *Hayemys* has the posterior temporal emargination, however, developed to the extent seen in *Eubaena*, *Stygiuchelys*, *Plesiobaena*, and *Palatobaena*. *Baena* and *Chisternon* have relatively large parietals that are more extensive posterolaterally than in other baenid genera. This feature is hypothesized as a synapomorphy for *Baena* and *Chisternon*.

The posterior temporal emargination shows an interesting taxonomic distribution within the baenids (Gaffney, 1979b, figs. 152–164). The primitive condition for baenids and cryptodires appears to be that seen in *Dorsetochelys* and *Mesochelys* in which the emargination is relatively shallow (but present in contrast to *Proganochelys*) and bordered only by the parietal and squamosal. The latter bones have a well-developed contact. *Trinitichelys* is advanced in comparison by having a more extensive emargination and a minute to absent parietal-squamosal contact. The Late Cretaceous baenids have the most extensive emargination characterized by no pa-



FIG. 3. Occipital view of *Trinitichelys hiatti* (MCZ 4070, 55 mm. in length), Early Cretaceous, Trinity Sand, Hardee Montague County, Texas. See Gaffney (1979b, fig. 157) for a labeled diagram of the occiput in *Eubaena*.

rietal-squamosal contact and a broad exposure of the postorbital. *Baena* and *Chisternon*, however, do have a parietal-squamosal contact which is hypothesized here as a synapomorphy for these two taxa. The parietal in *Baena* and *Chisternon* is larger and more extensive laterally than in the Cretaceous forms. In *Baena* the emargination is most limited and a well-developed parietal-squamosal contact is present. *Chisternon* has a limited parietal-squamosal contact but a more extensive emargination. *Baena*, however, has a distinctive degree of variation in its temporal emargination. This has been described in Gaffney (1972, figs. 26, 28, 29) and more thoroughly discussed in Archibald (MS).

The emargination in *Palatobaena* is generally comparable with that in the other Late Cretaceous and Paleocene baenids, but it is distinctly less developed than in such forms as *Eubaena*. The parietal in *Palatobaena gaffneyi* has the dorsal plate developed laterally much as in *Plesiobaena putorius* but in *Palatobaena bairdi* (CCM 77-11) the dorsal plate is more extensive and its posterior portion is aligned parasagittally, producing a distinctive parallel sided emargination.

JUGAL: The jugal (Gaffney, 1979b, figs.

152-164) consists of a flat, vertical cheek plate and a medially projecting ramus forming the posteroventral wall of the fossa orbitalis (fig. 6). The cheek portion of the jugal is roughly rectangular in outline and is bounded dorsally by the postorbital, posteriorly by the quadratojugal, ventrally by the cheek emargination, and anteriorly by the maxilla. The jugal is exposed along the orbital opening between the postorbital and maxilla in all baenids except *Eubaena*. In *Eubaena* the jugal is excluded from the orbital rim by a wide meeting of the maxilla and postorbital. The medial ramus of the jugal is usually exposed along the floor of the orbit and in the anterior wall of the fossa temporalis interior. Ventrally and anteromedially the jugal contacts the maxilla, dorsally it contacts the postorbital, and medially there is a short pterygoid contact. This pterygoid contact is at the anterior limits of the processus pterygoideus externus.

QUADRATOJUGAL: The quadratojugal (Gaffney, 1979b, figs. 152-164) is a flat, triangular bone forming part of the lateral wall of the fossa temporalis. It is sutured anteriorly to the jugal, dorsally to the postorbital, and posterodorsally to the squamosal. The posterior margin of the quadratojugal con-



FIG. 4. Occipital view of *Stygiochelys estesi* (AMNH 2601, 63 mm. in length), Late Cretaceous, Hell Creek Formation, Glendive, Montana. See Gaffney (1979b, fig. 157) for a labeled diagram of the occiput in *Eubaena*.

tacts the quadrate along the anterior edge of the cavum tympani forming a broadly curved suture. There is a posteroventral process covering some of the lateral surface of the processus articularis of the quadrate. The ventral margin of the bone is part of a limited ventral emargination of the cheek, which reaches its greatest extent in *Plesiobaena*.

There is not much variation of the quadratojugal among the baenid genera, but *Trinitichelys* has a somewhat longer quadratojugal and *Baena* and *Chisternon* lack the dorsal projection seen in other baenid genera. This latter feature is interpreted as a synapomorphy uniting *Baena* and *Chisternon*.

SQUAMOSAL: The squamosal of baenids is quite similar to that of other casichelydians, it is a roughly cone-shaped bone forming a cap above and somewhat behind the quadrate (Gaffney, 1979b, figs. 152–164). The interior of the squamosal (fig. 1) forms part of a cavity, the antrum postoticum, which is continuous with the cavum tympani. The squamosal is exposed along the lateral margin of the posterior temporal emargination. The posteroventral external surface usually has a trough for the attachment of the M. depressor mandibulae.

Anteriorly, the squamosal is bounded by the quadratojugal laterally and the postor-

bital medially in all baenids except *Chisternon*. In *Chisternon* the anterior margin is formed completely by the postorbital with no certain quadratojugal contact. Although most of the medial edge in *Chisternon* borders the temporal emargination, the parietal makes a short contact anteromedially, whereas *Baena* has a long medial suture with the parietal. The antrum postoticum is well developed in all baenids. Posteromedially the opisthotic covers the margin of the squamosal. The squamosal sends a process ventrally that covers the external surface of the quadrate posterior to the incisura columellae auris.

POSTORBITAL: As in other Casichelydia, the postorbital is a flat, rectangular bone forming part of the dorsolateral wall of the fossa temporalis. It forms the posterior border of the eye, contacts the frontal anteromedially, and borders the parietal medially. The postorbital contacts the maxilla anteroventrally in *Eubaena* but is prevented from doing so in other baenids by the jugal, which reaches the orbital margin. The posterolateral contact is a long suture with the quadratojugal and is always longer than the contact with the jugal. Posteriorly the postorbital reaches the squamosal, and in *Chisternon* the postorbital may also contact the quadrate at the dorsal edge of the cavum tympani.

In *Trinitichelys*, *Baena*, and *Chisternon* the

postorbital does not reach the temporal emargination, but in the remaining baenids the posteromedial edge of the bone forms the anterolateral border of the temporal emargination.

PREMAXILLA: The premaxilla of baenids (Gaffney, 1972, figs. 47–58; 1979b, figs. 152–164) does not have any systematic differences from other Casichelydia. The bone is roughly triangular in ventral view and forms the ventral margin of the apertura narium externa. The premaxilla is bordered by the other premaxilla medially and by the maxilla posterolaterally. The premaxilla forms the anteriormost portion of the labial ridge along its ventral edge and is continuous with the labial ridge of the maxilla. The anterodorsal edge of the premaxilla forms the ventral margin of the apertura narium externa. The dorsal surface of the premaxilla is the main element in the floor of the fossa nasalis. *Palatobaena* (Archibald and Hutchison, 1979) is characterized by a sulcus or recession of the premaxillae and maxillae along the margin of the apertura narium externa. Posteriorly the vomer contacts the premaxilla near the midline. The lingual ridge usually becomes reduced before reaching the premaxilla but some remnant of it usually continues nearly to the midline. The lingual ridges of the right and left sides are separated in the midline by a trough which is formed mostly by the premaxillae and the vomer. This trough in *Eubaena* is narrow in the region of the vomer and widens anteriorly in the region of the premaxillae. In the other baenids the trough is wide posteriorly and becomes indistinct anteriorly. The foramen praepalatinum usually lies in, or near, the suture between the premaxilla and the vomer.

MAXILLA: As in other turtles, the maxilla of baenids (figs. 2, 6; Gaffney, 1972, figs. 47–58; 1979b, figs. 152–164) consists of two regions, one vertical and one horizontal, joined at right angles. The vertical portion makes up much of the facial region and is limited anteroventrally by the premaxilla. A vertical process of the maxilla slopes posterodorsally from the premaxilla-maxilla suture to form the lateral edge of the apertura narium externa, and usually contacts the na-

sal anteriorly and the frontal posteriorly on the outer surface of the skull. The process in *Trinitichelys* seems to contact only the nasal, but in all other baenids this dorsal process contacts the frontal. In *Chisternon* an anterior extension of the frontal prevents a nasal-maxilla contact, whereas the apparent nasal-frontal fusion (or loss of the nasal) is characteristic of *Baena*.

Posterolateral to the dorsal process the lower rim of the orbit forms the dorsal margin of the vertical plate of the maxilla. In *Baena*, *Chisternon*, *Palatobaena*, *Stygiochelys*, *Plesiobaena*, *Trinitichelys*, and probably *Hayemys* (but this area is obscured by damage), the vertical plate of the maxilla ends posteriorly in a suture with the jugal which begins in the posteroventral corner of the orbit. In *Eubaena* the maxilla sends up a dorsally directed process behind the eye which articulates with the jugal posteriorly and also with the postorbital dorsally. The postorbital contact is lacking in the other taxa.

On the internal side of the maxilla (figs. 2, 6), in the posterior part of the wall of the fossa nasalis, is the foramen alveolare superius, which leads into the canalis alveolaris superior. In *Eubaena* the foramen is large and lies at the head of a groove leading posteriorly into the foramen orbito-nasale. In *Chisternon*, *Stygiochelys*, and *Palatobaena* the foramen alveolare superius lies near the edge of the foramen orbito-nasale rather than farther away from the edge of the foramen orbito-nasale as in *Eubaena*. *Plesiobaena* has the foramen alveolare superius in about the same position as it is in *Chisternon* but no groove seems to be present. None of the numerous specimens of *Baena* have this area sufficiently well preserved to determine the presence or absence of the foramen alveolare superius. *Trinitichelys* and *Hayemys* also yield no information about this area.

The horizontal plate of the maxilla makes up the main part of the triturating surface, forms some of the floor of the fossa orbitalis, and contacts buttresses of the palate. *Trinitichelys* and *Plesiobaena* have quite similar triturating surfaces. In these forms the labial ridge is straight and a deep channel is present just medial to the ridge. The lingual ridge

borders this channel anteriorly but quickly turns medially to form a posteromedial expansion of the triturating surface. The area where this expansion begins to take place is raised higher than the rest of the surface. *Trinitichelys* seems to differ from *Plesioabaena* in having a narrower triturating surface posteriorly and in not having the labial ridge as high but the specimen is not well preserved and further precision is not possible.

Eubaena has a labial ridge which is not straight as in most of the other forms, but has a bend anteriorly which results in the anterior portion of the ridge being oriented in a more anteroposterior direction than the rest of the ridge. The lingual ridge is so low as to be nothing more than the medial edge of the triturating surface. This surface begins quite close to the labial ridge just behind the premaxilla-maxilla suture and curves medially and then laterally to form a gently concave broad plate. *Stygiochelys* has the same form of the triturating surface as in *Eubaena* but the former differs in having the two maxillae set farther apart and at greater angles to one another thereby increasing the width of the snout region. *Stygiochelys* lacks the incipient secondary palate developed in *Eubaena*.

Palatobaena (Archibald and Hutchison, 1979) has the broadest and most distinctive triturating surfaces in the Baenidae. The labial ridge is lower than in the other baenids and the lingual ridge is virtually absent. The bone is thicker than in other forms but the overall morphologic relationships are the same as in *Stygiochelys*.

The maxilla in *Hayemys* has a very narrow dorsal process that is constricted between the expanded nasal and prefrontal. The limits of the vertical plate are difficult to determine but the maxilla probably did not reach the postorbital in life and its present contact with the postorbital is probably due to crushing. The triturating surface is obscured by the labial edge being folded over it during preservation (Gaffney, 1972, fig. 7).

VOMER: The vomer of baenids (Gaffney, 1972, figs. 47–58; 1979b, figs. 152–164) is a single, median element separating each aper-

tura narium interna, with the anterior and posterior portions expanded to articulate with the other palatal bones. The anterior expansion lies at a lower level than the posterior one and forms a roof for the ventrally concave trough developed between the triturating surfaces. The area exposed dorsally in the fossa nasalis (fig. 6) is convex upward and is wider in area than the ventral surface of this expansion. The anteriormost contact of the vomer is with the premaxillae. There is a lateral contact of the anterior expansion of the vomer with the maxilla that ends at the anterior edge of the apertura narium interna.

Between the apertura narium internae the vomer is rodlike and narrow, except in *Palatobaena* where it is broad. Above and behind the apertura the posterior portion is expanded into a flat plate of bone. This plate is above the level of the anterior expansion and carries a groove in its midline, the sulcus vomeri, which forms the ventral limits of the fissura ethmoidalis. At its posteriormost limits the posterior plate contacts the pterygoid in a short, transverse suture. For most of its length the posterior plate has a lateral contact with the palatine. Anterodorsolaterally, on either side of the sulcus vomeri, the posterior plate contacts the prefrontal.

Eubaena differs from the other baenids in having a narrower anterior vomerine expansion. *Baena* and *Chisternon* differ from *Plesioabaena* and *Eubaena* in having a vomer that extends posteriorly beyond the palatines, whereas the palatines extend farther posteriorly in the last two genera. In *Stygiochelys* and possibly *Palatobaena gaffneyi* (Archibald and Hutchison, 1979, figs. 5, 7) there is a minute vomer-basisphenoid contact. In *Hayemys* the anterior half of the vomer is badly damaged but the posterior half has an expansion that is wider than in other baenid genera.

PALATINE: The palatine of baenids (Gaffney, 1972, figs. 47–58; 1979b, figs. 152–164) does not differ significantly from other cryptodires. In baenids it is a platelike element forming the portion of the palate anterior to the pterygoid between the vomer and the maxilla and having a straight anteroposterior

suture with the vomer medially. Anteromedially it contacts the descending process of the prefrontal, and lateral to this contact the palatine forms the posterior half of the foramen orbito-nasale. The palatine has a long lateral suture with the maxilla. Ventrally this suture borders the triturating surface and extends posteriorly to the transverse suture with the pterygoid. In so doing, the foramen palatinum posterius is formed at least in part by the palatine. The palatine forms most of the dorsolateral wall of the internal nares ventrally, and part of the floor of the fossa orbitalis dorsally.

There is some difference in palatine morphology among baenids but it is not extensive. Most of the variation concerns width of the area between lingual ridges, that is, the choanal channel. The form of the choanal channels, paired grooves just posterior to the aperturæ narium internæ formed by the vomer and palatines, ranges from narrow (e.g., *Eubaena*) to broad (e.g., *Chisternon*). In *Chisternon* and *Stygiochelys* the foramen palatinum posterius is formed entirely by the palatines, and in the remaining baenid genera the pterygoid forms some of the margin of the foramen.

The anteroventral limits of the processus inferior parietalis come in contact with the posterior edge of the palatine in *Eubaena*, *Palatobaena*, and *Chisternon*. The condition is indeterminate in the other forms.

QUADRATE: The quadrate is a large C-shaped element lying at the posterolateral corner of the skull (Gaffney, 1979b, figs. 152–164). Its dorsal surface floors the lateral part of the fossa temporalis. Anterolaterally the quadrate has a broad vertical contact with the prootic (Gaffney, 1979b, fig. 13). At the anterior end of this contact they form the processus trochlearis oticum, the suture running down the middle of the process. Ventrally there is a vertical suture with the pterygoid. The quadrate forms much of the lateral floor and roof of the cavum acustico-jugulare (Gaffney, 1979b, fig. 94). In the anterior wall of the cavum, the canalis caver-nosus extends anteromedially and the aditus canalis stapedio-temporalis connects to the well-developed canalis stapedio-temporale.

The canalis stapedio-temporale trends dorsally where it reaches the fossa temporalis.

The lateral surface of the quadrate is the cavum tympani, a nearly circular cavity opening laterally. The incisura columellæ auris is a relatively narrow slit enclosing both the stapes and the eustachian tube in baenids. Above the incisura, the antrum postoticum extends posterodorsally into the squamosal. The suture with the squamosal is roughly oval in dorsal view. Ventrolaterally the quadrate sends down a short processus articularis which bears the condylus mandibularis, the lower jaw articulation.

The quadrate of baenids is typically cryptocodiran in its basicranial relations, that is, it has a broad sutural contact with the posterior part of the pterygoid rather than having a medial process that reaches the basisphenoid. The incisura columellæ auris is elongate, enclosing the stapes and eustachian tube, a feature common to nearly all pleurodires (but not *Bothremys* and *Taphrosphys*, see Gaffney and Zangerl, 1968; Gaffney, 1979b). Although many eucryptodires (cheloniods, for example) do not restrict the incisura, when they do, the restriction usually separates stapes and eustachian tube. Meiolaniids are the only eucryptodires that have an incisura columellæ auris enclosing stapes and eustachian tube in the baenid manner. At present, the baenid condition can be interpreted either as a derived character for baenids or as a primitive feature of Casichelydia retained independently in baenids and meiolaniids. I prefer the former interpretation.

PTERYGOID: A disarticulated right pterygoid (fig. 5; Gaffney, 1979b, fig. 24; also in Gaffney, 1975, fig. 21) from the Hell Creek Formation of Montana has been particularly useful and forms the basis for much of the following description. This bone (and MCZ 3566, a small pterygoid fragment that preserves the crista pterygoidea particularly well) is impossible to identify to genus, but *Palatobaena* can be ruled out on the basis of the pterygoideus muscle scar (see below) and the closest similarity is with *Eubaena* and *Plesiobaena* which occur in the Hell Creek Formation.

The crista pterygoidea rises sharply on the

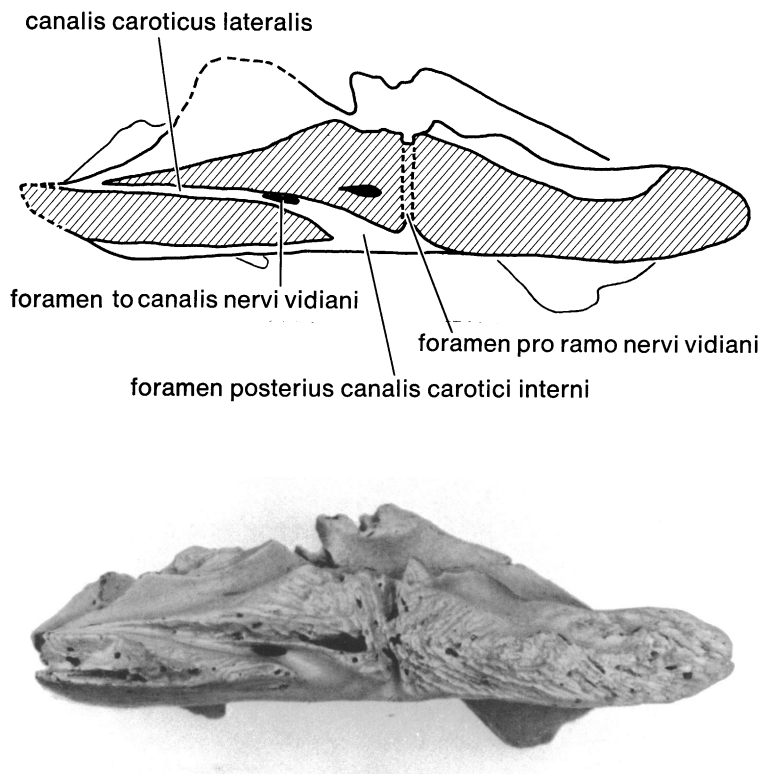


FIG. 5. Medial view of a baenid right pteryoid (MCZ 3563), Late Cretaceous, Hell Creek Formation, Bug Creek Anthills, McCone County, Montana. Compare with Gaffney (1979b, fig. 24) for a dorsal view of this specimen. Crista pterygoidea restored from MCZ 3566.

anterior part of the dorsal surface of the pterygoid then drops to form the lower border of the foramen nervi trigemini. Behind the foramen the crista again rises, forming the posterior margin of the foramen nervi trigemini then gradually tapers down to the level of the rest of the pterygoid at its posterior end. The contacts of the crista pterygoidea are of some interest systematically but due to the unfortunately common habit of sutural fusion in baenids, information on this area is scarce. The available material, however, does fit a single pattern. In nearly all other cryptodires (except *Dermochelys*) the epipterygoid ossifies as a distinct element and is sutured to the crista pterygoidea, but in baenids there is no separate epipterygoid ossification (Gaffney, 1979b, fig. 13). I have (*ibid.*, p. 106) interpreted this condition as due to fusion of pa-

rietal and epipterygoid but there is no compelling reason to accept this. The processus inferior parietalis extends ventrally and lodges in a groove on top of the crista pterygoidea. At the posteroventral end of this process is a space, the fossa cartilaginis epipterygoidea, which held the epipterygoid cartilage. Directly behind the foramen nervi trigemini is the laterally expanded portion of the crista pterygoidea which bears the prootic (best seen in *Baena arenosa*, AMNH 5952, and AMNH 5977). Posterior to this contact the lateral margin of the pterygoid is a broad surface sutured to the quadrate.

On the medial side of the crista pterygoidea lies the sulcus cavernosus. At the anterior point of prootic contact the pterygoid forms the foramen cavernosum and posterior to this structure the sulcus is called the canalis

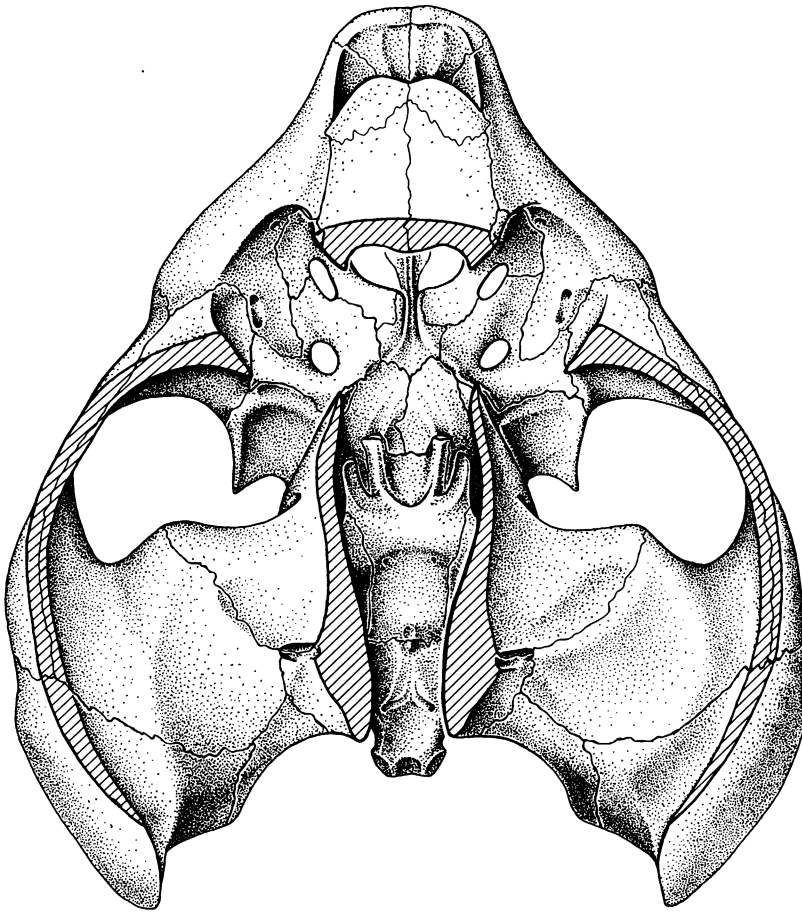


FIG. 6. Dorsal view of horizontally sectioned skull of *Eubaena cephalica* (composite, based primarily on AMNH 4948 but with additions from YPM 1785). From Gaffney (1979b).

cavernosus because it is roofed over by the prootic. The canalis cavernosus ends posteriorly on the floor of the cavum acustico-jugulare. Just medial to this point lies a circular concavity which represents the bony floor of the cavum labyrinthicum, the surface of which was probably covered with cartilage as in living turtles. The distinction between cavum labyrinthicum and cavum acustico-jugulare is not obvious in the disarticulated pterygoid (MCZ 3563) as the elements of the bony inner ear (prootic and opisthotic) are not fused to the pterygoid as in most other specimens. The posteromedial area of the pterygoid is a sutural contact with the basi-

occipital ventrally and the exoccipital dorsally.

In medial view MCZ 3563 and AMNH 8555 furnish important information about the arterial circulation (figs. 8, 9). The foramen posterior canalis carotici interni has its lateral wall formed by the pterygoid. The canalis caroticus internus curves medially into the basisphenoid very soon after entering the skull. The canalis caroticus lateralis, however, forms a groove continuous with the canalis caroticus internus and this groove extends anteriorly on the medial edge of the pterygoid until it exits at the foramen caroticum laterale. This structure is best seen in

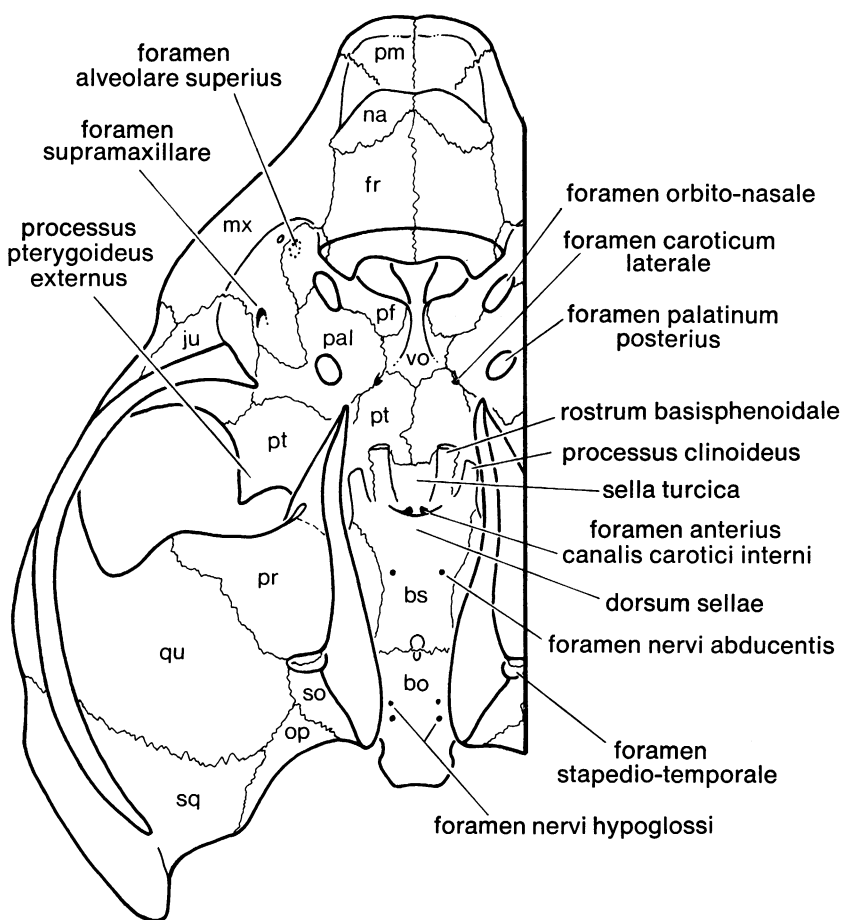


FIG. 6. Continued.

the following specimens: *Eubaena cephalica* (AMNH 4948, fig. 7), *Plesiobaena putorius* (PU 14984), and *Baena arenosa* (AMNH 5977, YPM 3941, USNM 211143). In these specimens the foramen caroticum laterale is formed between the pterygoid and palatine bones (as would be expected from an examination of MCZ 3563) and is just medial to the anteriormost part of the processus inferior parietalis-crista pterygoidea suture. At the posterior end of the foramen posterior canalis carotici interni lies the ventral opening of the foramen pro ramo nervi vidiani. This foramen extends dorsally to enter the sulcus cavernosus.

Although information on the vidian canals in baenids is limited, some conclusions can be drawn from the disarticulated pterygoid (MCZ 3563), a disarticulated skull of *Chisternon* (YPM 3930), and a fragmentary skull of *Baena* (YPM 3941). In the last specimen (YPM 3941) the canalis nervi vidiani has been prepared out revealing that it extends posteriorly from the foramen palatinum posterius through the palatine and into the pterygoid to the vicinity of the foramen pro ramo nervi vidiani. There may be a communication between the foramen and the canalis nervi vidiani but the material is not well enough preserved to confirm this and I have

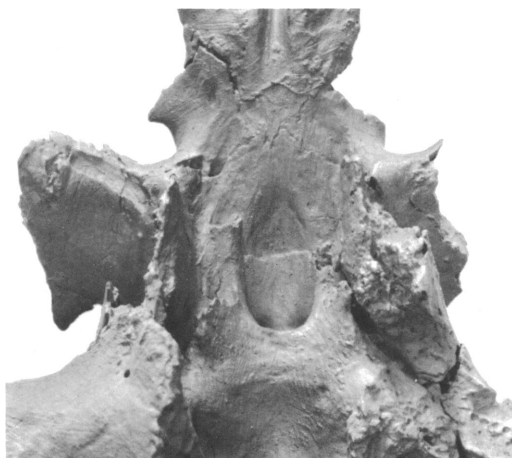


FIG. 7. Dorsal view of basicranium, *Eubaena cephalica* (AMNH 4948), Late Cretaceous, Hell Creek Formation, Bug Creek Anthills, McCone County, Montana. See figure 6 for identification of structures.

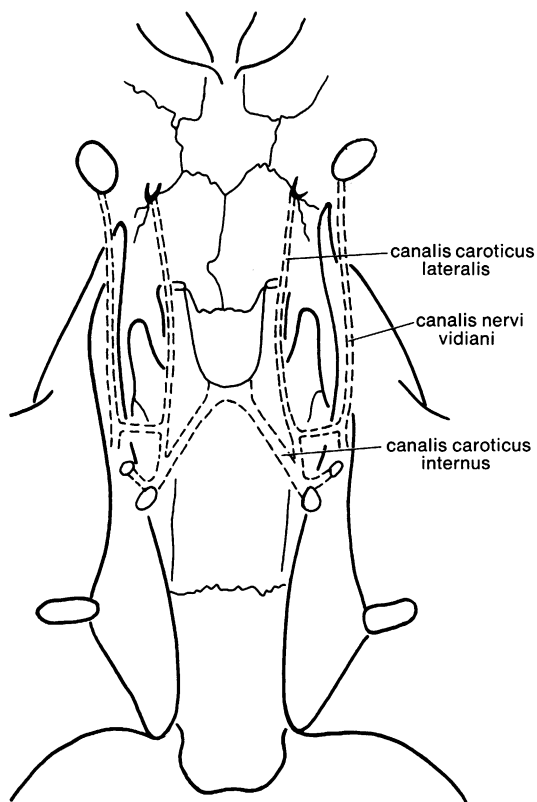


FIG. 8. Diagrammatic restoration of basicranial canals in a baenid. See figures 5 and 6 for further identification of structures, see text for discussion.

left out a connection in the restoration (fig. 8). There is a connection between the canalis nervi vidiani and the canalis caroticus lateralis in all three specimens as well as in AMNH 8555 but this is a short, lateral canal anterior to the foramen pro ramo nervi vidiani. The vidian canal and its relations then are quite similar to those described by Albrecht (1967) for *Chrysemys* (see also Gaffney, 1979b, fig. 28). This pattern could be primitive for Casichelydia or Cryptodira but at present our information on the taxonomic distribution of vidian canal types is too limited to be particularly useful.

SUPRAOCCIPITAL: The supraoccipital is exposed on the skull roof of baenids at the posteriormost extension of the midline in those specimens with determinable sutures. A free supraoccipital (fig. 1) from an unidentified Hell Creek baenid shows the flat plate on top of the crista supraoccipitalis that is part of the skull roof.

The crista supraoccipitalis (Gaffney, 1979b, figs. 94, 155, 157) forms a major attachment area for fibers of the M. adductor mandibulae externus, portio profundus of Schumacher (1973). The crista is high in *Eubaena*, *Plesiobaena*, and especially in PU 16838, an

unidentified Paleocene baenid, but very low in *Chisternon*. *Baena* and *Trinitichelys* seem to be intermediate. The crista supraoccipitalis is short in all baenids when compared with most casichelydians but quite comparable to chelids and *Proganochelys*, and is presumably the primitive condition. The crista is shortest in *Chisternon*, where it does not extend beyond the condylus occipitalis. In other forms it does extend beyond the condylus but not beyond the squamosal.

Anterodorsally the supraoccipital is overlapped by the paired parietals, anterolaterally it meets the prootic, posterolaterally it meets the opisthotic, and posteriorly it has a short suture with the exoccipital. The surface of the supraoccipital which is exposed in the cavum

carnii is trough-shaped and is continuous with the dorsal border of the foramen magnum. The hiatus acusticus (Gaffney, 1979b, fig. 71) is ossified in baenids but the area is often broken due to the thinness of the bone or fused with the adjacent element so that the ventral suture of the supraoccipital is not known. The foramen aquaducti vestibuli can be seen just above and behind the prootic contact.

The supraoccipital contribution to the cavum labyrinthicum is best seen in *Baena* (AMNH 5977) and an unidentified Paleocene baenid (PU 16838). The supraoccipital forms the dorsal portion of the cavum labyrinthicum and it is surrounded by a circular suture, the anterior half of it being a contact with the prootic and the posterior half being a contact with the opisthotic. The supraoccipital forms the posterodorsal portion of the canalis semicircularis anterior and the anterodorsal portion of the canalis semicircularis posterior. The recessus labyrinthicus supraoccipitalis takes up most of the area formed by the supraoccipital in the cavum labyrinthicum.

The dorsal plate of the supraoccipitalis varies from narrow to wide within *Palatobaena* (Archibald and Hutchison, 1979) with most baenids having a relatively narrow plate. This variation does not seem to have systematic significance.

EXOCCIPITAL: The exoccipital of baenids (Gaffney, 1979b, figs. 71, 94, 155, 157) does not differ significantly from that bone in other casichelydians. It is a paired element lying lateral to the foramen magnum, and can be described in two parts, a dorsolateral process and a ventral process. The dorsolateral portion contacts the supraoccipital dorsally but most of its lateral face is sutured to the opisthotic. The medial surface forms most of the lateral wall of the foramen magnum and part of the cavum cranii. Inside the cavum cranii the exoccipital forms the posterior border of the foramen jugulare anterius as well as the medial wall of the canal between the foramen jugulare anterius and the foramen jugulare posterius. The foramen jugulare posterius is incomplete laterally and the canal connecting the two foramina is also incomplete as it approaches the posterior foramen.

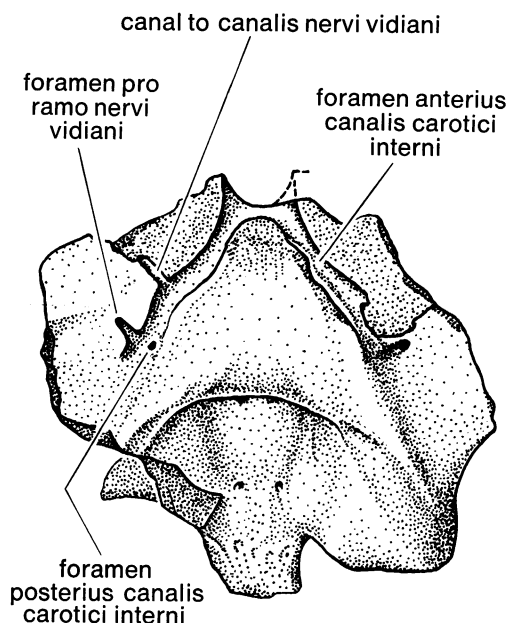


FIG. 9. Ventral view of baenid basicranial fragment (AMNH 8555) partially eroded and showing canalis caroticus internus and associated structures. Late Cretaceous, Hell Creek Formation, Bug Creek Anthills, McCone County, Montana. 27.5 mm. in length.

The exoccipital is sutured to the basisphenoid by a dorsolateral contact that runs the length of both bones. The exoccipitals do not meet

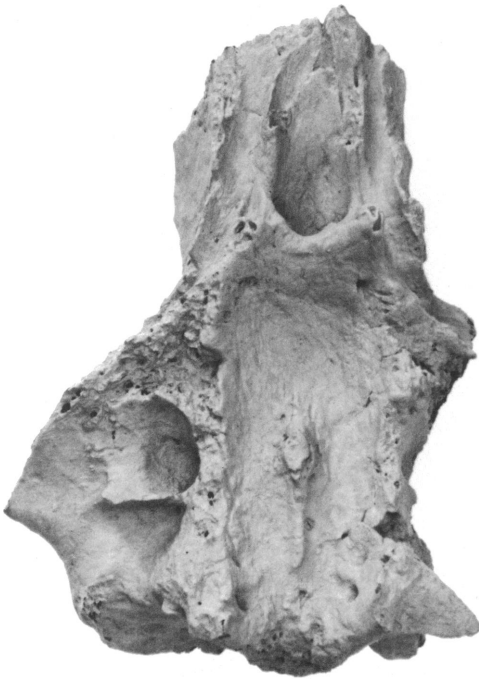


FIG. 10. Dorsal view of baenid basicranial fragment (MCZ 3532), same data as figure 9. 21.8 mm. in length.

at any point thus exposing the basioccipital dorsally in the foramen magnum and on the condylus occipitalis. The two paired foramina nervi hypoglossi penetrate the exoccipital between the foramen magnum and the path of the vena cerebialis posterior, the foramen jugulare anterius.

The condylus occipitalis is made up of both exoccipitals and the basioccipital. Ventromedially the exoccipital-basioccipital contact extends posteriorly to the well-developed tuberculum basioccipitale which includes a dorsolateral contribution from the exoccipital. Laterally, the lower portion of the exoccipital contacts the pterygoid above the basioccipital contact.

The variation of the exoccipital within the Baenidae is not easily observable since most specimens have the sutures fused in this region, however, there seem to be only two differences of interest. The tubercular con-

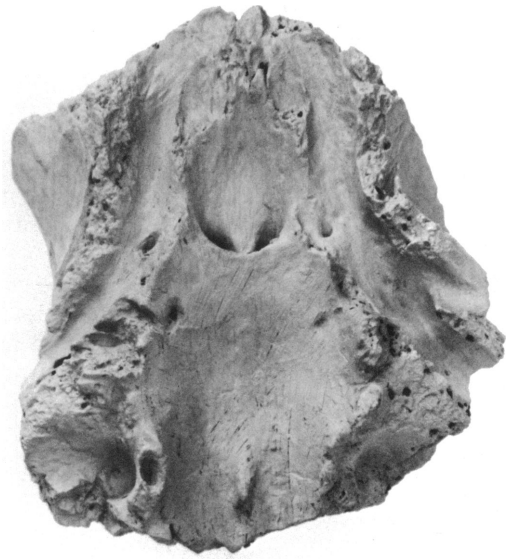


FIG. 11. Dorsal view of baenid basicranial fragment (AMNH 8554), same data as figure 9. 28.8 mm. in length.

tribution in *Plesiobaena* tends to be smaller than in other forms and *Chisternon* has a distinctly larger foramen magnum in comparison with other baenids.

BASIOCCIPITAL: The basioccipital (Gaffney, 1979b, figs. 71, 94, 155, 157) is a small, median element at the posteroventral end of the basicranium. It forms most of the condylus occipitalis. A disarticulated basioccipital (MCZ 3543) from a juvenile Hell Creek baenid shows the form of the element. The anterior contact is a transverse suture with the basisphenoid. Two winglike processes extend posteroventrally and are joined to the exoccipitals dorsally. Anterolaterally these processes meet the pterygoids which extend posteriorly where both elements form the paired tubercula basioccipitales. The basioccipital is excluded from the fenestra postotica. The condylus occipitalis has small dorsolateral contributions from the exoccipitals but otherwise is formed from the basioccipital in all specimens that are determinable in this area. The condylus occipitalis has a pit at its posterior end for the ligamentum apicis



FIG. 12. Dorsal view of basicranial fragment of *Palatobaena bairdi* (UCMP 114539), Late Cretaceous, Hell Creek Formation, V-75180, Garfield County, Montana. 35.8 mm. in length.

dentis. The posterior face is usually set off by a distinct neck. The central surface of the basioccipital is broadly concave and has two small foramina in its center.

PROOTIC: As in most turtles, the prootic of baenids (Gaffney, 1979b, figs. 13, 71) is a small cuboid element forming the anterior portion of the bony inner ear, part of the lateral wall of the cavum cranii, and the anteromedial portion of the fossa temporalis. Anterodorsally the prootic meets the parietal, posterodorsally it meets the supraoccipital. The lateral contact with the quadrate is interrupted by the canalis stapedio-temporalis. There is a small posterior suture with the opisthotic in the roof of the cavum labyrinthicum. Ventrally the prootic meets the pterygoid and medially it comes in contact with the basisphenoid. The anterior edge of the

prootic forms the posterior margin of the foramen nervi trigemini. Just lateral to this foramen the prootic roofs the canalis cavernosus. About midway along the canal the foramen pro ramo nervi vidiani emerges from the prootic to enter the canalis cavernosus.

The portion of the prootic contributing to the wall of the cavum cranii has a prominent fossa acustico-facialis. Two foramina nervi acustici and one foramen nervi facialis penetrate this fossa. Most of the prootic is formed around the cavum labyrinthicum, specifically, the recessus labyrinthicus prooticus. Anterodorsally the prootic forms the canalis semicircularis horizontalis. There is very little variation in the morphology of this element within baenids.

OPISTHOTIC: The opisthotic of baenids (Gaffney, 1979b, figs. 71, 94, 155, 157) does not differ significantly from that bone in other cryptodires. It is a triangular element forming the posterior part of the bony inner ear, much of the roof of the cavum acustico-jugulare, and the posterior part of the fossa temporalis. Anteroventrally it meets the prootic, but anterodorsally this contact may be interrupted by a contact of the supraoccipital and quadrate. Laterally there is a broad contact with the quadrate and medially the opisthotic is sutured to the supraoccipital. Ventromedially the exoccipital dorsal process reaches the opisthotic.

A prominent processus interfenestralis extends ventrally from the opisthotic to divide the cavum acustico-jugulare into two regions. Posterior to the processus interfenestralis is the processus scallae tympani, whereas lateral to the processus is the cavum acustico-jugulare proper. The foramen externum nervi glossopharyngei pierces the process dorsally. The anterior edge of the process forms the posterior margin of the fenestra ovalis. Anteromedial to the processus interfenestralis is the recessus labyrinthicus opisthoticus. The canalis semicircularis posterior extends into the supraoccipital from this chamber.

BASISPHEOID: As in other Casichelydia, the basisphenoid of baenids (figs. 6–12; Gaffney, 1979b, figs. 71, 152–164) is triangular in ventral view with the pterygoids meeting

anteriorly ventral to the rostrum basisphenoidale (except in *Stygiochelys*). The general morphology of the baenid basisphenoid is common to other casichelydian groups and there seem to be only two features of systematic significance: first, the position of the foramen posterius canalis carotici interni, and second, the degree of ossification of the rostrum basisphenoidale. Except for these features, discussed below, the baenid basisphenoid agrees with other casichelydians and differs from *Proganochelys* in the following characters:

1. Broad sutural attachment of pterygoid to lateral and anterior margins of basisphenoid.
2. Absence of basiptyergoid processes and basicranial articulation.
3. Flattened, platelike ventral surface of basisphenoid.
4. Foramen posterius canalis carotici interni not formed or formed only in part by basisphenoid.

The formation of the foramen posterius canalis carotici interni midway along the length of the basisphenoid-ptyergoid suture is typical in baenids and glyptopsids. This character has been interpreted both as derived (Gaffney, 1972, 1975) and as primitive (Evans and Kemp, 1975, 1976; Gaffney, 1979a) for the Cryptodira. The implications of these contradictory hypotheses are discussed more fully in Gaffney (1979a). Within the Baenidae the size and positions of the canalis caroticus internus and the foramen posterius canalis carotici interni do not offer systematically useful variations. The diameter of the foramen and canalis are roughly one-half the diameter of the canalis stapedio-temporalis which is the common pattern in chelonoids but in testudinoids the canalis caroticus internus is usually less than half the diameter of the canalis stapedio-temporalis and in trionychoids the canalis caroticus internus is usually larger than the canalis stapedio-temporalis. The baenid pattern is probably primitive for cryptodires but I did not see that any phylogenetic significance can be obtained from this.

The entire canalis caroticus internus can be seen in AMNH 8555 (fig. 9), a Hell Creek baenid braincase that has been naturally eroded, revealing this structure. The canalis is seen to curve medially anterior to the foramen posterius canalis carotici interni then it straightens somewhat before ending at the foramen anterius canalis carotici interni. Evidence for an arterial anastomosis is present below the dorsum sellae in the smooth, convex connection between the two foramina anterius canalis carotici interni. All other baenid basisphenoids that I have seen simply have the foramina end directly into the concave sella turcica without a smoothly curved wall connecting them. An anastomosis could still have been present in these.

The ossification of the trabeculae into a median rostrum basisphenoidale is incomplete in baenids. The condition is as yet unknown in *Proganochelys* but pleurodires have the rostrum well ossified into a distinctive median bar anterior to the sella turcica. Eucryptodires, however, cannot be characterized so easily, well-developed rostra being common in chelonoids and testudinoids, unossified rostra being typical of trionychoids. Enough exceptions are present to give this character low resolving power.

The degree of overhang of the dorsum sellae over the sella turcica in baenids is typically that seen in *Eubaena cephalica*, AMNH 4948 (figs. 6–7). In this specimen the foramina anterius canalis carotici interni are just barely hidden by the dorsum sellae. In some baenids (e.g., *Palatobaena bairdi*, UCMP 114539, fig. 12) the foramina are placed more anteriorly in the sella turcica while in others (e.g., unidentified Hell Creek baenid, MCZ 3532, fig. 10; and *Plesiobaena putorius*, PU 14984) the foramina are more posterior. As far as I can determine at present, only *Chisternon* has a unique morphology in this region. In the only two specimens showing this area, YPM 3939 and AMNH 5904, the posterior wall of the dorsum sellae has paired anteriorly facing concavities just below the processus clinoides with a median concavity between them.

ENDOCRANIAL CAST

One of the *Plesiobaena antiqua* skulls (UCMP 49759; Gaffney, 1979b, fig. 162) has a matrix-free endocranium and a cast of the endocranium has been made by dripping liquid latex into the various skull openings and rotating the skull while the latex dried. The figures of the resulting endocast (fig. 13) are partially reconstructed by using the skull as well as the endocast. The reader is referred to Edinger (1934), Zangerl (1960), Gaffney and Zangerl (1968), and Gaffney (1977) for other descriptions of turtle endocasts.

The roof of the fossa nasalis consists of two ventrally open concavities housing the olfactory region in life. Nasal bones occur in *Plesiobaena* but the nasal-frontal suture is not distinct. The hypothesized position of this suture indicates that the major portion of the fossa nasalis roof is formed by the nasals and that the frontal has an anterior extension along the midline. The dorsal portion of the fissura ethmoidalis is marked by a constriction (seen in dorsal view) in the endocast between the area of the fossa nasalis and the sulcus ethmoidalis. This region of the fissura was broad and not constricted as in some emydids. The sulcus ethmoidalis is a ventrally open trough extending from the fossa nasalis to the region of the cerebral hemisphere. The sulcus is broad and without high boundary ridges in *Plesiobaena* in contrast to some turtles that have a narrow, well-defined sulcus ethmoidalis. The endocast shows the dorsal and posterior margins of the foramen interorbitale, a large open space in the ethmoid region.

The dorsal region of the endocast is dominated by relatively well-developed convexities that presumably housed the cerebral hemisphere in life. The cerebral convexities are relatively well developed in comparison to the *Bothremys barberi* endocast figured by Gaffney and Zangerl (1968, fig. 21E) but they are smaller than in *Bothremys cooki* (*ibid.*, fig. 21C). Between the swellings is the cartilaginous "rider" mentioned by Zangerl (1960, p. 29) that in life contained the cartilaginous anterior end of the supraoccipital.

In *Plesiobaena* the "rider" is W-shaped rather than knoblike as in *Bothremys*.

The brain flexure referred to by Edinger (1929) and Zangerl (1960) as occurring between the olfactory lobes and the cerebrum is not as marked in *Plesiobaena* and *Bothremys* as it is in sea turtles. However, an endocast made from an unidentified baenid braincase (PU 16838, discussed in Gaffney, 1972, p. 269) shows a flexure very similar in degree to that seen in cheloniids. This braincase and cheloniids both are characterized by a deep crista supraoccipitalis and it is likely that this feature of the endocast is more related to jaw muscle architecture than brain architecture. The hindbrain region on the endocast is marked by a slight median rise, absent in most turtle endocasts I have seen. This raised area would appear to be posterior to the optic lobes and lie in the cerebellum region. Whether or not the endocast morphology reflects brain morphology in this instance is an open question.

The side walls of the braincase show the cranial nerve exits and vessel positions. Beginning anteriorly the foramen nervi trigemini and the foramen cavernosum (the anterior opening of the canalis cavernosus) extend laterally near the ventral part of the endocast. The distinct swelling formed at the junction of these two extensions presumably housed the trigeminal ganglion as in recent turtles. Posterior to the trigeminal area is the fossa acustico-facialis, a low convexity (concavity in the bone) containing three foramina. The anteriormost foramen is the foramen nervi facialis, whereas the posterior two are presumably the foramina nervi acustici.

The hiatus acusticus is the wall that lies between the cavum labyrinthicum and the cavum acustico-jugulare. In most turtles this wall is cartilaginous but in baenids it is characteristically ossified (Gaffney, 1979b, fig. 71). The *Plesiobaena* endocast shows this typical baenid condition and the region of the hiatus is marked by a shallow concavity. Although the occurrence is too poorly known to generalize, it would appear that most turtles have a branch of the acoustic (VIII) nerve that traverses the hiatus (Gaffney, 1979b).

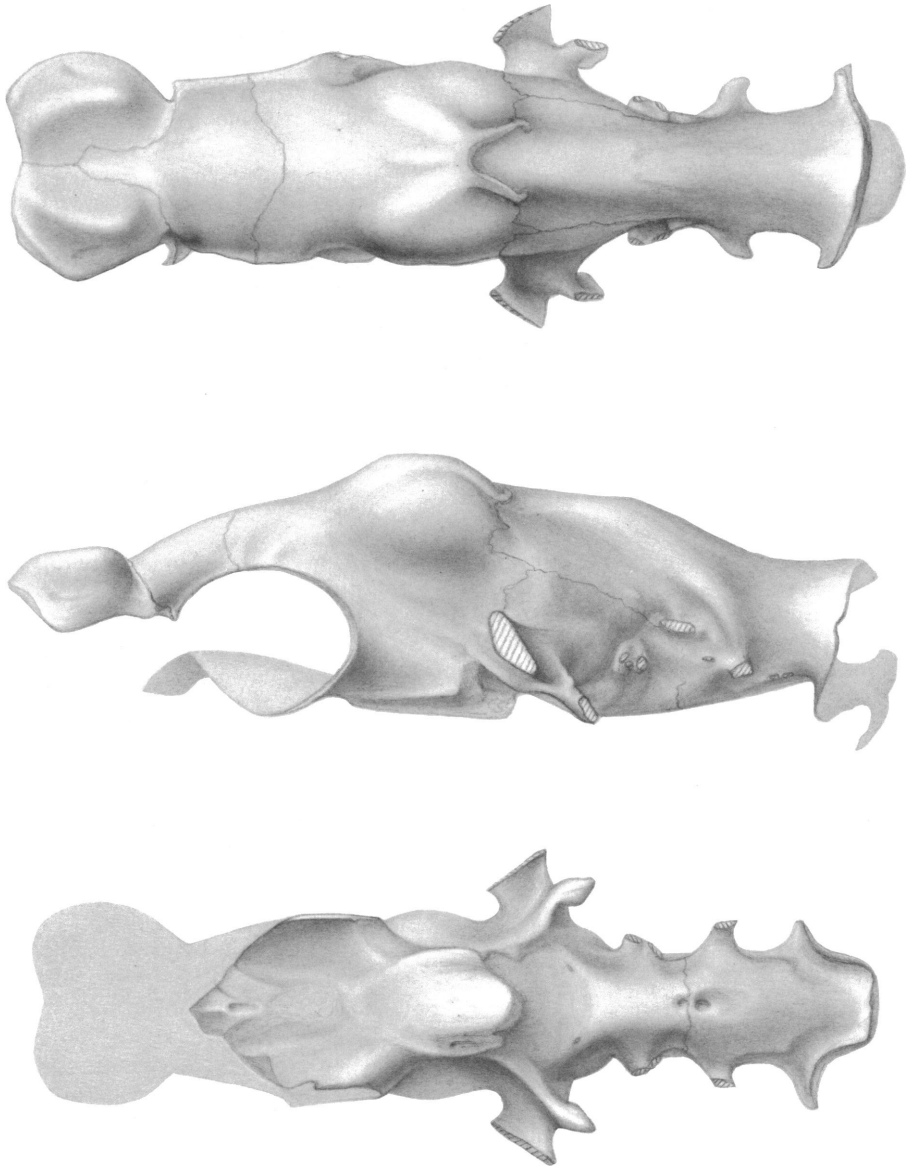


FIG. 13. Endocranial cast of *Plesiobaena antiqua* (UCMP 49759), Late Cretaceous, Lance Formation, Lusk (V-5620), Wyoming. Midline skull length 63 mm.

Such a branch seems to be present in the skull of *Baena arenosa* (YPM 3933) but not in the *Plesiobaena* endocast. It is possible, however, that the foramen was obstructed on both sides and did not affect the endocast.

Posterodorsal to the fossa acustico-facialis

is a well-defined foramen aquaducti vestibuli. This foramen is often on the margin or within the cartilage of the hiatus acusticus in other turtles and may be used as a landmark for this region. Two sutures are visible extending from the foramen, an anterior one separating

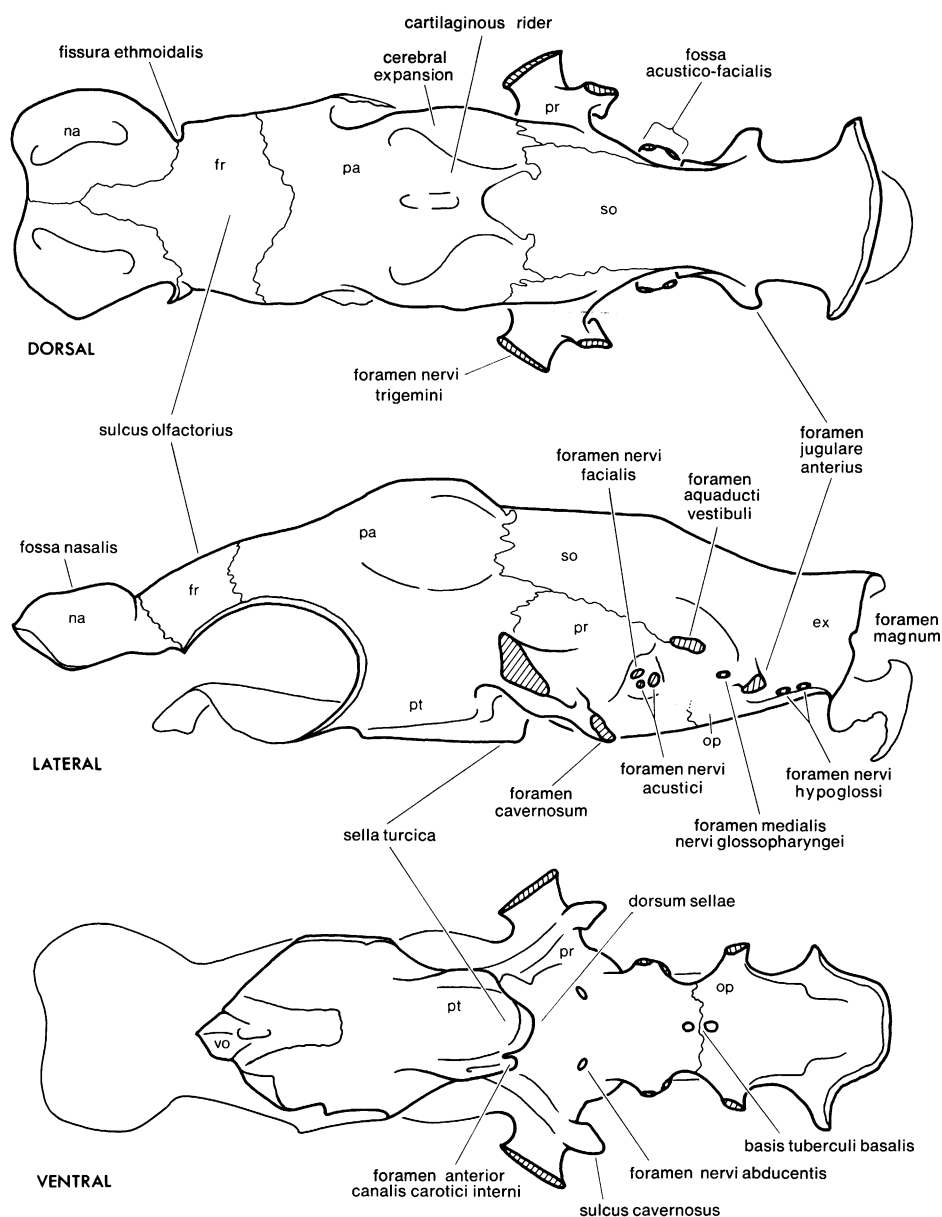


FIG. 13. Continued.

the supraoccipital and the prootic and a ventral one separating the prootic from the opisthotic. Within the opisthotic region lies the foramen medialis nervi glossopharyngei and the foramen jugulare anterius. That opening is usually formed by the opisthotic anteriorly

and the exoccipital posteriorly but sutures separating these elements are lacking. Two foramina nervi hypoglossi are present posterior to the foramen jugulare anterius, as in nearly all turtles. The endocranium of *Plesio-*
baena was extended to the margins of the

foramen magnum and around the dorsal and posterior surface of the condylus occipitalis.

The ventral surface of the endocast is imperfect anteriorly, so the complexities of palatal morphology were ignored. The sella turcica seems to be obscured along its left edge by matrix but the right foramen arterius canalis carotici interni can be identified. The dorsum sellae and the dorsal surface of the basisphenoid are readily identifiable. The sulcus cavernosus and foramen cavernosum are apparent in ventral and lateral views. The right sulcus and foramen are obscured by matrix and the figures are restored from the left side.

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