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**Revision of the Genus *Palatobaena*
(Testudines, Baenidae), with the Description
of a New Species**

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Abstract

Recovery of three new partial skulls of *Palatobaena bairdi* from the latest Cretaceous (Lancian) and middle Paleocene (Torrejonian) of Montana and from the early Paleocene of Colorado adds greatly to the knowledge of this peculiar baenid turtle. Although there is some variation in the temporal emargination, *Palatobaena* primitively appears to have had a deep emargination as seen in eubaenines. The wide triturating surfaces align *Palatobaena* with the Eubaeninae. A skull of a new species found in the Wasatch Formation (Wasatchian), Wyoming, belongs to this genus and extends the record of *Palatobaena* into the early Eocene. The new species has a relatively shorter skull and its jaw mechanics represents a further specialization from the morphology seen in *P. bairdi*.

FMNH Field Museum of Natural History
PU Princeton University
UCM University of Colorado Museum
UCMP University of California Museum
of Paleontology
YPM Yale Peabody Museum of Natural
History

Introduction

Recently, Gaffney (1972a) revised the turtles of the family Baenidae. Unlike earlier workers he relied heavily on cranial morphology and convincingly showed (1972a and 1975) that baenids are true cryptodires. A major portion of his revision (1972a) was devoted to the description of new genera and species. The most unusual new taxon described was *Palatobaena bairdi*. Due to this species' unusual features and also the fragmentary nature of the material, Gaffney (1972a, p. 304-308) was unable to determine the relationships of this taxon.

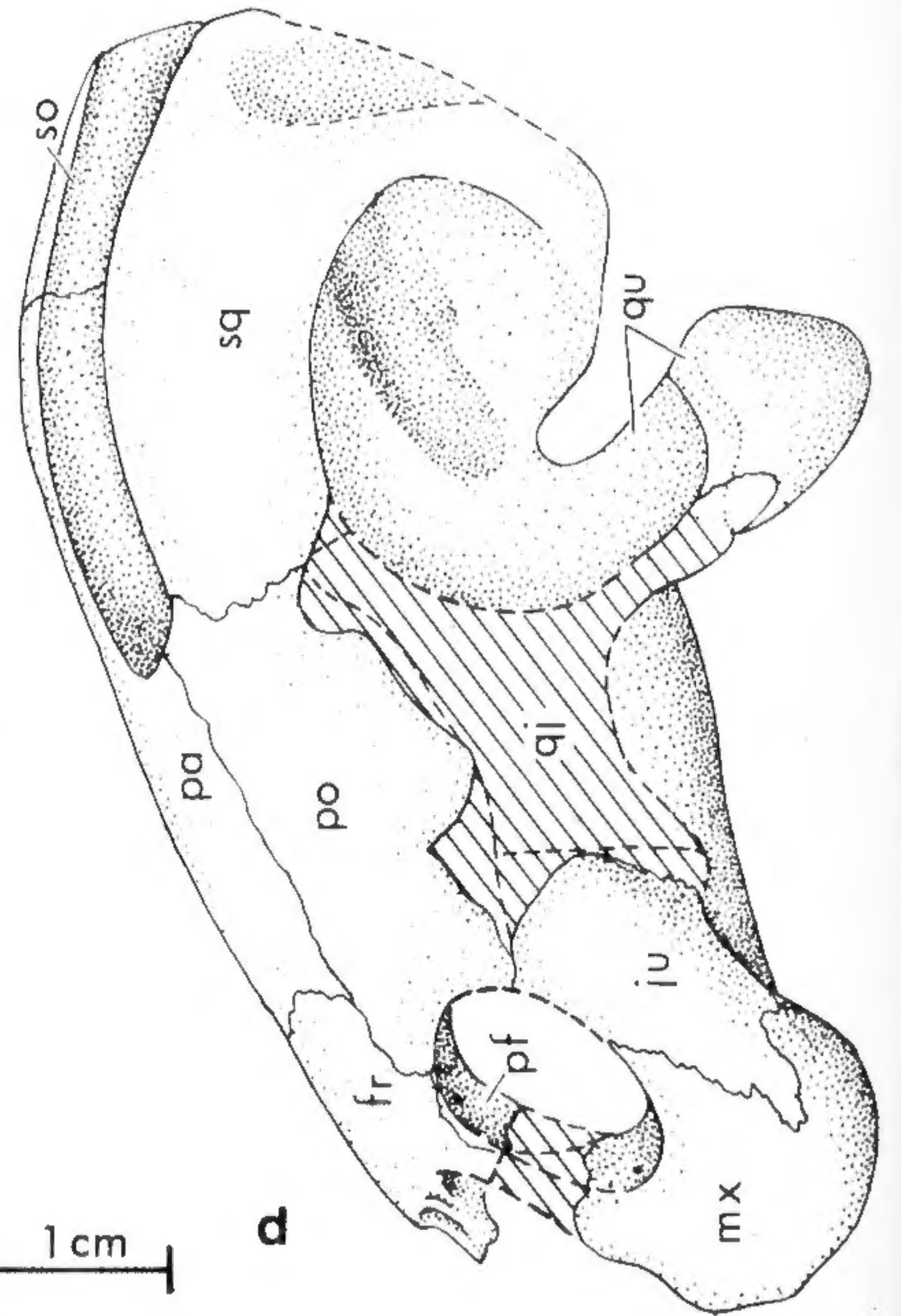
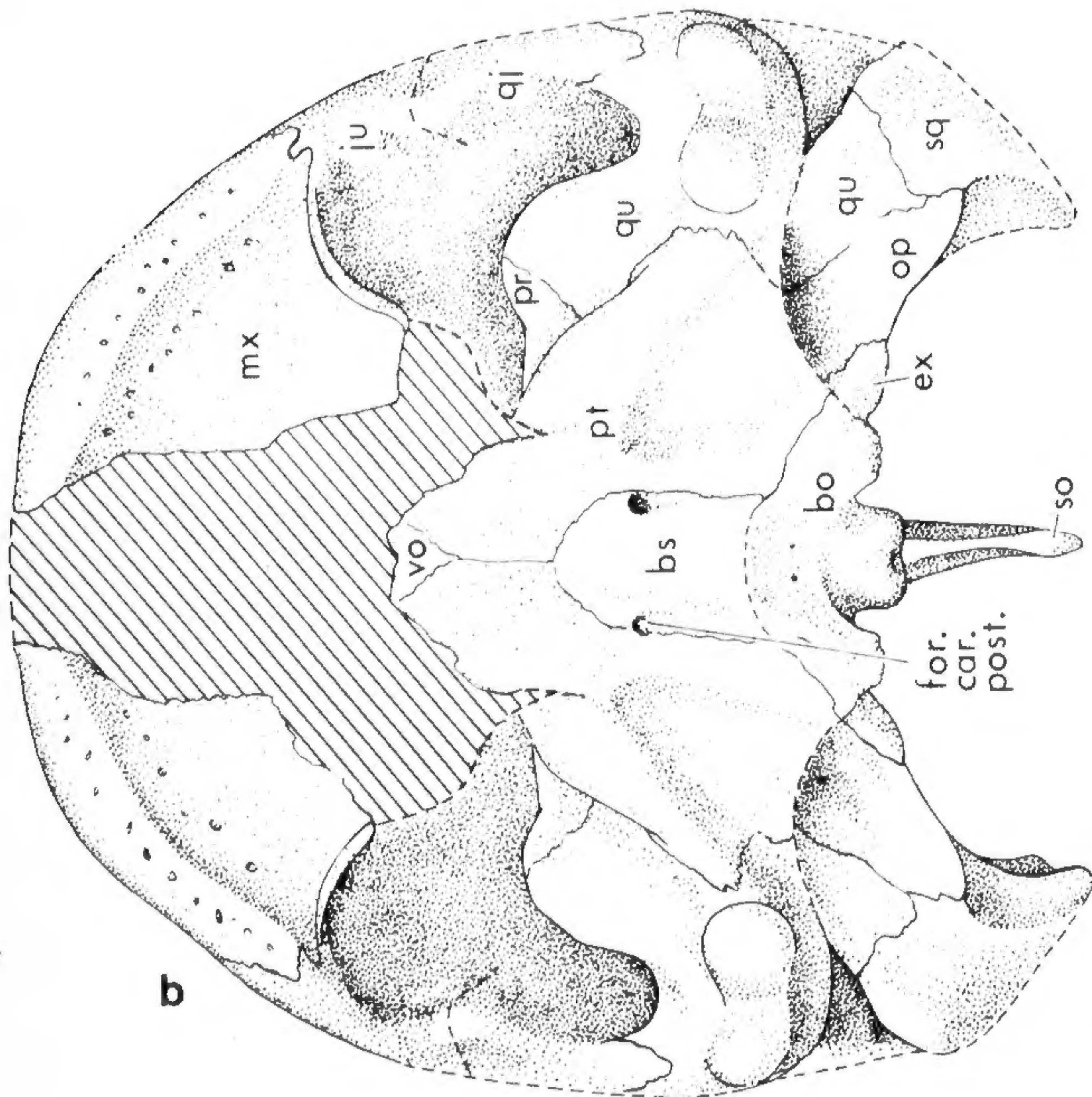
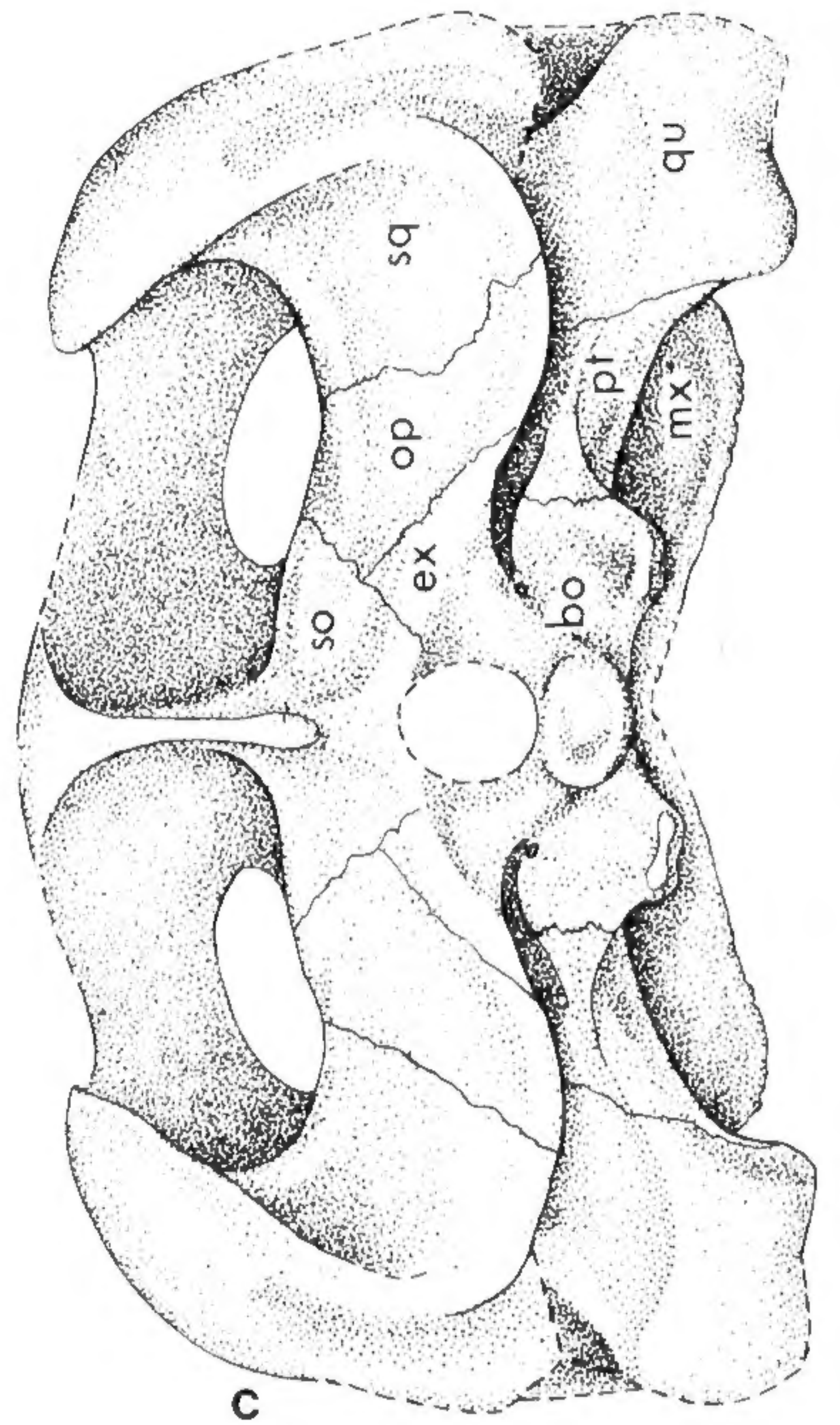
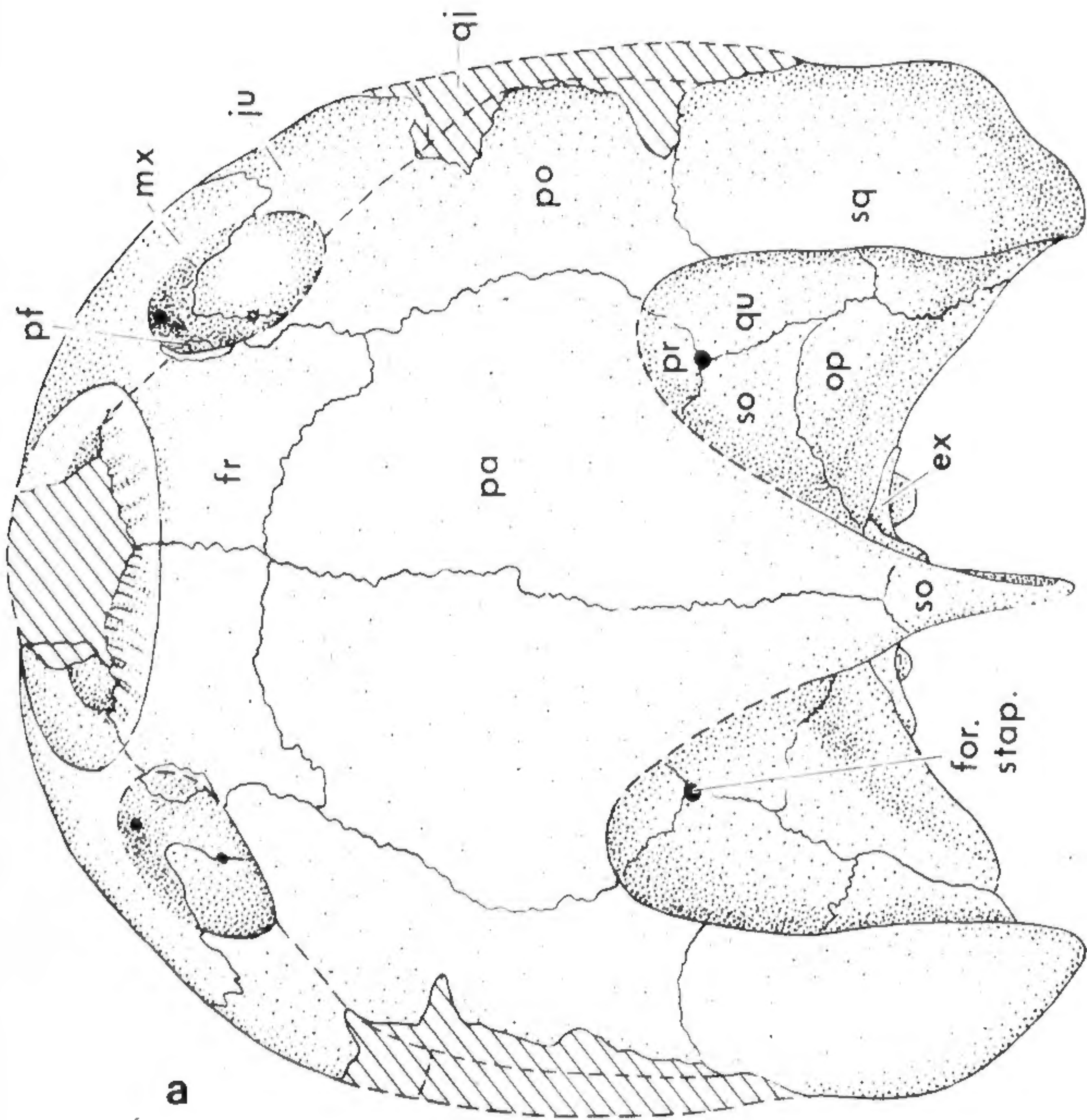
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Abbreviations

The following institutions are referred to in the text:

AMNH The American Museum of Natural
History
CCM Carter County Museum, Montana

Palatobaena bairdi was based largely on the right half of a skull (type specimen) from Cedar Point Quarry, Wyoming (Tiffanian) and the anterior portion of a skull from the Cretaceous of Montana. Gaffney (1972a, figs. 22; 23) restored the skull of *Palatobaena* with a rather circular outline in dorsal view and with a relatively shallow temporal emargination. In 1975, a joint University of California Museum of Paleontology (UCMP) - Los Angeles County Museum field party recovered portions of a skull (UCMP 114539) of this genus from the Hell Creek Formation (Lancian), Montana. Though fragmentary, this specimen preserves the posterior portion of the skull roof



1 cm

◀ **Fig. 1**

Palatobaena bairdi Gaffney. Restored skull based on UCM 114539 with additions from FMNH PR 829, PU 16839 (type), and UCM 37738: a. dorsal view, b. ventral view, c. posterior view; d. lateral view.

Abbreviations for this and following figures: *ant. crs.*, anterior crista of processus inferior parietalis; *aper. nar. int.*, apertura narium interna; *bo*, basioccipital; *bs*, basisphenoid; *cav. acust. jug.*, cavum acusticojugulare; *ex*, exoccipital; *for. ant. can. car. int.*, foramen anterior canalis carotici interni; *for. car. post.*, foramen posterior canalis carotici interni; *for. ner. hypo.*, foramen nervi hypoglossi; *for. pal. post.*, foramen palatinum posterius; *for. prepal.*, foramen praepalatinum; *for. stap.*, foramen stapediotemporale; *for. supmax.*, foramen supramaxillare; *fos. orb.*, fossa orbitalis; *fr*, frontal; *ju*, jugal; *lat. crs.*, lateral crista of processus inferior parietalis; *mx*, maxilla; *na*, nasal; *op*, opisthotic; *pa*, parietal; *pal*, palatine; *pf*, prefrontal; *pm*, premaxilla; *po*, postorbital; *pr*, prootic; *proc. inf. par.*, processus inferior parietalis; *pt*, pterygoid; *qj*, quadratojugal; *qu*, quadrate; *so*, supraoccipital; *sq*, squamosal; *sul. cav.*, sulcus cavernosus; *vo*, vomer.

allowing for a somewhat different restoration (Fig. 1). Another skull fragment (UCM 37738) from the Dawson Formation (Puercan), Colorado, agrees in most characters with UCM 114539.

In 1977 during the preparation of this study, Dr. Eugene S. Gaffney called our attention to a skull of this genus recovered by Mr. Marshall Lambert from the Tongue River Formation (Torrejonian), southeastern Montana. This skull (CCM 77-11) is approximately three-quarters complete and is undistorted (Figs. 2; 3; 7a, b). In 1972 and 1975, pieces of a skull of this genus were recovered by UCM parties in the Wasatch Formation, Wyoming. Though fragmentary when found, this specimen represents an almost complete skull of a new species of *Palatobaena*. It also extends the range of this genus into the early Eocene.

Family **Baenidae** Cope, 1882

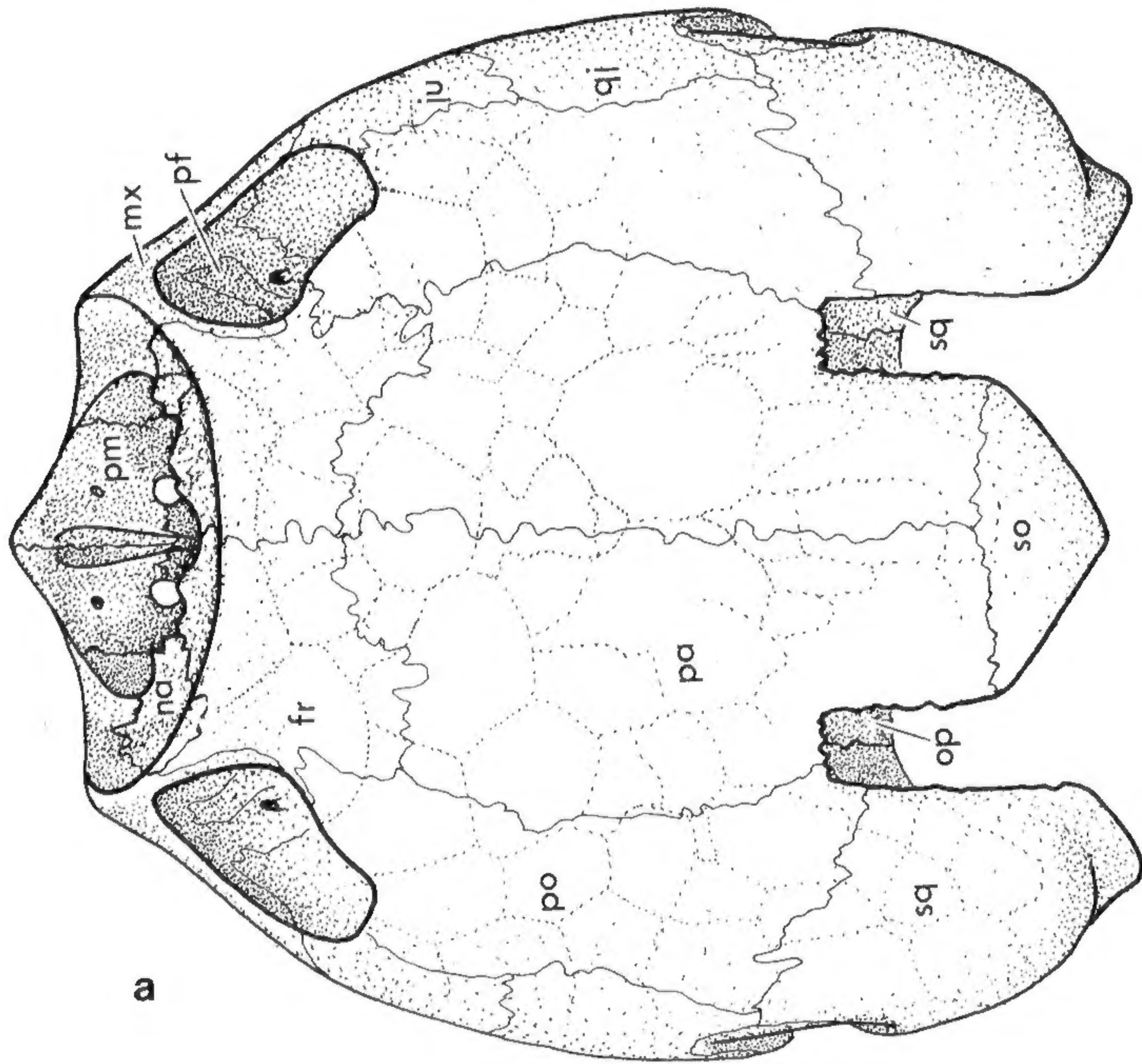
Subfamily **Eubaeninae** (Williams, 1950)

Palatobaena Gaffney, 1972a

Type species *Palatobaena bairdi* Gaffney, 1972a

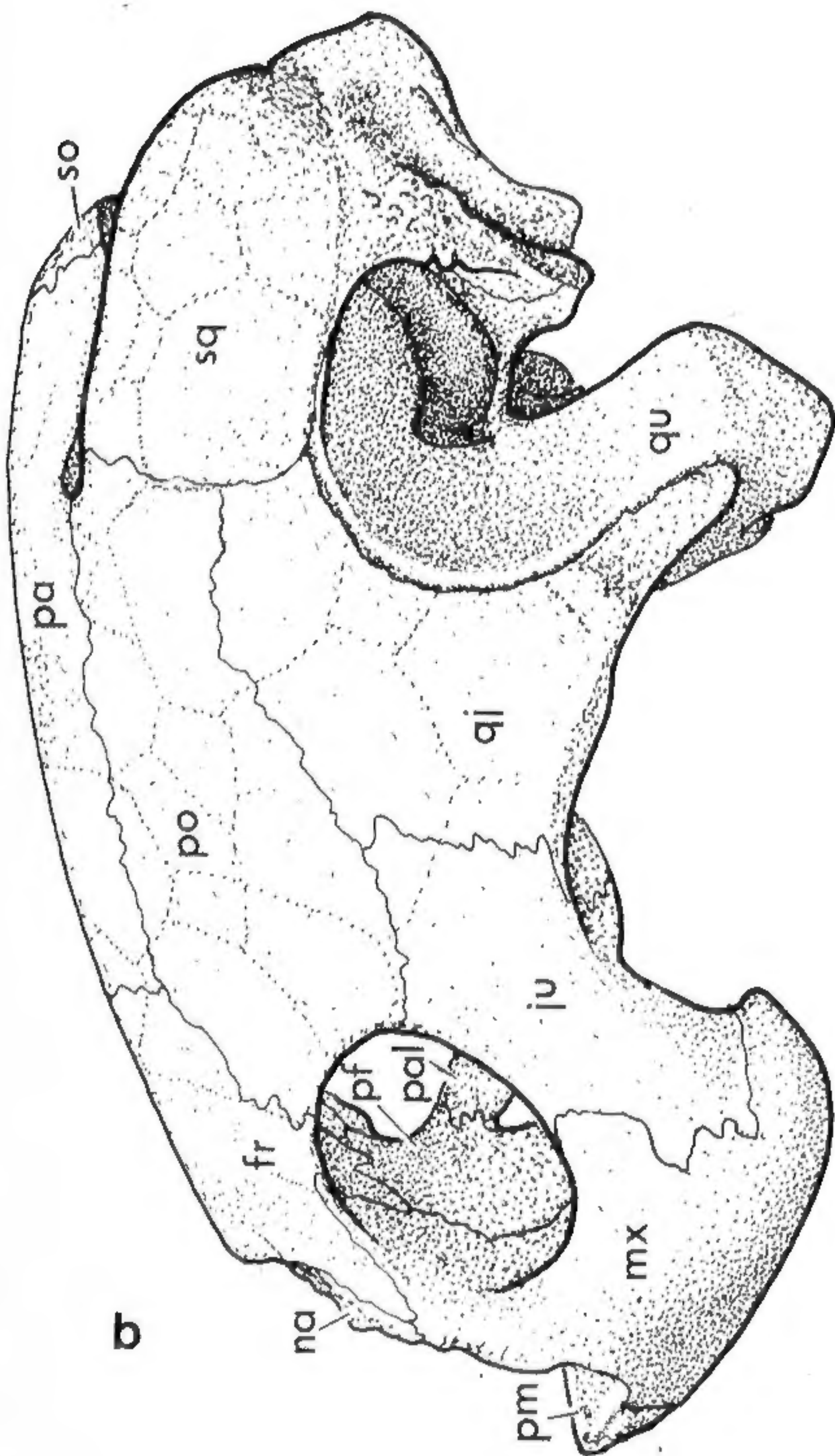
Known distribution Latest Cretaceous (Maestrichtian correlative, Lancian) of Montana, early (Puercan) Paleocene of Colorado, middle (Torrejonian) Paleocene of Montana, late (Tiffanian) Paleocene and early (Wasatchian) Eocene of Wyoming.

Revised Diagnosis Eubaenines with wide, subrectangular skulls; anterior portion of skull broadly curving in dorsal view; preorbital skull length shortest of any baenoid; labial ridges of maxilla and lower jaw forming larger angle with sagittal plane than other baenoids; temporal emargination deep to moderate; ridge separating orbital floor from cheek; nasals small and not contacting in midline; distinct, smooth sulcus surrounding narial opening ventrally and laterally; upper triturating surfaces very wide forming triangular crushing

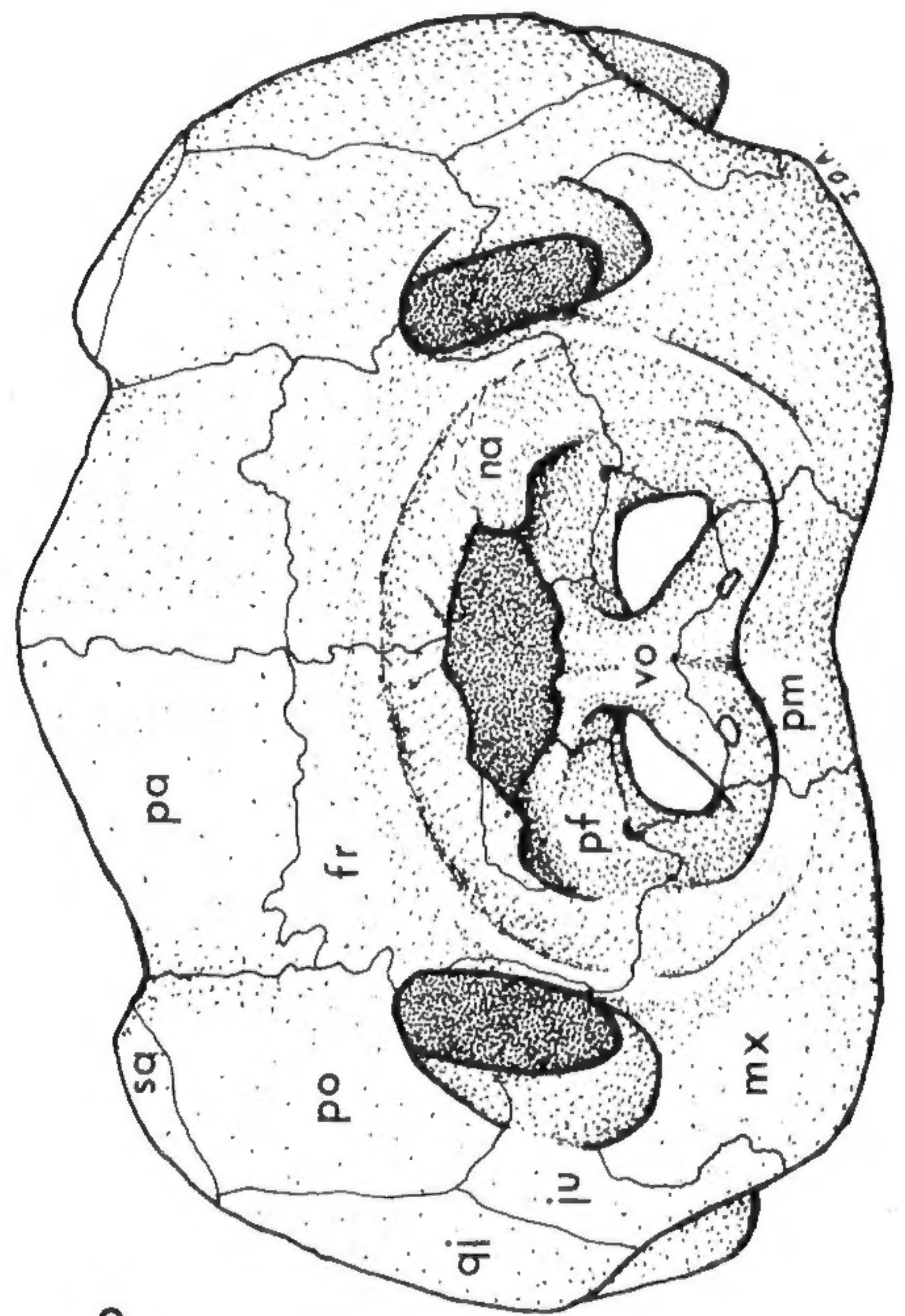


a

~1 cm



b



c

areas, surfaces flat to concave, narrowing in anteromedial portion and forming small continuous lingual ridge on premaxillae; processus pterygoideus externus very small; anterior process of jugal extending below orbit; posterolateral process of frontal distinct; processus trochlearis oticum more prominent than in other baenids, except possibly *Eubaena*; antrum postoticum slightly narrowing dorsoventrally; lower jaws with wide triangular triturating surfaces sloping labially, processus coronoideus tall and massive; two deep fossae on labial side of jaw, first large one posteroventral to processus coronoideus and second small one anteroventral to area articularis manibularis. Lower jaws known only for *P. bairdi*.

Palatobaena bairdi Gaffney, 1972a

(Figs. 1; 2; 3; 4a, b; 6d, e; 7a, b)

Type Specimen PU 16839, the right half of a skull, partially distorted (Gaffney, 1972a, p. 269).

Type Locality Cedar Point Quarry, Bighorn Basin, Wyoming.

Horizon Fort Union Formation, early Tiffanian (late Paleocene).

Collector Princeton Party, 1949.

Referred Specimens Only specimens not listed by Gaffney, 1972a, p. 269–272 are noted.

UCMP 114539, fragmentary skull and jaws. Locality: V75180, Baenid Skull Locality, Garfield County, Montana. Horizon: Hell Creek Formation, Maestrichtian correlative (Lancian). Collector: David Lawler, 1975.

◀ **Fig. 2**

Palatobaena bairdi Gaffney. Restored skull based on CCM 77-11: a, dorsal view; b, lateral view; c, anterior view. Abbreviations as in Fig. 1.

UCMP 114644, left maxilla; UCMP 114656, right quadrate. Locality: V65127, Bug Creek Anthills-General, McCone County, Montana. Horizon: Hell Creek Formation, Maestrichtian correlative (Lancian). Collector: UCMP Party, 1970.

UCMP 114680, right and left jaw halves; UCMP 114686, left maxilla. Locality: V70201, Bug Creek Anthills C, McCone County, Montana. Horizon: Hell Creek Formation, Maestrichtian correlative (Lancian). Collector: UCMP Party, 1970.

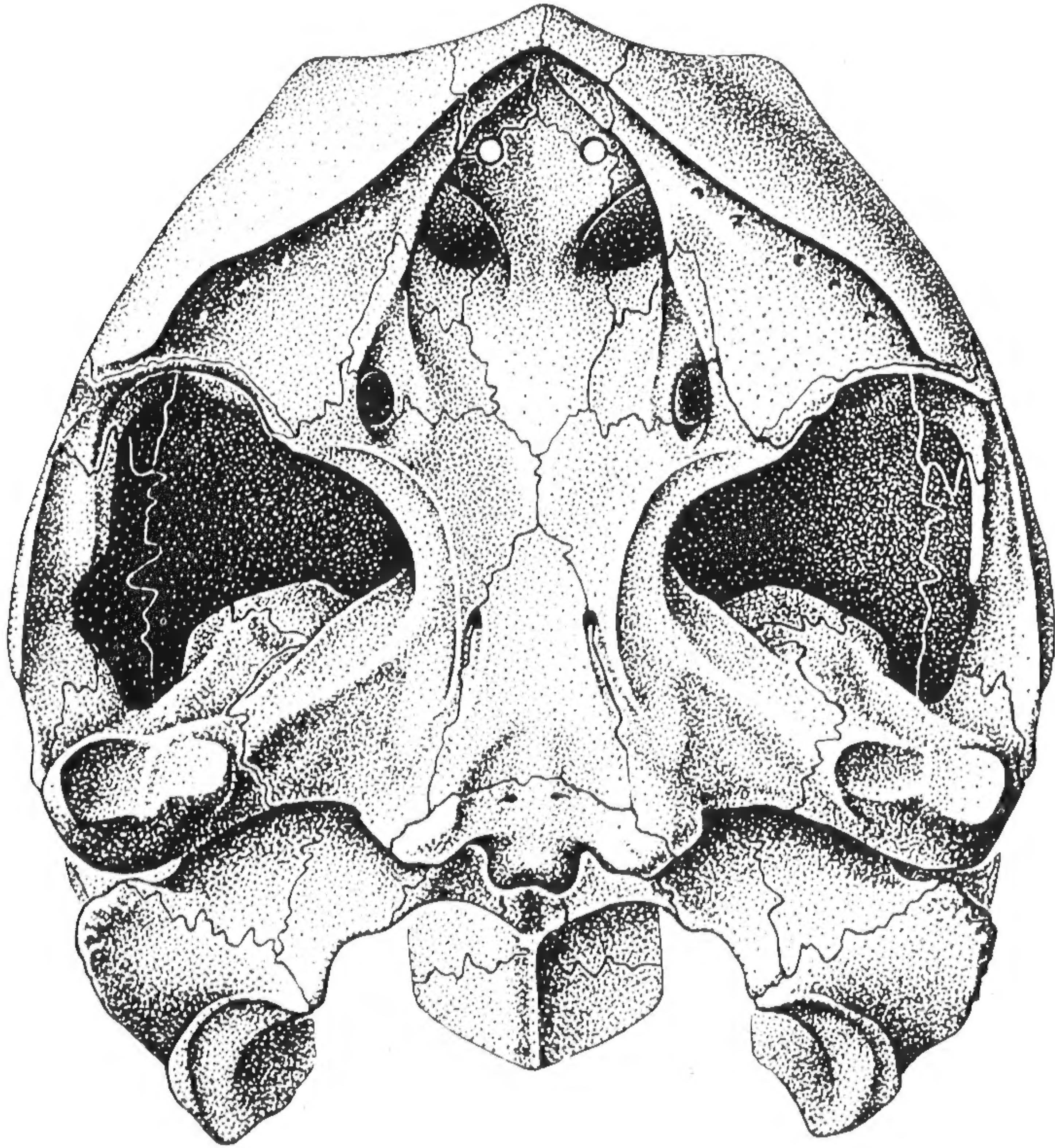
AMNH 8277, complete lower jaws. Locality: Bug Creek Anthills, McCone County, Montana. Horizon: Hell Creek Formation, Maestrichtian correlative (Lancian).

AMNH 2603, nearly complete lower jaws. Locality: Lismas, Montana (label). Horizon: Hell Creek Formation, Maestrichtian correlative (Lancian).

UCM 37738, skull and jaw fragments. Locality: Corral Bluffs, El Paso County, Colorado. Horizon: Dawson Formation, Paleocene (Puercan). Collector: UCM Party, 1974.

CCM 77-11, three-quarters of undistorted skull. Locality: Medicine Rocks, Site 1, Carter County, Montana. Horizon: Tongue River Formation, Paleocene (Torrejonian). Collector: Marshall Lambert, 1977.

Revised Diagnosis Temporal emargination deep to moderate; tomial ridge deflecting ventrally about 10° and vomer about 25° from the plane of the basicranium; skull roof over crista supraoccipitalis varying from sharp point with little dorsal exposure to laterally wide triangular surface; crista supraoccipitalis terminating posteriorly to level of occipital condyle and about in line with, or slightly anteriorly to posterior termini of squamosals; processus inferior parietalis forming anteriorly two distinct cristae (anterior and lateral); frontals wider than long and terminating posteriorly to anterior margin of premaxillae; narial

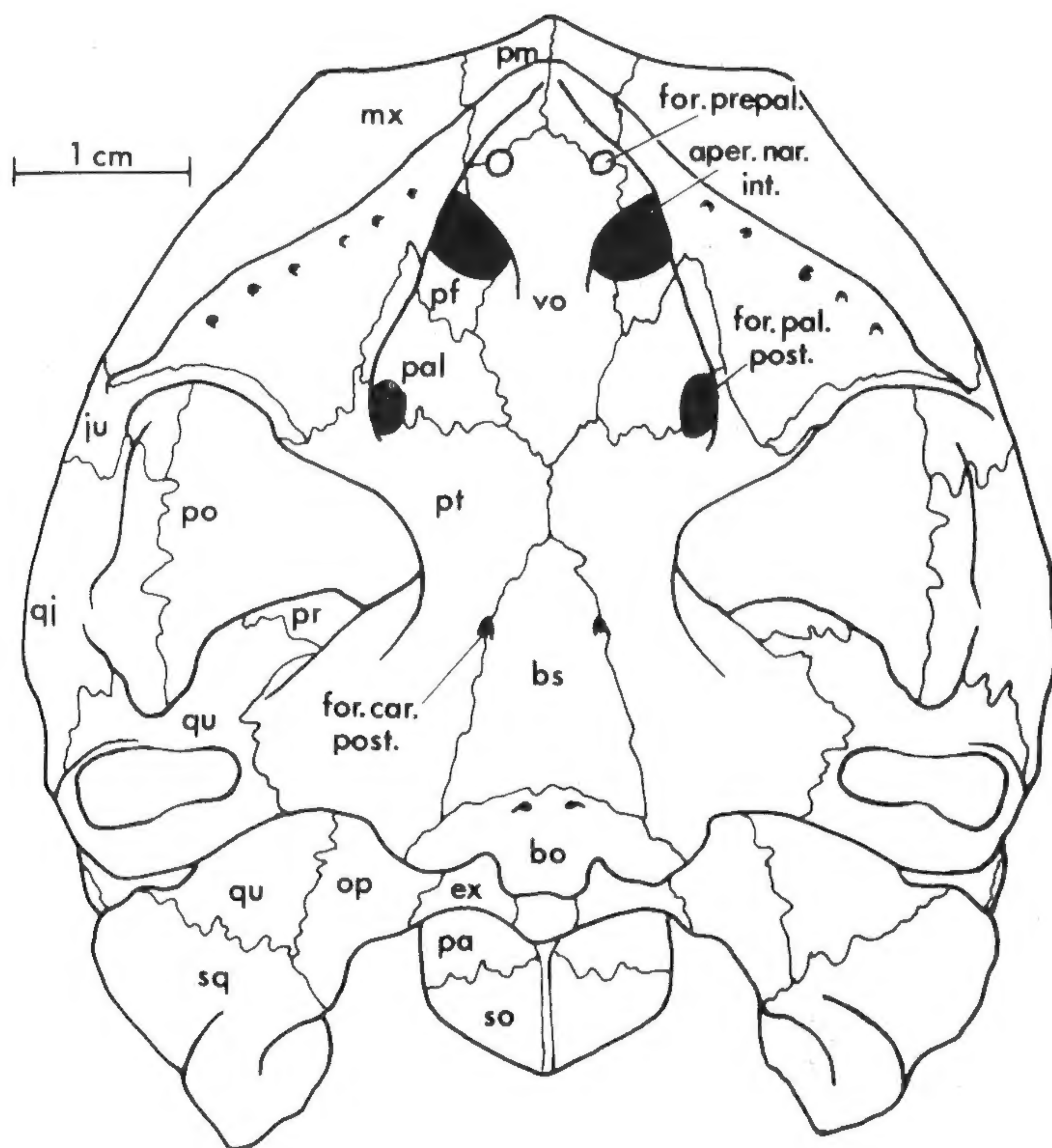
**Fig. 3**

Palatobaena bairdi Gaffney. Restored ventral view of skull, facing page, based on CCM 77-11. Abbreviations as in Fig. 1.

sulcus extending across anterior margin of frontals; anterior termination of maxillae well anterior to orbits; dorsal margin of cheek emargination with distinct tubercle on medial side and no smooth shelf on lateral side; tubercula basioccipitalia divergent and extending posteriorly as far as occipital condyle articulation; processus paroccipitalis with distinct transverse ridge extending onto squamosal; processus paroccipitalis extensively contacting squamosal posteriorly; posterior surface of squamosal and quadrate above the incisura columellae auris forming a broadly U-shaped surface. Features of the lower jaws same as those given in the generic diagnosis.

Discussion The record of *Palatobaena* has been greatly augmented since the original description of Gaffney (1972a). Material referable to this genus is now known from each of the land mammal ages from Lancian (latest Cretaceous) through Wasatchian (early Eocene), except possibly for the Clarkforkian (late Paleocene or early Eocene; see Gingerich and Rose, 1977). The genus is still represented only by skull material, but Archibald (1977) has speculated that its shell, probably unrecognized in existing collections, resembles that seen in eubaenines and baenines.

Although the stratigraphic record of this genus has greatly improved, the sample in each interval is usually represented by only one specimen. Thus, variability can only be



estimated for each sample. Conservatively we have recognized only two species, but the recovery of additional material may warrant further subdivision. All but the new Eocene skull described below are referred to *Palatobaena bairdi*.

The depth and shape of the temporal emargination are the most variable characters in the skulls referred to *Palatobaena bairdi*. In Gaffney's restoration of the type specimen (1972a, figs. 22, 23) he tentatively reconstructed the skull with a shallow temporal emargination. The skull roof of this specimen is somewhat distorted and the posterolateral margin of the parietal is quite thick indicating more bone may have been present posteriorly. However, in the Eocene skull (new

species), which preserves the temporal emargination, the parietal remains thick until almost the very border of the emargination.

In the new Cretaceous specimen of *Palatobaena bairdi*, UCM 114539, the posterior part of the skull roof is relatively intact and undistorted. Here the temporal emargination is deep, the anterior border reaching anteriorly beyond the level of the cavum tympani (Fig. 1d). The bone near the emargination is thin, and the dorsal exposure of the crista supraoccipitalis is extensive, but much narrower than in the Eocene species. In the portion of the skull roof preserved in the early Paleocene specimen, UCM 37738, the parietal is slightly wider and thicker along the temporal emargination than in UCM 114539.

In the well-preserved middle Paleocene skull, CCM 77-11, the left temporal emargination is complete (Fig. 2a). The bone surrounding the emargination is as thick as in UCM 37738. However, the anteroposterior depth in CCM 77-11 is noticeably less than in UCMP 114539 (and probably UCM 37738) with the anterior border only reaching the level of the anterior margin of the cavum tympani. This depth is comparable to that seen in the new Eocene species described below.

The shape of the temporal emargination is very distinctive in CCM 77-11. In the other skulls of *Palatobaena* preserving the emargination, including the new Eocene species, the lateral border of the emargination is approximately in a parasagittal plane while the medial border diverges anteriorly. In CCM 77-11 both the lateral and medial borders are in an approximately parasagittal plane. The distinctive parallel-sided temporal emargination in CCM 77-11 is the result of the lateral expansion of the supraoccipital and the posterior portion of the parietal. Although this distinctive shape of the temporal emargination may prove to be of taxonomic value upon recovery of additional specimens, we prefer to regard it as variability within one species.

The general shallowing of the temporal emargination and the thickening of the bordering bones going from the latest Cretaceous to early Eocene specimens of *Palatobaena* suggest that the temporal emargination in the type specimen of *P. bairdi*, PU 16839, may have been shallower than in UCMP 114539, but not as shallow as restored by Gaffney (1972a, fig. 22A).

Additional variability can be observed in the position and in the presence or absence of the anterior and lateral cristae of the processus inferior parietalis. Three character states are present within the sample of *Palatobaena*. In the first condition, present in the latest Cretaceous skull fragments, UCMP 114539 and FMNH PR 829, and the early Paleocene specimen, UCM 37738, the anterior and lateral

cristae form an angle of 80–90° to one another (Fig. 6d). The second state is represented in the middle and late Paleocene skulls, CCM 77-11 and PU 16839, respectively. In these specimens the cristae are both more anterior to anterolateral in orientation and parallel each other in their more dorsal portions (Fig. 6e). The third character state is present in the new Eocene species described below. Here lateral cristae are totally absent and the anterior cristae, although present, are less prominent (Fig. 6f). Only in this last skull are the differences such as to probably be of taxonomic value in view of the small sample size of this genus.

A marked sulcus almost completely encircles the apertura narium externa in all specimens of *Palatobaena bairdi* preserving this region of the skull. Only CCM 77-11 preserves the premaxillae showing that the sulcus, although less distinctive in this region, continues on to the anteroventral surface of the premaxillae. There is some variation in the development of the rim that surrounds the sulcus and the apertura. As can be seen in dorsal view of CCM 77-11 (Fig. 2a), the lateral rim of this sulcus is slightly flared, interrupting the otherwise rounded outline of the anterior aspect of the skull. Most of the other specimens of *P. bairdi* including the type, PU 16839, do not show this flaring (see Fig. 1a). This could be due to the poorer preservation of the other specimens, but it seems doubtful. The only other specimen of *P. bairdi* that shows a similar flaring is FMNH PR 829, an anterior skull fragment (Gaffney, 1972a, fig. 25A). The overall size of FMNH PR 829 cannot be estimated, but it was probably a smaller individual than CCM 77-11 which has a condyle–premaxilla length of 48 cm. This compares to a condyle–premaxilla length of 63 cm for UCMP 114539 and 54 cm for PU 16839. The apparent absence of flaring in these larger skulls is probably due to one or more factors related to allometry (e.g., differences in ontogenetic age or sexual dimorphism). Similarly the size of the apertura narium externa appears to be relatively larger in CCM 77-11

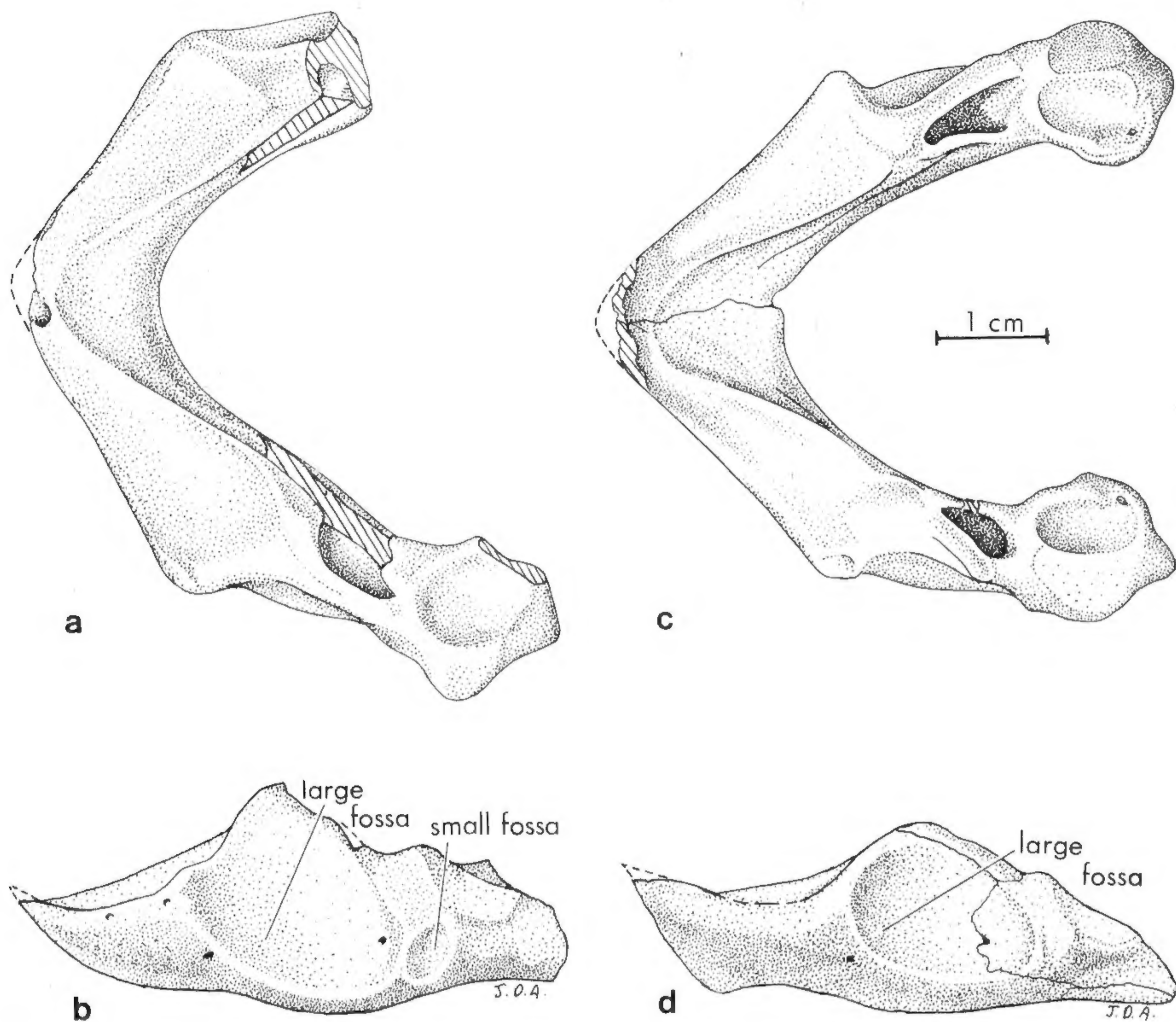


Fig. 4
Lower jaws. *Palatobaena bairdi* Gaffney,
AMNH 2603: a, dorsal view; b, lateral view.
Plesiobaena putorius Gaffney, PU 17108: c,
dorsal view; d, lateral view.

than as reconstructed here for UCMP 114539 (Fig. 1a) and by Gaffney for the type, PU 16839 (Gaffney 1972a, fig. 22A).

Gaffney (1972a) suggested that the frontals and nasals may be fused in *Palatobaena bairdi*. CCM 77-11 is well enough preserved to show that the nasals are present (recognized by Gaffney, personal communication) although they are highly modified from the arrangement present in other baenoids. In CCM 77-11, and presumably *P. bairdi* in general, the nasals are reduced to small, irregular slivers of bone exposed in the dorso lateral aspect of the apertura narium externa (Fig. 2). They do not contact each other in the

midline. Some of the sutures between the nasals and surrounding bones are difficult to ascertain in CCM 77-11, but the nasals extensively contact the frontals and prefrontals, and probably the maxillae. The other specimens of *P. bairdi* are not well enough preserved to identify the nasals. In the new Eocene species of *Palatobaena* a small pit is present at the anterolateral corner of the left frontal that may have received a small nasal bone (Fig. 6f). Most of its contact was with the frontal bone, but very reduced contact with the maxilla and prefrontal cannot be eliminated as a possibility.

Lower jaw fragments were found with UCMP 114539 and UCM 37738, which are the first associations of jaws and skulls of this genus. This has allowed for a more certain identification of complete isolated lower jaws of the genus. No comparative study of baenid lower jaws has been published; therefore, detailed comparisons with other taxa are not attempted here. However, lower jaws are now known for all the baenid species (based on skulls) described by Gaffney (1972a) except for *Trinitichelys hiatti* and *Hayemys latifrons*, and considerations in our paper are based on a comparison with these other taxa. The bone relationships in a complete lower jaw of *Palatobaena bairdi*, AMNH 8277, will be discussed elsewhere by E. Gaffney. A second, almost complete lower jaw of *P. bairdi* (AMNH 2603) from the Hell Creek Formation, Montana, and a complete lower jaw of *Plesiobaena putorius* (PU 17108) from the Polecat Bench Formation (Torrejonian), Wyoming, are illustrated (Fig. 4) for comparison. The latter specimen (mentioned by Gaffney 1972a, p. 264) is included because of the close similarities of this lower jaw to those assigned to *Palatobaena bairdi* and both are discussed in the section dealing with speculations on jaw mechanics.

The scalation pattern on the skull of the type-species was figured by Gaffney (1972a, figs. 22; 24). Of the new material only CCM 77-11 and the Eocene skull, UCMP 114529, preserve much of this pattern. The scalation pattern becomes more pronounced in going from the Cretaceous to Paleocene to Eocene specimens. This could be a phylogenetic trend, but could also be a preservational bias or a vagary resulting from small sample sizes.

Palatobaena gaffneyi Hutchison, new species (Figs. 5; 6a, b, c, f; and 7c, d)

Type Specimen UCMP 114529, nearly complete skull lacking right orbital region, sutures not co-ossified, slightly distorted. Only known specimen of species.

Type Locality V71238, Upper *Meniscotherium* locality, Sweetwater County, Wyoming.

Horizon Main Body of Wasatch Formation, Eocene (Wasatchian).

Collectors J.A. Lillegraven, 1972, and J.H. Hutchison, 1975.

Etymology For Dr. Eugene S. Gaffney, The American Museum of Natural History, in recognition of his contributions to our knowledge of the Baenidae.

Diagnosis Temporal emargination moderate; tomial ridge deflecting ventrally about 20° and vomer about 60° from the plane of the basicranium; skull roof over crista supraoccipitalis terminating posteriorly at about level of occipital condyle and anteriorly to level of posterior termini of squamosals; processus inferior parietalis forming anteriorly only one distinct crista (anterior); frontals about equally wide as long and terminating anteriorly to anterior margin of premaxillae; narial sulcus only on maxillae and premaxillae; maxillae terminating immediately anterior to orbits; dorsal margin of cheek emargination

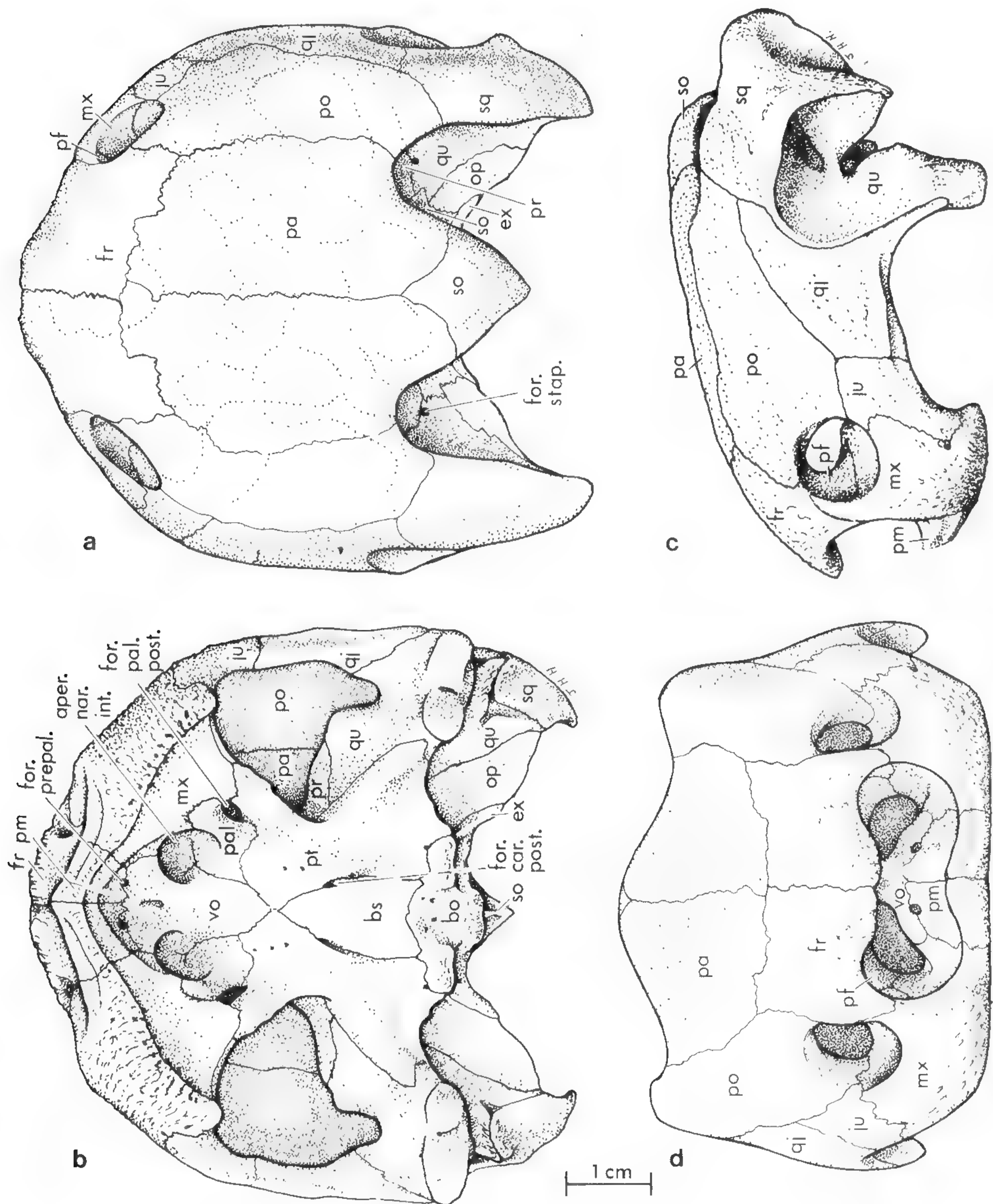
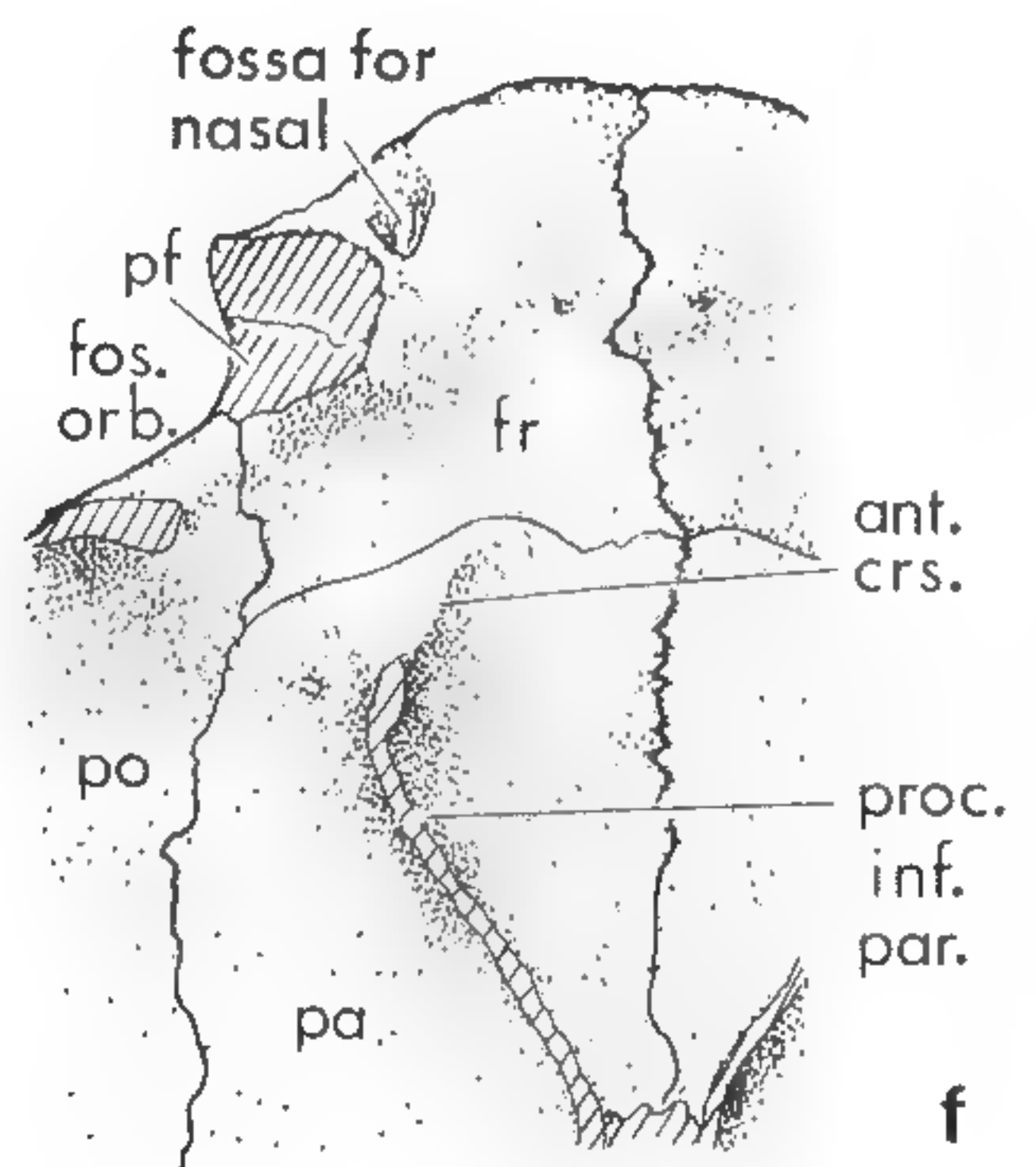
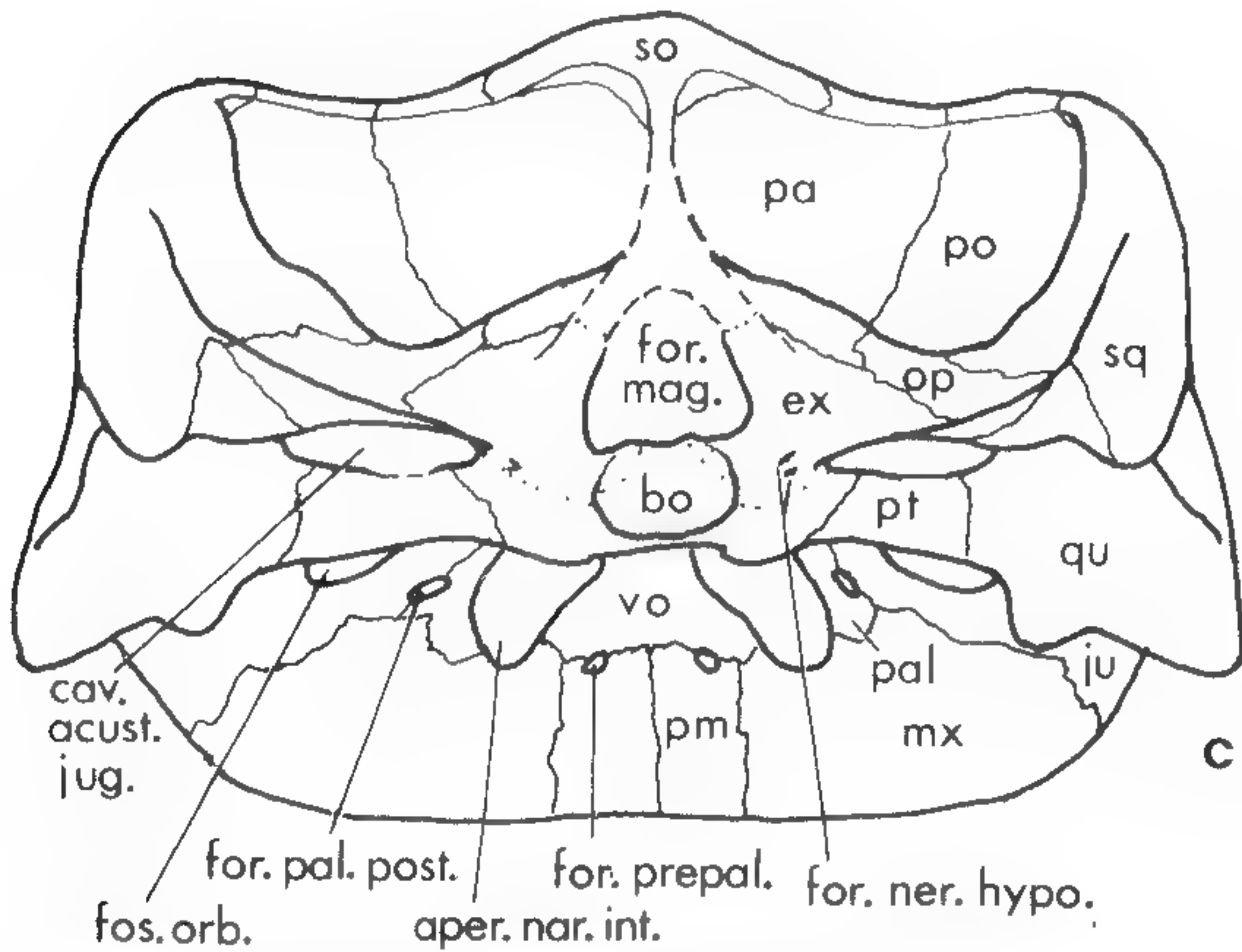
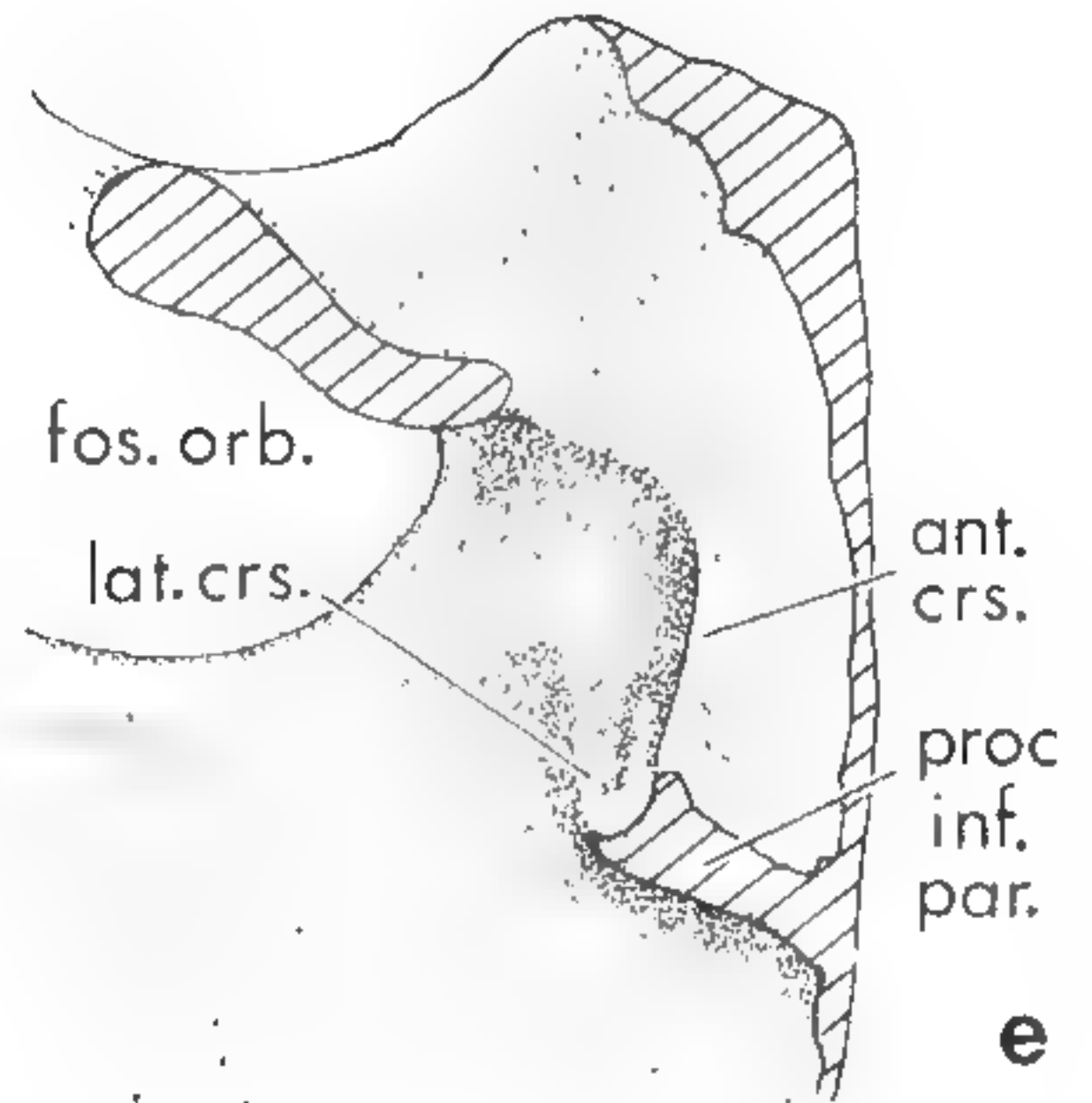
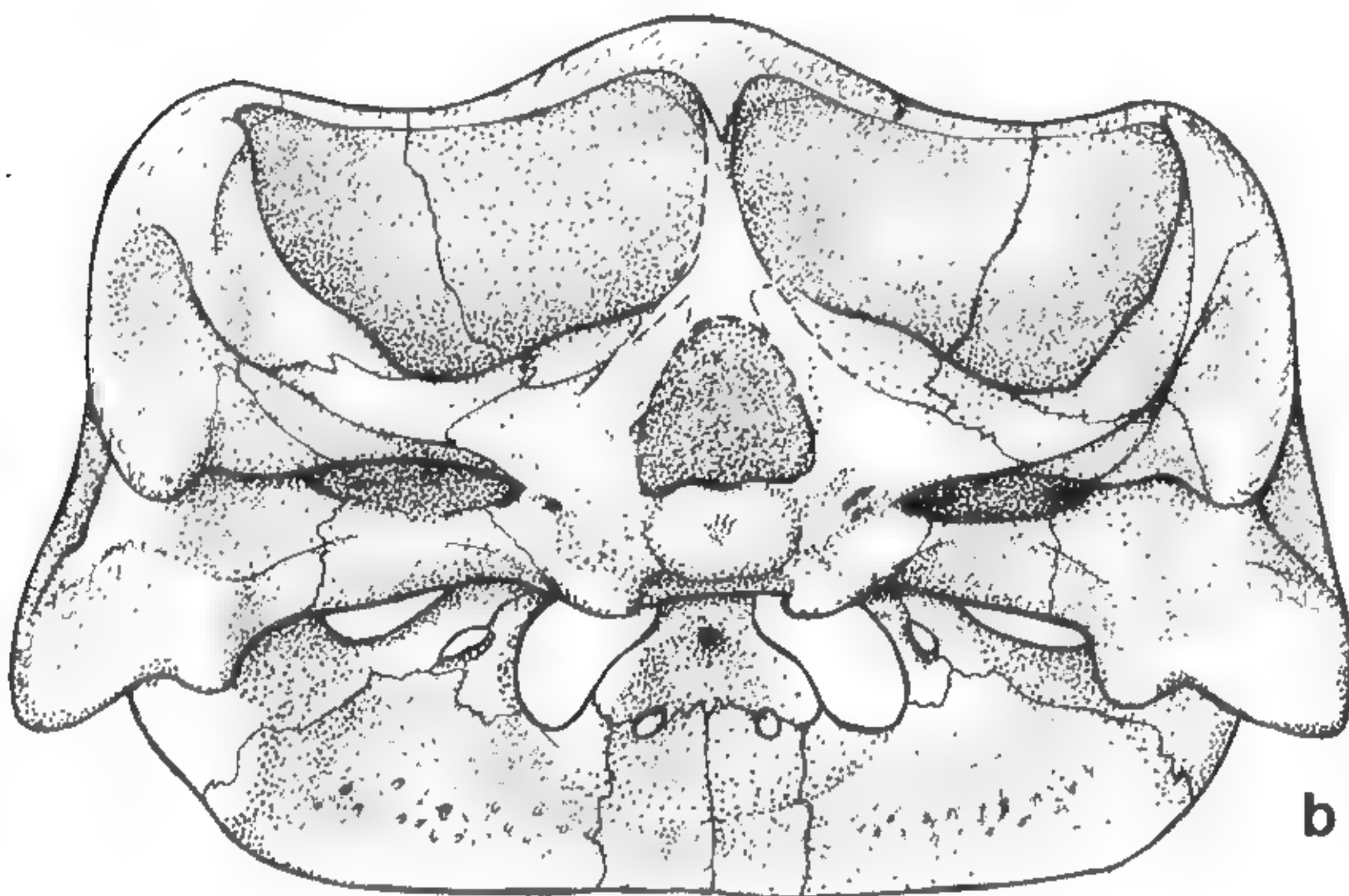
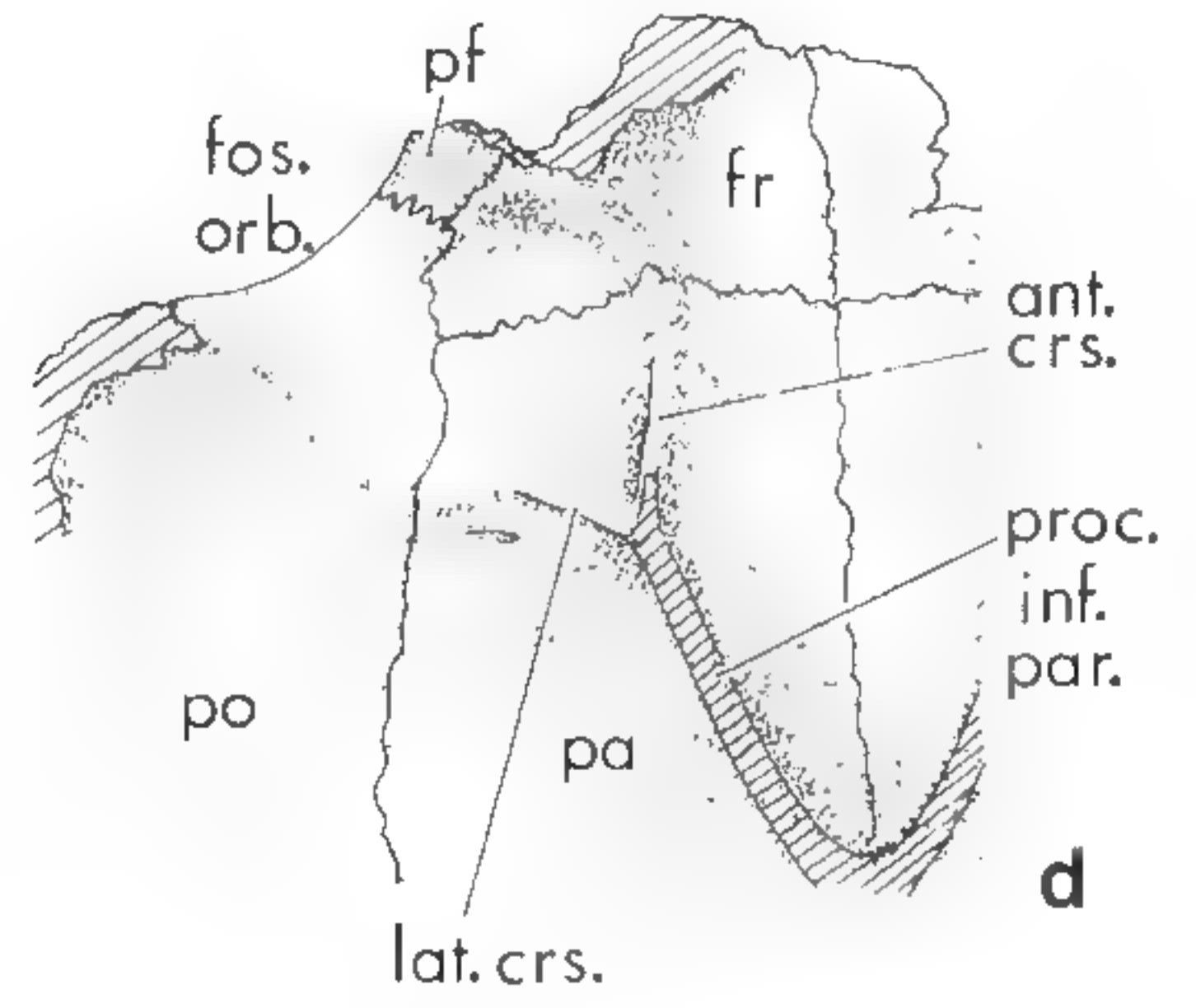
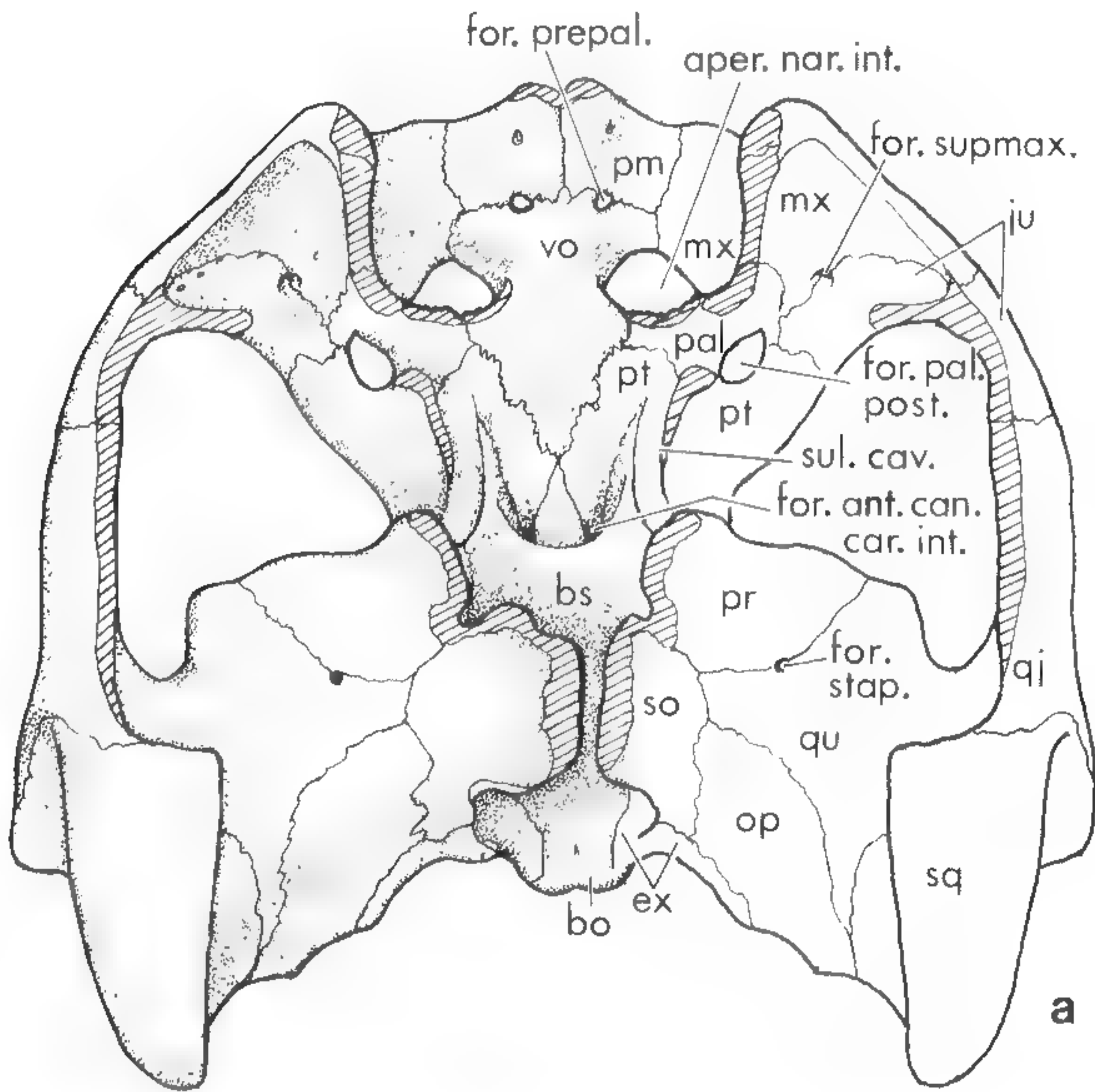


Fig. 5
Palatobaena gaffneyi Hutchison, n. sp.
 Restored skull based on type, UCMP 114529:
 a, dorsal view; b, ventral view; c, lateral view;
 d, anterior view. Abbreviations as in Fig. 1.



with smooth step along lateral side and no medial tubercle; tubercula basioccipitalia parallel and falling short of occipital condyle; processus paroccipitalis is without distinct transverse ridge, contacting squamosal in small posterolateral area; posterior surface of squamosal and quadrate basally forming a narrow, sharply angled canal. Lower jaws are not known.

Description All the noted differences between *Palatobaena gaffneyi* and *P. bairdi* seem to be related to the feeding mechanism which involves a further shortening of the rostrum and concomitant modifications of the masticatory musculature. In comparison with *P. bairdi*, these resolve into different character states in diverse parts of the skull.

The preorbital portion of the ventral part of the maxilla is markedly shortened in *Palatobaena gaffneyi* so that the labial ridge is within 15–20° of perpendicular to the sagittal plane compared to an angle of 30–40° in *P. bairdi*. The sulcus surrounding the nasal aperture in *P. bairdi* is reduced in size and restricted to the maxilla and premaxilla in *P. gaffneyi*. The orbit of *P. gaffneyi* appears to be more vertically aligned. The fossa orbitalis forms a smaller and rather triangular basin in the dorsal surface of the maxilla. Processus inferior parietalis forms only a simple ridge with the anterior part of the parietal roof rather than dividing into anterior and lateral cristae.

The frontals are relatively longer than in *Palatobaena bairdi*, terminating in a simple, blunt point that extends anteriorly beyond the level of the premaxillae. As noted previously, evidence from CCM 77-11 suggests *P. gaffneyi*

also possessed reduced nasals. In the latter, the anteriorly elongated frontals dorsally override and more completely separate the nasals.

The dorsal margin of the cheek emargination has a smooth reflected rim probably for the origin of an adductor muscle (see discussion of jaw mechanics below). No such rim is present in *Palatobaena bairdi*, but just medial to the cheek rim lies an elongate and ventrally projecting tubercle which probably serves for attachment of the same muscle. No other baenids possess either of these structures.

Palatobaena gaffneyi is less robust in the area of the opisthotic-quadrate suture. The dorsally exposed area between the processus trochlearis oticum and the tip of the processus paroccipitalis is generally depressed in *P. gaffneyi*, whereas in *P. bairdi* there is a strong transverse ridge across this region in the area of the opisthotic-quadrate-squamosal suture. In *P. gaffneyi* the squamosal has almost lost contact with the opisthotic, touching only at the extreme tip of the processus paroccipitalis in contrast to the extensive contact between these two bones in *P. bairdi*. The posterior face of the squamosal-quadrate above the incisura columellae auris is rather constricted and is marked by a narrow, sharply angled channel in contrast to the shallow broadly U-shaped surface in *P. bairdi*. In *P. gaffneyi*, the tubercula basioccipitalia are less divergent, more medial, and terminate more anteriorly than in *P. bairdi*. The crista supraoccipitalis is shorter, more broadly pointed (except in CCM 77-11) and has greater dorsal exposure than in *P. bairdi*.

The expression of the scale pattern on the skull roof varies in *Palatobaena bairdi*, but the type of *P. gaffneyi*, despite its probably more immature age, shows a well-defined scale pattern as in CCM 77-11 and a better defined pattern than the type of *P. bairdi*.

All character states distinguishing *Palatobaena gaffneyi* from *P. bairdi* can be derived from those seen in *P. bairdi*, most being exten-

◀ Fig. 6

Palatobaena gaffneyi Hutchison, n. sp.
Restored skull based on type UCMP 114529:
a, dorsal view with skull roof removed; b and c,
posterior view. Ventral view of skull roof: d, *P.*
bairdi, UCMP 114539; e, *P. bairdi*, PU 16839
(type); f, *P. gaffneyi*, UCMP 114529 (type).
Abbreviations as in Fig. 1.

sions of those characters which distinguish *P. bairdi* from other baenids. Morphologically and temporally, *P. bairdi* is a suitable ancestral species for *P. gaffneyi*; however, there are no specimens of *P. bairdi* that show any tendency for the anterior extension of the frontals.

Speculations on Jaw Mechanics

Most of the characters in the skull of *Palatobaena* compared to those in the presumably more primitive *Plesiobaena antiqua* (see Gaffney, 1972a) point to changes in diet. The majority of the speculations discussed below indicate *Palatobaena* was molluscivorous. Probably the most obvious single feature is the development of large triangular triturating surfaces on the maxilla and lower jaw. However, other baenids—*Stygiochelys estesi*, *Eubaena cephalica*, and *Plesiobaena putorius*—have variously developed wide triturating surfaces. Only in *Palatobaena bairdi* and finally in *P. gaffneyi* are the width of the triturating surfaces plus other features in the skull and jaws carried to an extreme.

The reduction in the crista supraoccipitalis from *Palatobaena bairdi* to *P. gaffneyi* is probably related to the similar shortening and downward rotation of the face in the latter species. The shortening of the face in *P. gaffneyi* is clearly seen in the more abbreviated preorbital region of the premaxillae and maxillae, and in the greater angle the labial ridges of the maxillae make with the sagittal plane. The downward rotation of the face is evident from the greater angles that the vomer and tomial ridges make with the plane of the basicranium in *P. gaffneyi* relative to *P. bairdi*. Schumacher (1973) noted that the *M. pterygoideus*, which originates partially behind the orbit, helps to counteract the force of the *M. adductor mandibulae externus*, which partially originates along bones in the temporal emargination. Thus the shortening of the face and of the region surrounding the temporal emargination in *P. gaffneyi* probably occurred simultaneously.

At least one other feature suggests the *M. pterygoideus* has been shortened (or somewhat reduced) in *P. gaffneyi*. As noted earlier only the anterior crista of the processus inferior parietalis is present in *P. gaffneyi*. Other baenids (i.e., *Stygiochelys*, *Eubaena*, *Plesiobaena antiqua*, and *Baena*) have both anterior and lateral cristae as in *Palatobaena bairdi*. Two of the better-preserved UCMP baenid specimens of *Plesiobaena antiqua* (UCMP 49759) and *Baena arenosa* (UCMP 117348) possess a low curved ridge connecting the two cristae anteriorly, thus forming a small pocket. Probably this pocket and parts of the lateral crista served as points of origin for parts of the *M. pterygoideus*. The absence of this pocket or a lateral crista in *P. gaffneyi* suggests that the origin of *M. pterygoideus* has moved ventrad along the processus inferior parietalis or has become somewhat reduced. It is doubtful that the muscles for retraction or protraction (Schumacher, 1973) have been relatively or absolutely reduced. It is more likely that with the shortening and relative deepening of the skull the muscles have moved closer to the site of insertion increasing the power of the bite. It is also interesting to speculate that the anteroposterior arching of the palate in *P. gaffneyi* (partially caused by downward flexure of the face) was produced in part to offset powerful muscles of protraction and retraction.

The extremely large processus trochlearis oticum in *Palatobaena bairdi* and *P. gaffneyi* over which the tendon for the *M. adductor mandibulae externus* rides (Schumacher, 1973; Gaffney, 1975) is almost directly dorsal to the large processus coronoideus, suggesting the capability of a very powerful bite.

Other modifications in the skull of *Palatobaena* probably are related to its mode of feeding and are unique for baenids, and possibly among cryptodires.

It cannot be determined if the Cretaceous and early Paleocene specimens or the late Paleocene type specimen of *Palatobaena bairdi*

have a processus pterygoideus externus. Both Gaffney's (1972a, Fig. 23) and our restorations suggest it was present. Gaffney (1972b, p. 31) noted that the "lateral edge [of the process] is generally produced into a vertical plate that acts as a guide for the lower jaw during adduction of the lower jaw." The well-preserved specimen of *P. bairdi* CCM 77-11, possesses a remnant of the processus pterygoideus externus, but the vertical plate is absent (Fig. 3). In *P. gaffneyi* even the remnant of the process is almost completely gone (Fig. 5b). The reduction and final loss of the process and vertical plate suggest other features probably arose in the skull, the lower jaws, or in both to stabilize the lower jaws during adduction. At least part of the answer may be found in the curious development of a slightly medially positioned tubercle in the dorsal margin of the cheek emargination in *P. bairdi*. In *P. gaffneyi* this tubercle is absent, but a shallow sulcus positioned on the lateral margin of the cheek emargination is present. Both of these structures presumably were for the origin of a superficial portion of the M. adductor mandibulae externus (Pars superficialis) or an analog of the M. zygomaticomandibularis of trionychids (Schumacher, 1973). Depending on the point of insertion on the lower jaw, this "de novo" muscle may have 1) served to stabilize the lower jaw during adduction, 2) increased muscle mass for adduction, 3) served as a muscle for protraction to counteract the retraction of the M. adductor mandibulae externus, or in a combination of these functions. There are two probable places on the lower jaw where this muscle may have been inserted. The first is along the lower border of the large fossa on the labial side of the jaw ventral to the coronoid (see Fig. 4b). If it inserted here, it probably served as an adductor and stabilizer, but not for protraction. The second possible point of insertion is the small fossa on the lateral side of the lower jaw below the anterior edge of the area articularis mandibularis (Fig. 4b). This fossa is posterior and ventral to the area of origin on the skull, and if the "de novo" muscle inserted here it could serve for adduction, lower jaw stabilization, and protraction to counteract the

retraction of the M. adductor mandibulae externus. It is also possible but unlikely that the M. pterygoideus inserted here and served a similar purpose. However, among baenids only *Palatobaena bairdi* possessed this small fossa on the lateral side of the lower jaw (lower jaws are not known for *P. gaffneyi*, but it presumably possessed an homologous fossa) plus a tubercle or sulcus along the cheek emargination. This suggests, but by no means proves, that these new structures were respectively for the insertion and origin of the "de novo" muscle.

A lower jaw from the middle Paleocene (Torrejonian) of Wyoming, PU 17108, was included in the hypodigm of *Plesiobaena putorius* by Gaffney (1972a, p. 264) and is shown here in Figure 4c, d. This lower jaw could also belong to *Palatobaena bairdi*, but because of several characters it is probably best included in *Plesiobaena putorius* as done by Gaffney (1972a). It shows the high degree of parallelism between *Palatobaena* and *Plesiobaena putorius*.

In Gaffney's comments and figures (1972a) it can be seen that *Plesiobaena putorius* has not developed the extreme specializations of *Palatobaena*. Although it has wide triturating surfaces on the maxilla and lower jaws as in *Palatobaena* it still retains the presumably more primitive triangular-shaped face of other baenids. It is difficult to determine, based on Gaffney's illustration (fig. 16A); however, it appears that the one specimen of *Plesiobaena putorius* which preserves the cheek emargination (PU 16837) does not show the presence of a tubercle (as in *Palatobaena bairdi*) or a sulcus (as in *Palatobaena gaffneyi*). In addition, the lower jaw (PU 17108), probably assignable to this species, lacks the small fossa below the area articularis mandibularis as seen in *Palatobaena bairdi* (compare Fig. 4b and d). PU 17108 is somewhat laterally compressed as evidenced by a crack in the midline of the lower jaw; however, even when this is accounted for the triturating surfaces clearly do not rotate outwards from the midline to the degree seen in the lower

jaws of *Palatobaena* (compare Fig. 4a and c). This is also true of the triturating surfaces on the maxilla of *Plesiobaena putorius* (Gaffney, 1972a, fig. 15) compared to both species of *Palatobaena*. These differences support Gaffney's (1972a) allocation of PU 17108 to *Plesiobaena putorius*.

Hypotheses concerning jaw mechanics and feeding habits based solely on skull and lower jaw morphology are always speculative. Nevertheless, the combination of structural features in the skull of both species of *Palatobaena* strongly suggest that this genus had developed masticatory muscles especially designed for a powerful bite (possibly at the expense of rapid jaw movements). Combined with greatly widened triturating surfaces this indicates a probable molluscivorous diet.

A final point of speculation concerns the presence of a sulcus around the apertura narium externa variously developed in the two species of *Palatobaena*. The simplest explanation is that the sulcus was for the origin of muscles inserting on a moveable proboscis. If this is true, *Palatobaena* was undoubtedly a very odd looking creature with a rounded face and a moveable snout.

Intrafamilial Relationships of *Palatobaena*

Gaffney erected a new subfamily, Palatobaeninae (1972a, p. 269) for his new genus *Palatobaena*. The modifications in the anterior region of the skull are strikingly different from eubaenines (or other baenoids). The blunting of the snout, the expansion of the triturating surface, and the expansion of the muscle attachment along the cheek emargination as noted above suggest a very specialized feeding mechanism, probably for crushing molluscs. However, the recovery of material preserving the posterior portion of the skull indicates *Palatobaena* is very similar to

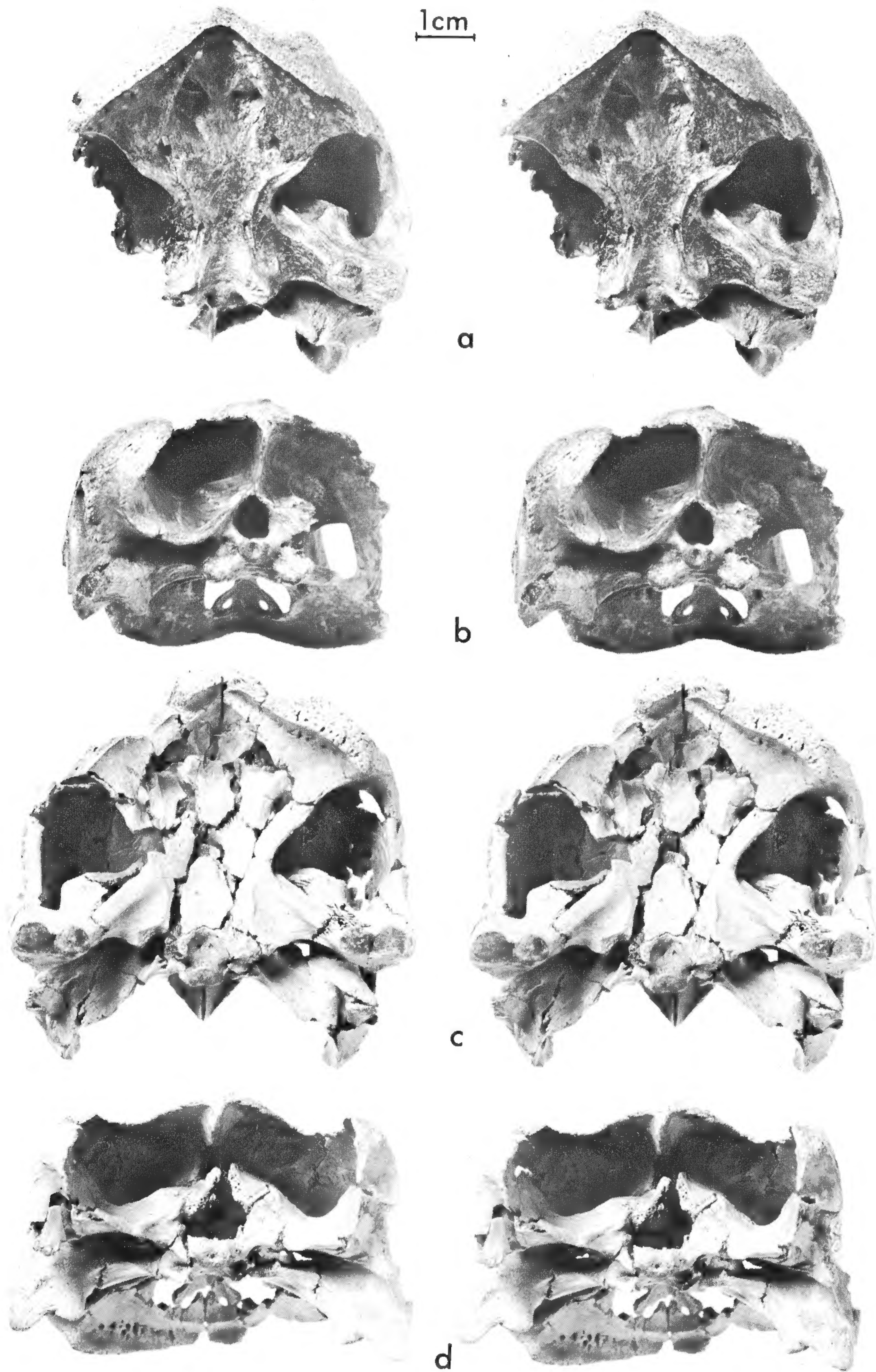
eubaenines. As in eubaenines the temporal emargination is deep at least in stratigraphically lower specimens and the parietal and squamosal are separated by a flange of the postorbital. As in *Eubaena cephalica* the skull roof overlying the crista supraoccipitalis narrows and extends beyond the foramen magnum in the latest Cretaceous specimen of *P. bairdi*, UCMP 114539. However, in this specimen of *P. bairdi* the narrowing and posterior extension are more exaggerated. The quadratojugal is reminiscent of other eubaenines. There is no broad anterior process and the quadratojugal is C-shaped with a dorsal process.

Gaffney tentatively associated *Palatobaena* with the baenines (1972a, p. 306 and Figs. 45 and 46). His criteria were the fusion of the nasals to the frontals and a presumed shallow temporal emargination. The additional material, as described above, has shown that the nasals are present but greatly reduced and that the temporal emargination is like other eubaenines.

The most important feature aligning *Palatobaena* with the eubaenines is the expanded triturating surface found in all members of the subfamily, except *Plesiobaena antiqua*. The polarity of this character state is more easily adduced than others in the skull. The expanded triturating surface is regarded as a derived character. It is not clear whether this character state is to be regarded as a shared derived character of eubaenines or as a parallel development. The former conclusion is favored here and accordingly we place *Palatobaena* with the eubaenines. If it can be shown that the similarities in the posterior portion of the skull of *Palatobaena* and other eubaenines are also shared derived characters for the subfamily,

Fig. 7

Stereophotographs of *Palatobaena bairdi* Gaffney, CCM 77-11: a, ventral view; b, posterior view and *Palatobaena gaffneyi* Hutchison, n. sp., UCMP 114529 (type): c, ventral view; d, posterior view.



then this could be used as additional evidence for aligning these taxa. Our study indicates that the character state seen in the posterior region of the skull of eubaenines is primitive for both eubaenines and baenines, and possibly for the family Baenidae. *Plesio-baena antiqua* lacks the expanding triturating surface and for that reason is tentatively excluded from the Eubaeninae (Archibald, 1977). The slight expansion of the triturating surface seen in the late Paleocene *Plesio-baena putorius* is regarded as a development parallel to that seen in the Cretaceous and later eubaenines. The Eubaeninae is here considered to comprise the following genera recognized by Gaffney (1972a, p. 248) *Eubaena*, *Stygiochelys*, and *Palatobaena*.

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Literature Cited

- Archibald, J. D.** 1977. Fossil Mammalia and Testudines of the Hell Creek Formation, and the geology of the Tullock and Hell Creek Formations, Garfield County, Montana. Ph.D. dissertation, Univ. Calif., Berkeley.
- Cope, E. D.** 1882. Contributions to the history of the Vertebrata of the Lower Eocene of Wyoming and New Mexico, made during 1881. Proc. Amer. Philos. Soc. 20:139-197.
- Gaffney, E. S.** 1972a. The systematics of the North American family Baenidae (Reptilia, Cryptodira). Bull. Amer. Mus. Nat. Hist. 147:243-319.
- 1972b. An illustrated glossary of turtle skull nomenclature. Amer. Mus. Novitates, no. 2486:1-33.
- 1975. A phylogeny and classification of the higher categories of turtles. Bull. Amer. Mus. Nat. Hist. 155:389-436.
- Gingerich, P. D.** and **K. E. Rose.** 1977. Preliminary report on the American Clark Fork mammal fauna, and its correlation with similar faunas in Europe and Asia. Géobios. Mém. Spécial 1:39-45.
- Schumacher, G. H.** 1973. The head muscles and hyolaryngeal skeleton of turtles and crocodilians, p. 101-199. In C. Gans and T. S. Parsons [eds.] Biology of the Reptilia, Vol. 4. Academic Press, New York.
- Williams, E. E.** 1950. Variation and selection in the cervical central articulations of living turtles. Bull. Amer. Mus. Nat. Hist. 94:505-562.

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