The Supraotic Bone in Neopterygian Fishes (Osteichthyes, Actinopterygii)*

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ABSTRACT

The supraotic is a chondral bone that has a relatively restricted phylogenetic occurrence, since it occurs only in some extinct neopterygian fishes. Like the supraoccipital in teleosts, coelacanths, and tetrapods, the supraotic is positioned at the dorsal midline in the posterior part of the braincase, but the supraotic and supraoccipital have been distinguished on topographic grounds. The supraotic is situated anterior to the occipital segment, presumably within the synotic tectum. The supraoccipital may be confined to the occipital segment (as in the Jurassic stem teleost *Pholidophoroides*), or it can extend into the otic region following fusion of the synotic tectum and occipital arch (as in many modern teleosts and tetrapods). In some Recent teleosts (e.g., *Oryzias, Danio, Betta*) the supraoccipital may form entirely within the synotic tectum, a presumably secondary arrangement. The topographic distinction between the supraotic and supraoccipital is therefore obscured secondarily in Recent teleosts and is more evident in fossils. In *Amia* and extinct stem teleosts such as *Pholidophoroides*, the dorsal part of the cranial fissure persists during development, separating the occipital pila from the synotic tectum even in the adult. Such persistence of the cranial fissure dorsally in extinct halecomorphs may have prohibited the supraotic from extending onto the occipital arch.

The supraotic bone is present in the early Cretaceous amiid *Calamopleurus cylindricus*, but it is absent in the Recent *Amia calva*, suggesting a previously unsuspected bone loss in amiid evolution. In *Calamopleurus cylindricus* and *Ionoscopus cyprinoides* the supraotic encloses the dorsal parts of the anterior and posterior semicircular canals. In *I. cyprinoides* the supraotic also forms the mesial wall of the lateral cranial canal, which in pholidophorid teleosts lies

within the pterotic. The supraotic may be exposed in the skull roof at the posterior midline (as in *Ionoscopus, Oshunia*), or it may be located entirely beneath the parietals (as in *Calamopleurus*). A peculiar median chondral bone in the roof of the otic region in the pycnodontiform *Neoproscinetes penalvai* is probably also a supraotic, although its morphology is highly specialized.

INTRODUCTION

The supraotic is a median chondral bone from the otic region of the braincase. The bone is known only in some Mesozoic non-teleostean neopterygians and is not well documented in the literature; for example, it was not mentioned in Rojo's (1991) dictionary of fish osteology, nor in Jollie's (1986) primer of actinopterygian skull bones, even though the supraotic was first recognized more than a decade earlier (Patterson, 1975) in isolated Bathonian "caturid" braincases that had been previously referred to *Aspidorhynchus* (Rayner, 1948). For many years, this remained its only documented occurrence.

Patterson (1975: 436) considered the supraotic to be a phylogenetically novel ossification, and distinguished it from the supraoccipital by its different topographic position relative to the occipital fissure (he observed that the supraotic ". . .does not appear on the posterior face of the braincase, the normal position of the ossification centre of a supraoccipital, and only intrudes between the anterior extension of the epioccipitals"). This has remained the principal distinguishing criterion between the two bones, but data concerning supraotic morphology and supraoccipital ontogeny are sparse. In this paper additional examples of the supraotic are documented and compared with the supraoccipital from paleontological and ontogenetic perspectives.

Additional examples of the supraotic are described here from three extinct Mesozoic halecomorph taxa known from complete skeletal remains; *Ionoscopus cyprinoides,* from the Late Jurassic of Europe, plus *Oshunia brevis* and *Calamopleurus cylindricus* (= *Enneles audax* Jordan and Branner, 1908) from the Early Cretaceous of Brazil. These taxa not only help confirm Patterson's (1975) original topographic observations about the supraotic, but also show that the bone is present in a variety of Mesozoic halecomorphs (figs. 1, 6–10, 13, 14). Besides these occur-

rences, a supraotic may also be present in an Early Jurassic (Toarcian) braincase referred to *Caturus* by Rayner (1948; see fig. 11 below). Additionally, the "endochondral supraoccipital" (Nursall and Maisey, 1991; Nursall, 1996) found in *Neoproscinetes* and some other pycnodontiforms is reinterpreted here as a highly specialized supraotic (see below and figs. 15, 6), but the supposed supraotic noted in a specimen of *Lepidotes* by Patterson (1975) is here considered to be some other bone.

The evolutionary distribution of the supraotic is uncertain, as its occurrences are phylogenetically restricted but disjunct. The supraoccipital in primitive teleosts such as *Pholidophorus* and *Leptolepis* certainly has a very different appearance from the supraotic in primitive halecomorphs such as *Ionoscopus* and "*Aspidorhynchus,*" suggesting that these bones probably evolved independently. According to hypotheses by which pycnodontiforms and teleosts are closely related (e.g., Nursall, 1996; Gardiner et al., 1996), the supraotic could be interpreted as an apomorphic feature of halecomorphs and the teleost-pycnodontiform clade, even though the bone has not been reported in any teleost (unless it is masquerading as the supraoccipital) and it is apparently absent in semionotids. Alternatively, pycnodontiforms might be allied more closely to halecomorphs than to teleosts; that hypothesis is supported by presence of the supraotic in pycnodontiforms, and also by some other features, e.g., inclusion of the dermosphenotic into the skull roof, fusion of the symplectic to the preopercle (Maisey, in Gardiner et al., 1996: fig. 6).

A supraoccipital is primitively present in all Recent teleosts, as well as in many extinct stem teleosts including Mesozoic leptolepids and pholidophorids, and its presence has been regarded as a teleost synapomorphy (Brito, 1992). In some extinct stem teleosts (e.g., *Pholidophorus bechei, Hulettia, Vinctifer*) the bones of the occipital region are

indistinguishably fused (Patterson, 1975; Schaeffer and Patterson, 1984: 22; Brito, 1992). It is possible that the supraoccipital was primitively absent in some of these taxa, although it is present in other "pholidophorid-level" teleosts.

The supraoccipital in primitive extinct teleosts (e.g., "pholidophorids," *Leptolepis,* and perhaps ichthyodectids) is chondral, but in some modern teleosts there may also be a secondary dermal contribution (e.g., in *Mastacembelus*; Taverne, 1973: fig. 1). In some extinct stem teleosts (e.g., *Pholidophoroides limbata*) the chondral supraoccipital is separated from the occipital region by the cranial fissure (Patterson, 1975: 314). In *Pholidophorus bechei* the supraoccipital develops membrane bone outgrowths extending anteriorly into the otic region, and in most other "pholidophorids" and "leptolepids," the supraoccipital extends anteriorly as chondral bone, as in modern teleosts. Here the dorsal part of the occipital fissure is usually closed, so that cartilage of the occipital pila is fused indistinguishably with that of the synotic tectum (de Beer, 1937). This probably represents a derived condition that is shared by many pholidophorids, leptolepids and most Recent teleosts (Patterson, 1975). Brito's (1992: 154) suggestion that having the supraoccipital extending into the otic region is a synapomorphy only of *Ichthyokentema* and *Leptolepides sprattiformis* is not supported by data from Recent teleosts, in which the bone is commonly located on the synotic tectum.

In some Recent teleosts the supraoccipital is positioned so far anteriorly that it actually first appears on the *anterior* margin of the synotic tectum, e.g., in the medaka *Oryzias* (Atherinomorpha), the zebrafish *Danio* (Cyprinidae) and the percomorph *Betta splendens* (Langille and Hall, 1987; Cubbage and Mabee, 1996; Mabee and Trendler, 1996). Moreover, according to an illustration by Langille and Hall (1987: fig. 12; also see fig. 17 of this paper), the occipital cartilages (?) in *Oryzias* are still separated from the synotic tectum even after the supraoccipital appears, suggesting that this bone is entirely confined to the synotic tectum. In such an anterior position, the supraoccipital mimics the topographic relations of the supraotic in haleco-

morphs, but it presumably represents a secondary condition in teleosts. The chondral part of the supraoccipital may arise from a single ossification center at the midline (e.g., in *Salmo*; de Beer, 1937), but in *Oryzias* and *Danio* there is a bilateral pair of ossifications that subsequently fuse medially as ossification proceeds (Langille and Hall, 1987; Cubbage and Mabee, 1996); this may also represent a secondary condition.

No median supraoccipital or supraotic is known in living or extinct gars (Jollie, 1984b; Wenz and Brito, 1992; 1996), nor in the living *Amia* (fig. 2B). The presence of a supraoccipital in teleosts is widely accepted as a synapomorphy of the group, although Gardiner (1984: 206) has argued that its presence may be primitive for actinopterygians or even for osteichthyans. The enormity of the phylogenetic gap between teleosts and sarcopterygians nevertheless provides circumstantial support that the teleost supraoccipital is not homologous with that of tetrapods and actinistians. Furthermore, the phylogenetic distribution of the supraoccipital in coelacanths suggests that it evolved independently from that in tetrapods (Forey, 1998). In Recent cladistians and some primitive extinct actinopterygians, the midregion of the braincase immediately behind the otico-occipital fissure is ossified dorsally, in the vicinity of the posterior dorsal fontanelle (as in *Mimia, Moythomasia, Perleidus, Caturus groenlandicus, Ospia,* and *Watsonulus*; Gardiner, 1984; Aldinger, 1932: 22: fig. 6; Stensiö, 1932: figs. 72, 73; Olsen, 1984: fig. 7). This does not constitute evidence of a dorsal center of ossification, however, and no supraotic or supraoccipital bone has been identified in these taxa.
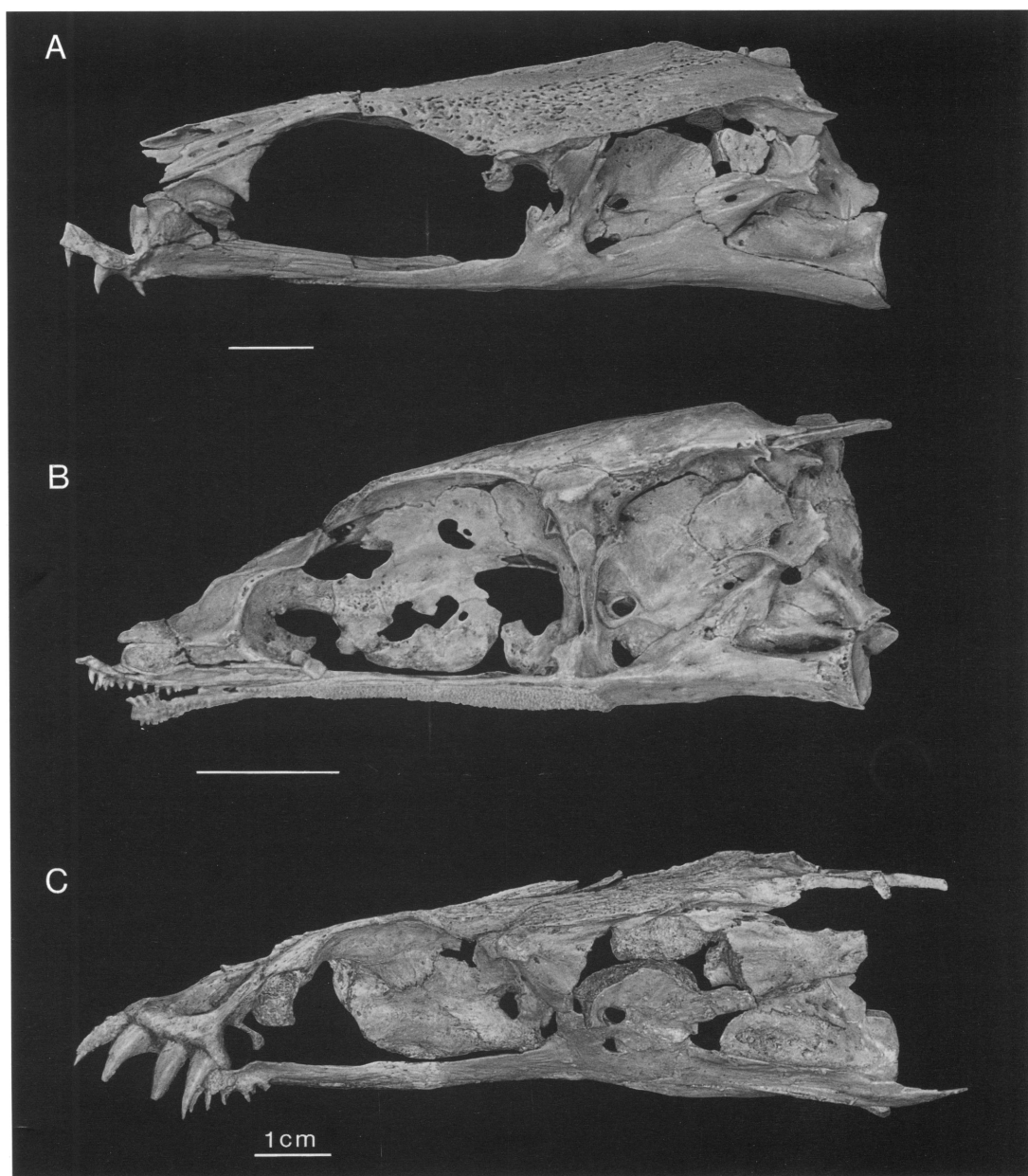
Fig. 1. The braincase of three fossil halecomorphs following acid preparation, all in lateral view, with annotated diagrams of otico-occipital regions. (**A**) *Ionoscopus cyprinoides* BM(NH) 37795a (Late Jurassic, Solnhofen Limestone, Germany). Pterotic bone is not visible in lateral view but is illustrated in Figure 8B; (**B**) *Oshunia brevis* AMNH 12793 (Early Cretaceous, Santana Formation, Brazil); (**C**) *Calamopleurus cylindricus* AMNH 11840 (Early Cretaceous, Santana Formation, Brazil), a reversed image of the specimen shown in Figure 6. Epiotic is hidden by intercalar in this view, but can be seen in Figure 6A. Unfinished spongy endochondral bone shown stippled.
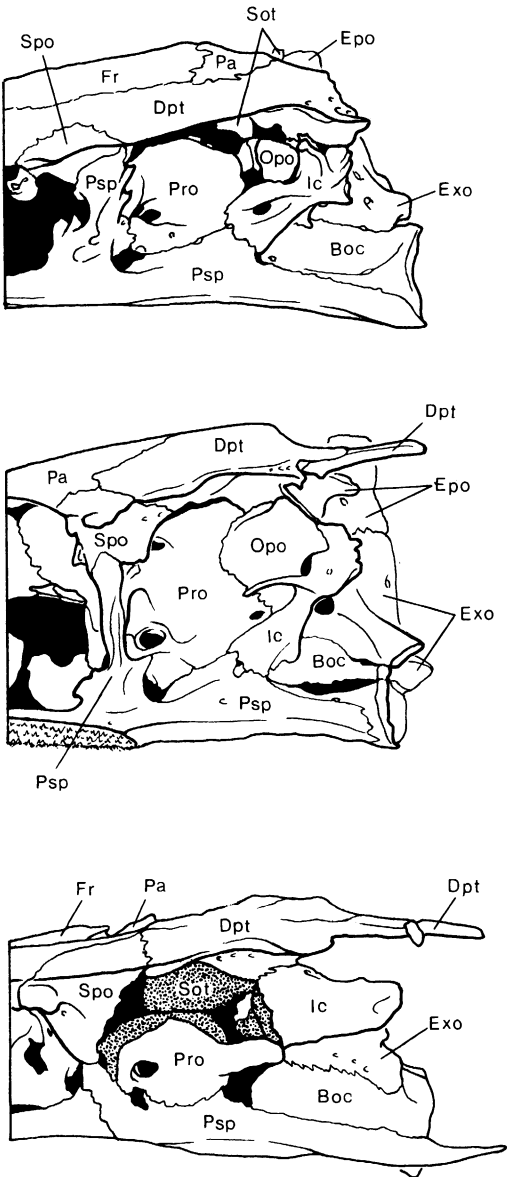
Fig. 1. Continued.

a single slab). All the illustrations and reconstructions of the labyrinth region in the fossils were prepared by Lorraine Meeker, whose efforts and patience are greatly appreciated. I thank Melanie Stiassny for many helpful discussions about Recent teleost osteology and for providing access to specimens and pertinent literature, and I also thank Lance Grande and Willi Bemis for providing information about their phylogeny of

amiids in advance of its publication. I am grateful to Herbert R. and Evelyn Axelrod for their support of paleoichthyological research at the American Museum of Natural History.

ABBREVIATIONS

Note: Some abbreviations are followed by (l) = left or (r) = right; the same abbreviations are used to denote cavities in bones occupied by semicircular canals and actual canals where the labyrinth is illustrated.

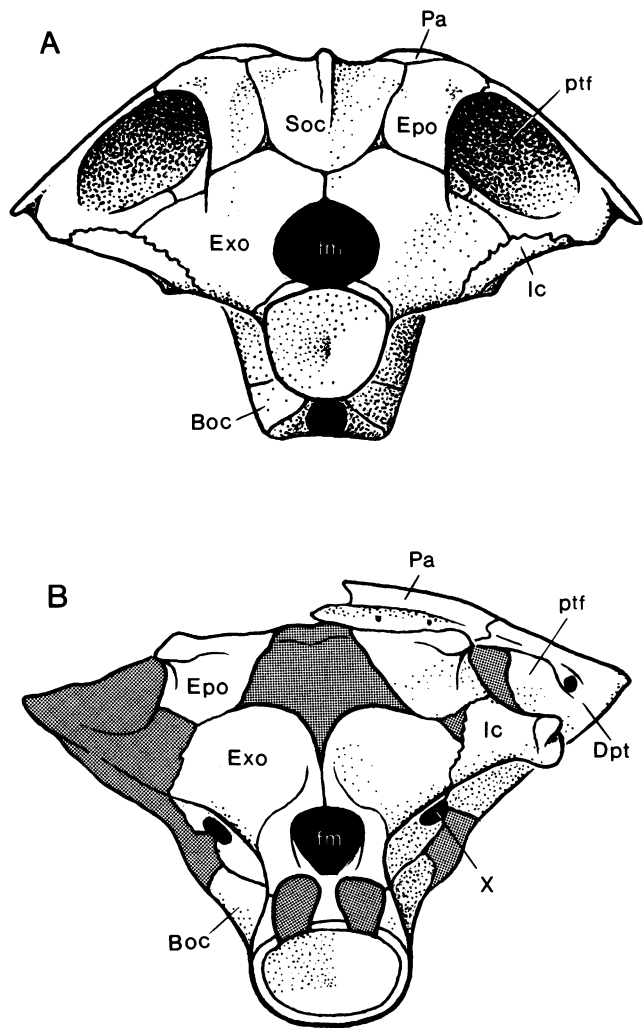|	
aamp	anterior ampulla
ac	auditory capsule
alcc	anterior lateral cranial canal
asc	anterior semicircular canal or cavity it occupies
Asp	Autosphenotic
assu	apex of superior utricular sinus
Boc	Basioccipital
Bsp	Basisphenoid
cpro	supraoccipital cartilaginous connection with prootic
cpts	supraoccipital cartilaginous connection with pterosphenoid
dldpt	descending lamina of dermopterotic
Dpt	Dermopterotic
Dsp	Dermosphenotic
eamp	external ampulla
eb	epiphyseal bar
ed	endolymphatic duct
edp	pit in supraotic for endolymphatic duct
epi	epiphyseal cartilage
Epo	Epioccipital (epiotic)
esc	external semicircular canal, or cavity it occupies
eth	ethmoid cartilage
Exo	Exoccipital
"f"	"foramen" (Pehrson, 1922) between synotic tectum and occipital pila
fis	metotic fissure (embryos) or otico-occipital fissure (adult)
fm	foramen magnum
focn	foramen for occipital nerve
Fr	Frontal
Ic	Intercalar
ips	internal perichondral surface of supraoccipital
lag	lagena
lps	lateral perichondral surface of supraoccipital
mp	median pocket
n	notochord
occ	occipital condyle
op	occipital pila
Opo	Opisthotic

Fig. 2. Occipital views of the braincase. (A) *Elops*, a teleost, with the supraoccipital situated between the epioccipitals, after Patterson (1973); (B) *Amia*, a halecomorph, with cartilage (stippled) between the epioccipitals (left parietal, dermopterotic and intercalar excluded for clarity). Allis (1897) and Patterson (1973) depicted the epioccipital and exoccipital in *Amia* separated by cartilage, but these bones may contact each other in some individuals (as shown here).

Ors	Orbitosphenoid	psc	posterior semicircular canal, or cavity
Pa	Parietal		it occupies
pamp	posterior ampulla	Psp	Parasphenoid
pb	paraphyseal bar	ptf	posttemporal fossa
pep	pre-epiotic pocket	Pto	Pterotic
plcc	posterior lateral cranial canal	Pts	Pterosphenoid
pmgt	posterior marginal tectum	sac	sacculus
pmt	posterior medial tectum	sacr	saccular recess
pps	posterior perichondral surface of su-	sepo	supraoccipital suture with epioccipital
	praoccipital	sexo	supraoccipital suture with exoccipital
Pro	Prootic	Soc	Supraoccipital

sop	supraotic pocket
Sot	Supraotic
Spo	Sphenotic
spro	supraoccipital suture with prootic
ssu	superior utricular sinus
st	synotic tectum
tff	trigemino-facialis foramen
ut	utriculus
utr	utricular recess
vf	vagus foramen
VII	facial nerve
VIII	acoustic nerve
VIII(lag)	lagenar ramus of acoustic nerve
VIII(sac)	saccular ramus of acoustic nerve
VIII(ut)	utricular ramus of acoustic nerve
IX	glossopharyngeal nerve
X	vagus nerve

SYSTEMATIC NOTE

Taxonomic nomenclature used here agrees with that established by Grande and Bemis (1998) and taxa examined in the present work are placed within a simplified version of their classification as follows:

Subdivision Halecomorphi Cope, 1872
  Order Parasemionotiformes Lehman, 1966
    Family Parasemionotidae Stensiö, 1932
      Watsonulus eugnathoides (Pivetau, 1935)
  Order Ionoscopiformes Grande and Bemis, 1998
    Family Ionoscopidae Lehman, 1966
      Ionoscopus cyprinoides (Wagner, 1863)
    Family Oshuniidae Grande and Bemis, 1998
      Oshunia brevis Wenz and Kellner, 1986
      ?"*Aspidorhynchus*" (sensu Rayner, 1948)
    Family Ophiopsidae Bartram, 1975
      Macrepistius arenatus Cope, 1894
    Family indet.
      "*Caturus*" (sensu Rayner, 1948)
  Order Amiiformes Hay, 1929
    Family Caturidae Owen, 1860
      Caturus furcatus Agassiz, 1843
    Family Amiidae Bonaparte, 1838
      Amia calva Linnaeus, 1766
      Calamopleurus cylindricus Agassiz, 1841

Previous descriptive and systematic work on ionoscopids is inadequate (Saint-Seine, 1949; Steutzer, 1972) and a thorough review of the group is required. Such an undertaking is in preparation but is beyond the scope of this paper; nevertheless, one concern needs to be aired here. Published phylogenetic discussions about ionoscopids (e.g., Saint-Seine, 1949; Patterson, 1973; Grande and Bemis, 1998) are based mainly on Late Ju-

rassic taxa from Solnhofen, Germany, and Cerin, France (e.g., *I. cyprinoides, I. desori*). These taxa seem to differ morphologically in several respects from the type species, *I. petraroiae* from the Early Cretaceous of Benevento, Italy (D'Erasmo, 1915), which is in need of revision. The Brazilian ionoscopid *Oshunia brevis* resembles *I. petraroiae* and differs from *Ionoscopus cyprinoides* in its general head shape and proportions, depth and arrangement of the infraorbital bones, jaw proportions (particularly length of the maxilla, which terminates below the orbit in *Oshunia brevis* and *I. petraroiae* rather than extending farther posteriorly, as in *I. cyprinoides*; D'Erasmo, 1915: fig. 18), and in the dentition (particularly in size and form of the teeth). *Oshunia brevis* also differs from *I. cyprinoides* in number of ural centra, hypurals and other caudal elements, but their numbers are not yet known in *I. petraroiae*.

Grande and Bemis (1998) separated *Oshunia* from *Ionoscopus* at family level, and regarded the family Oshuniidae as a sister taxon to ophiopsids on the basis of two characters (most anterior infraorbital bone deeper than long, and presence of lateral line canal in maxilla). In view of the close morphological agreement between the braincase of *Oshunia* and those referred to "*Aspidorhynchus*," the latter are provisionally classified here within the family Oshuniidae although they are not renamed. In *Ionoscopus cyprinoides* the most anterior infraorbital bone is much wider than deep, and the maxilla does not include a sensory canal (Saint-Seine, 1949; Steutzer, 1972; Grande and Bemis, 1998). From D'Erasmo's (1915) figure 18, however, the most anterior infraorbital appears to at least as long as wide in *Ionoscopus petraroiae*, and the maxilla has never been reexamined in this taxon to see whether it bears a sensory canal. *Oshunia brevis* may thus be more closely related to the type species of *Ionoscopus* than to *I. cyprinoides*, and future nomenclatural adjustments may be required among these taxa, e.g., by removing *I. cyprinoides* from the Ionoscopidae and replacing *Oshunia* (and "*Aspidorhynchus*"?) within it. At the present time, the braincase is still unknown in *I. petraroiae* and thus, unless otherwise specified, in the following
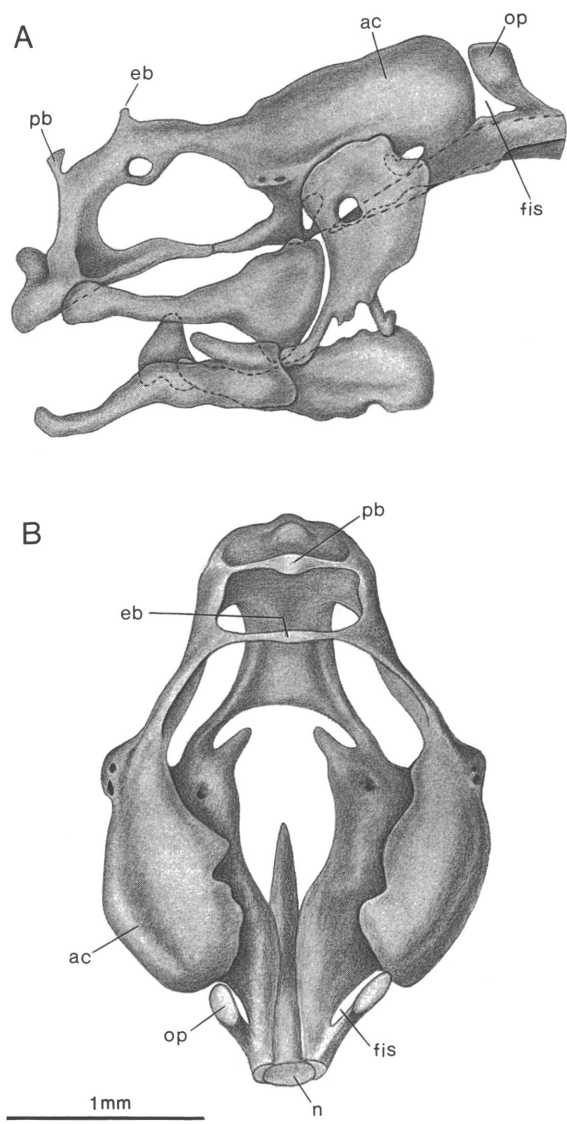
Fig. 3.   *Amia calva:* developing chondrocranium of Stage 9 embryo (13.6–14 mm). (**A**) Lateral; (**B**) dorsal view (modified from Pehrson, 1922). The paired outgrowths of the occipital pila lie on either side of the notochord, and are separated by the metotic fissure from the otic capsule.

pages the name *Ionoscopus* refers only to *I. cyprinoides.*

THE OTIC REGION AND SUPRAOTIC BONE

THE OTICO-OCCIPITAL REGION IN *AMIA CALVA*

The morphology of the braincase in *Amia calva* was described in the well-known monograph by Allis (1897) and was revised

recently by Grande and Bemis (1998). Chondral bones of the braincase include paired pre-ethmoids, lateral ethmoids, orbitosphenoids, pterosphenoids, basisphenoids (small, and sometimes fused together), prootics, sphenotics, exoccipitals, and epioccipitals. The median basioccipital is large, and during ontogeny becomes fused with two or even three vertebral centra (Grande and Bemis, 1998: 75). Pterotics and opisthotics are ab-
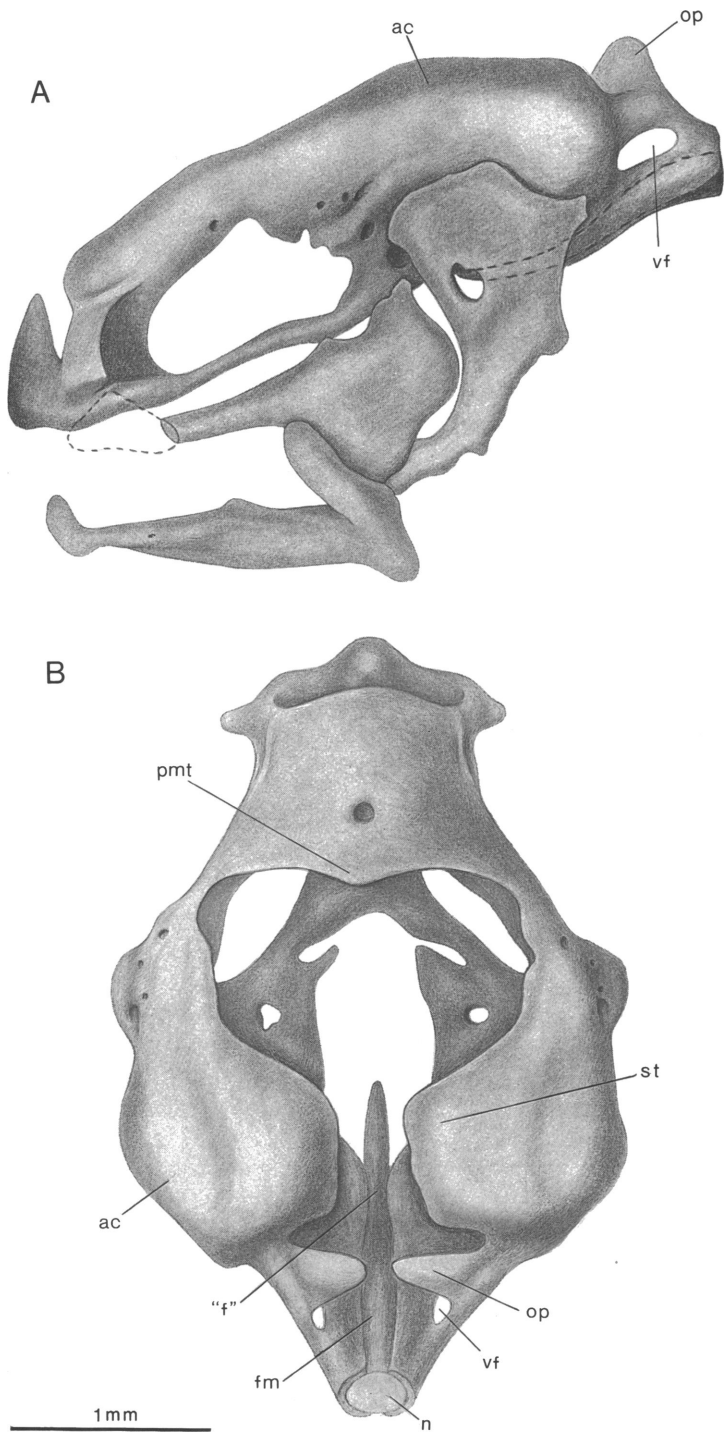
Fig. 4. *Amia calva:* developing chondrocranium of Stage 10 embryo (19.5 mm). **(A)** Lateral; **(B)** dorsal view (modified from Pehrson, 1922). Outgrowths of the occipital pila are now attached to the posterior wall of the otic capsule, but are separated) from paired ingrowths of the capsular cartilage farther anteriorly by a large space (f = the "foramen" of Pehrson). The ingrowths of the capsules eventually fuse (by Stage 11 of Pehrson) to form the synotic tectum, and the occipital pila fuse to become the occipital tectum, but this remains separated dorsally by a space from the occipital cartilage.
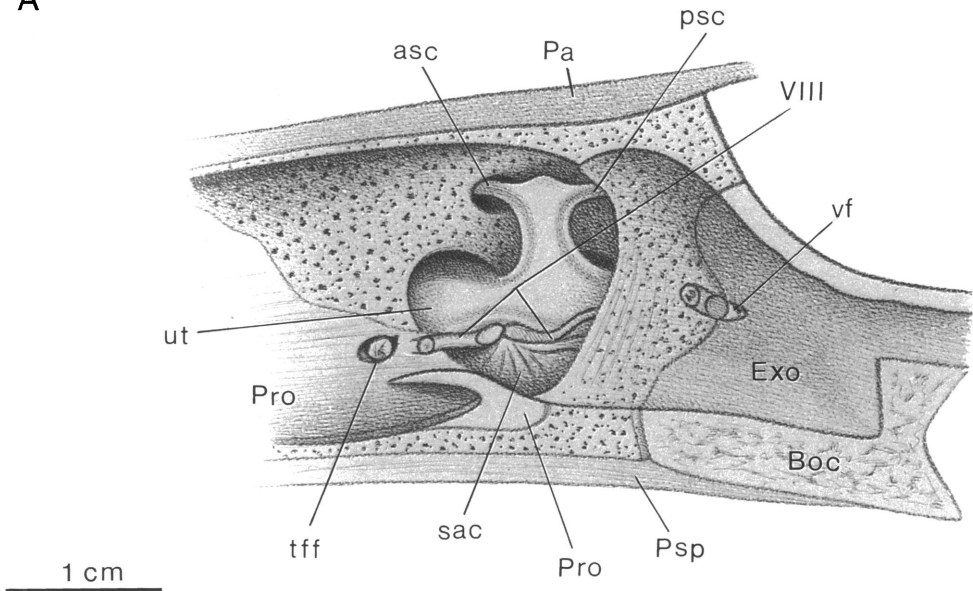
A

Fig. 5. The labyrinth in *Amia* (from Retzius, 1881; annotations have been emended from the original figures). (**A**) Right half of braincase in sagittal view showing the general relations of the labyrinth and acoustic nerve. No structures were identified in the original figure, and all labels are new. The utricular and saccular-lagenar chambers are incorrectly depicted as confluent, whereas in the other views they are more accurately shown as separate entities. The utricular branch of the acoustic nerve seems to be entering the braincase wall behind the trigemino-facialis foramen in this view, which is also incorrect; (**B**) lateral view of right labyrinth organ and acoustic nerve, anterior to right; (**C**) medial view of right labyrinth organ and acoustic nerve, anterior to left. Note the vertical extent of the endolymphatic duct, the raised apex of the superior sinus and the alignment of this sinus with the saccular recess.

sent in *Amia,* and no supraoccipital or su-praotic has been found there even in large individuals.

Norman (1926: 437) recognized six prin-cipal areas of chondrification in the neopter-ygian cranial roof behind the ethmoid region: the *paraphyseal bar* (present in gars and *Amia,* but generally absent in teleosts); the *epiphyseal bar* (apparently a primitive fea-ture, but having a disjunct distribution among teleosts); the *anterior medial tectum* (median longitudinal bar connecting the pa-raphyseal and epiphyseal bars, found in some teleosts); the *synotic tectum* formed from the otic capsules; the *posterior medial tectum* (a posterior median longitudinal bar, often in-complete or absent, connecting the epiphy-seal bar and synotic tectum); and the *occip-ital tectum* (= posterior tectum; de Beer, 1937; formed from the occipital pila). Ad-ditionally, the epiphyseal bar may be con-nected to the auditory capsules by the paired

posterior marginal tectum (e.g., *Amia*; Pehr-son, 1922: figs. 11, 13; *Danio*; Cubbage and Mabee, 1996: fig. 5).

In adult *Amia* the entire roof of the brain-case is chondrified (Allis, 1897: pl. 21). A considerable part of this chondrification is represented by the epiphyseal bar. In this re-spect *Amia* differs from most teleosts (*Salmo* is an exception), where there is usually a large fontanelle in the roof of the endocra-nium and the epiphyseal bar may be absent (Norman, 1926; de Beer, 1937). Extensive chondrification of the endocranial roof ante-rior to the synotic tectum, as seen in *Amia,* may have been a prerequisite for the evolu-tion of a median supraotic bone, as it prob-ably could not be formed where a large dor-sal fontanelle persisted (e.g., as in *Ospia*; Stensiö, 1932). Instead, large paired pterotics may have been present within the synotic tectum and lateral to the dorsal fontanelle, as
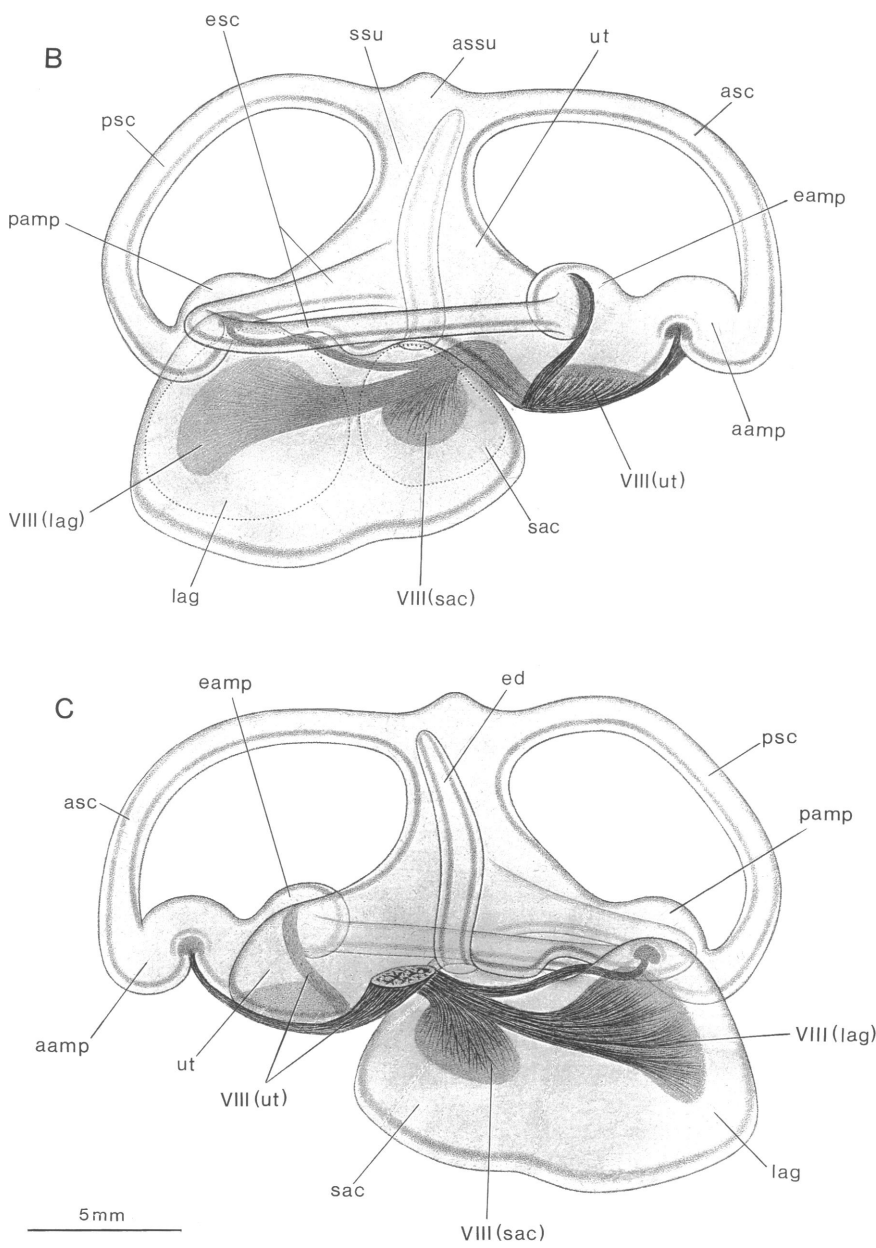
Fig. 5. Continued.

in the extinct stem teleost *Pholidophoroides limbata* (Patterson 1975: fig. 82).

The supraotic is known only from fossils, where its ontogeny cannot be investigated directly. Cranial development in modern *Amia* nevertheless provides some clues regarding the ontogenetic history of the supraotic. According to Schreiner (1902) and Pehrson (1922), in *Amia* the occipital tectum begins to develop in 9–10-mm embryos as paired cartilaginous outgrowths (the occipital pila) on either side of the notochord, behind the metotic fissure (fig. 3). These paired outgrowths eventually become attached to the posterior wall of the otic capsule (Pehrson's stage 10), thereby defining the vagus fora-

men, but the occipital pila remain separated dorsally even at that stage (fig. 4). Eventual fusion of the occipital pila leads to formation of the foramen magnum later in ontogeny (de Beer, 1937).

Pehrson (1922: 26) showed that in embryos of *Amia* the synotic tectum remains separated from the occipital pila farther posteriorly by a large dorsal "foramen," which is essentially a relic of the median dorsal part of the fissure between the otic and occipital tectum of the embryonic braincase (fig. 4). A similar fenestra occurs in the roof of the braincase in *Eusthenopteron* (Jarvik, 1980: vol. 1: fig. 88A; fe.p), partially separating the occipital plug from the rest of the cranium. By contrast, in most teleosts (and many tetrapods; de Beer, 1937) the synotic tectum and occipital pila become fused at an early stage in ontogeny and the structure thus formed may contain cartilage from both arches. As noted earlier, however, in *Oryzias* the synotic tectum (containing a median dorsal bone usually termed the supraoccipital) appears to be separated by a continuous dorsal fissure from paired (occipital?) cartilages (fig. 17A). Persistence of the corresponding space in *Amia* provides a clue as to why the supraotic is restricted to the region anterior to the occipital fissure in fossils; continued separation of the synotic and occipital tecta probably would have prohibited any ossification center situated on the synotic tectum from extending onto the occipital cartilage.

The labyrinth organ in *Amia* is well described in the literature, but is often depicted separately from the braincase (e.g., Allis, 1897: pl. XXXV; Jarvik, 1980: vol. 1, fig. 54). Retzius (1881: pl. V, fig. 12) provided a thumbnail illustration of its position in lateral view within the cranium, and its position in a 35-mm cleared and stained specimen was shown in dorsal view by Grande and Bemis (1998: fig. 26A). For convenience, some of Retzius (1881) original illustrations are reproduced here with new annotations (fig. 5). These illustrations are worthy of brief comment as they have played such an important role in the present reconstructions.

Retzius (1881) figured the labyrinth organ in *Amia* as a transparent object in mesial, lateral and dorsal views (the dorsal view has not been reproduced here), as well as a me-

sial view of the organ within the braincase. This last view is somewhat misleading (see fig. 5A), since it depicts the sacculus and utriculus as a single confluent chamber, and also inaccurately suggests that the utricular branch of the acoustic nerve passed through the braincase wall behind the trigemino-facialis foramen.

The reconstructions of *Amia*'s labyrinth organ reproduced here (fig. 5B,C) show the superior utricular sinus terminating distally in a short apex that rises above the junction of the anterior and posterior semicircular canals. Mesial to the sinus is an elongate endolymphatic duct, extending almost as far dorsally as the apex of the sinus and flexed slightly toward the anterior. The acoustic nerve divides almost at the base of the endolymphatic duct, with branches extending to the three main ampullae and the utricular and saccular-lagenar chambers. The saccular-lagenar chamber is located mainly beneath the superior utricular sinus and the posterior semicircular canal, unlike the condition in cladistians, *Acipenser,* gars, and *Pteroniscus magnus,* in which the saccular-lagenar chamber is positioned more centrally and the anterior region part of the chamber extends farther anteriorly beneath the anterior semicircular canal (Retzius, 1881; Popper, 1978: figs. 1, 5; Coates, 1998: fig. 12G,H). A similar configuration is also noted in the extinct amiid *Calamopleurus* (fig. 7B), suggesting that the arrangement in *Amia* is derived. A different slightly different arrangement is suggested in *Ionoscopus* and "*Caturus*", where the saccular-lagenar chamber was positioned farther anteriorly (figs. 10B, 11B); even allowing for the slight forward upturn of the entire labyrinth organ in these fossils, relatively little of the chamber is positioned below the posterior semicircular canal.

MORPHOLOGY OF THE SUPRAOTIC

(a) *Calamopleurus* (figs. 1C, 6, 7)

Calamopleurus cylindricus (also known in the literature as *Enneles audax;* e.g., Silva Santos, 1960) is an extinct amiid. It is a primitive amiine (Maisey, 1991b) and has been classified within the subfamily Vidalamiinae by Grande and Bemis (1998). Its fossils are common in the Santana Formation of

Brazil (Albian, Early Cretaceous), and the species is also known from the Codó Formation (Albian, southern Parnaíba Basin; Maisey, in prep.). *Calamopleurus* has been documented from the Albian or Cenomanian of Morocco (Grande and Bemis, 1998: 669; Forey and Grande, 1998). Additionally, "*Megalurus*" *mawsoni* Woodward, 1902 (Berriasian-Hauterivian, Bahía, Brazil) was referred to *Calamopleurus* by Grande and Bemis (1998: 443).

The braincase of *Calamopleurus* was first described by Silva Santos (1960, as *Enneles audax*) in fossils from the Santana Formation, and additional material has been described by Maisey (1991b) and by Grande and Bemis (1998). The cranium in *Calamopleurus* is morphologically similar to that of *Amia,* although the pre-ethmoid, orbitosphenoid, and basisphenoid are more extensive; furthermore, there is a large descending frontal lamina meeting the orbitosphenoid in *Calamopleurus* which is absent in *Amia.* Besides these relatively minor differences in the extent of ossification, arguably the most significant osteological difference between the neurocrania of *Calamopleurus* and *Amia* is the presence in the former of a supraotic bone beneath the parietals.

Calamopleurus is at present the only amiid known to have possessed a supraotic, and so far the bone has been recognized only in specimens from the Santana Formation. In some previous descriptions the bone either was not observed (e.g., Silva Santos, 1960) or was misidentified as a pterotic (e.g., Tav-

erne, 1974; Maisey, 1991b). The bone is completely internal and its presence would not be suspected from a superficial examination of unprepared fossils, which may explain why it was not observed by Silva Santos (1960) and came to light only following the application of acid during specimen preparation. The braincase is unknown or poorly known in the majority of extinct amiids, including all other taxa included within the Vidalamiinae by Grande and Bemis (1998). The majority of fossil amiid skeletons are crushed flat, however, and even if they possessed an internal supraotic like that of *Calamopleurus* the bone would be extremely difficult to observe. On the other hand, the bone is absent in *Sinamia,* the only other extinct amiiform in which the braincase is known from three dimensional fossils (Stensiö, 1935: fig. 1; Grande and Bemis, 1998). The distribution of the supraotic among the extinct relatives of *Amia* is thus incompletely documented.

In *Calamopleurus* the supraotic is located dorsal to the prootics and anterior to the presumed position of the otico-occipital fissure (fig. 6A; see also Grande and Bemis, 1998: figs. 299, 304). It is a thick chondral bone, attached to the ventral surface of the parietals, and only its ventral surface is perichondrally ossified (figs. 1C, 6A,B). In some specimens the unfinished posterior margin of the supraotic just makes contact with the exoccipitals, but usually there is a narrow space between them. A wider gap (presumably cartilage-filled) separates the supraotic and

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Fig. 6. *Calamopleurus cylindricus* AMNH 11760 (the same specimen as in fig. 1C): (**A**) Otico-occipital part of the braincase in lateral view (right side, stereopair, anterior toward top). The supraotic is visible deep within the braincase, posterior to the sphenotic and mesial to the prootic. The intercalar has been removed, exposing the supraotic and the position of the vagus foramen within the exoccipital (compare with fig. 1C, where the same braincase is shown with the intercalar in place); (**B**) supraotic in right lateral view (anterior toward top, dorsal surface to left, with fragments of parietal bones attached). Openings for the anterior and posterior semicircular canals are located within the spongy bone; (**C**) supraotic in ventral view (stereopair, anterior toward top). Several features are defined within the perichondrally finished bone, including the raised apex of the superior utricular sinus, pits for the endolymphatic ducts and openings for the anterior and posterior semicircular canals; (**D**) reconstruction of the supraotic and semicircular canals (dorsal view, anterior toward top, canals depicted on right side); (**E**) floor of otic region (stereopair, anterior toward top) showing the saccular and utricular recesses within the prootic. The large myodome is visible beneath the prootics, as in *Amia.* Unfinished spongy endochondral bone is indicated by mechanical stipple and diagonal parallel lines denote broken areas in C and E.
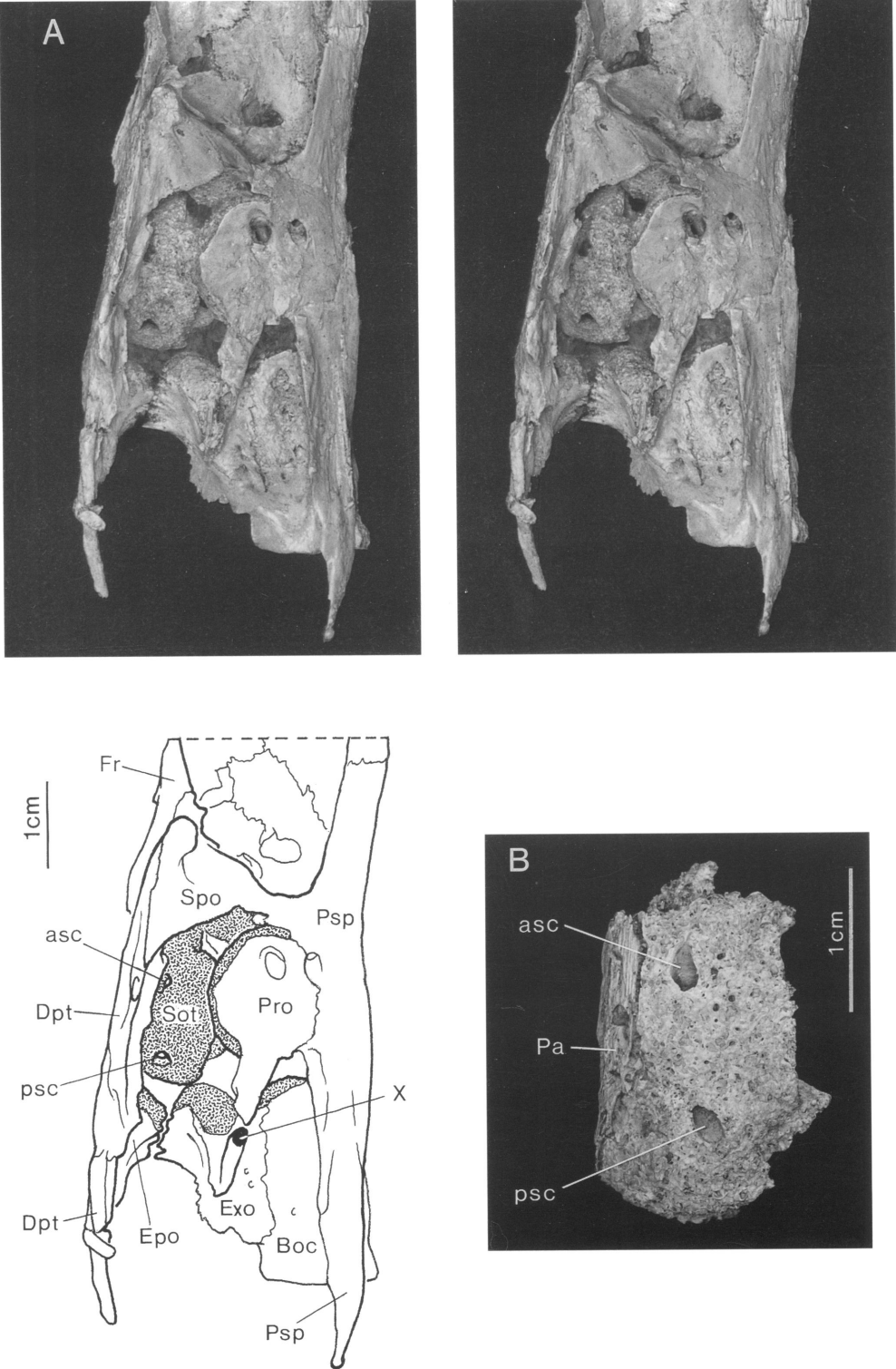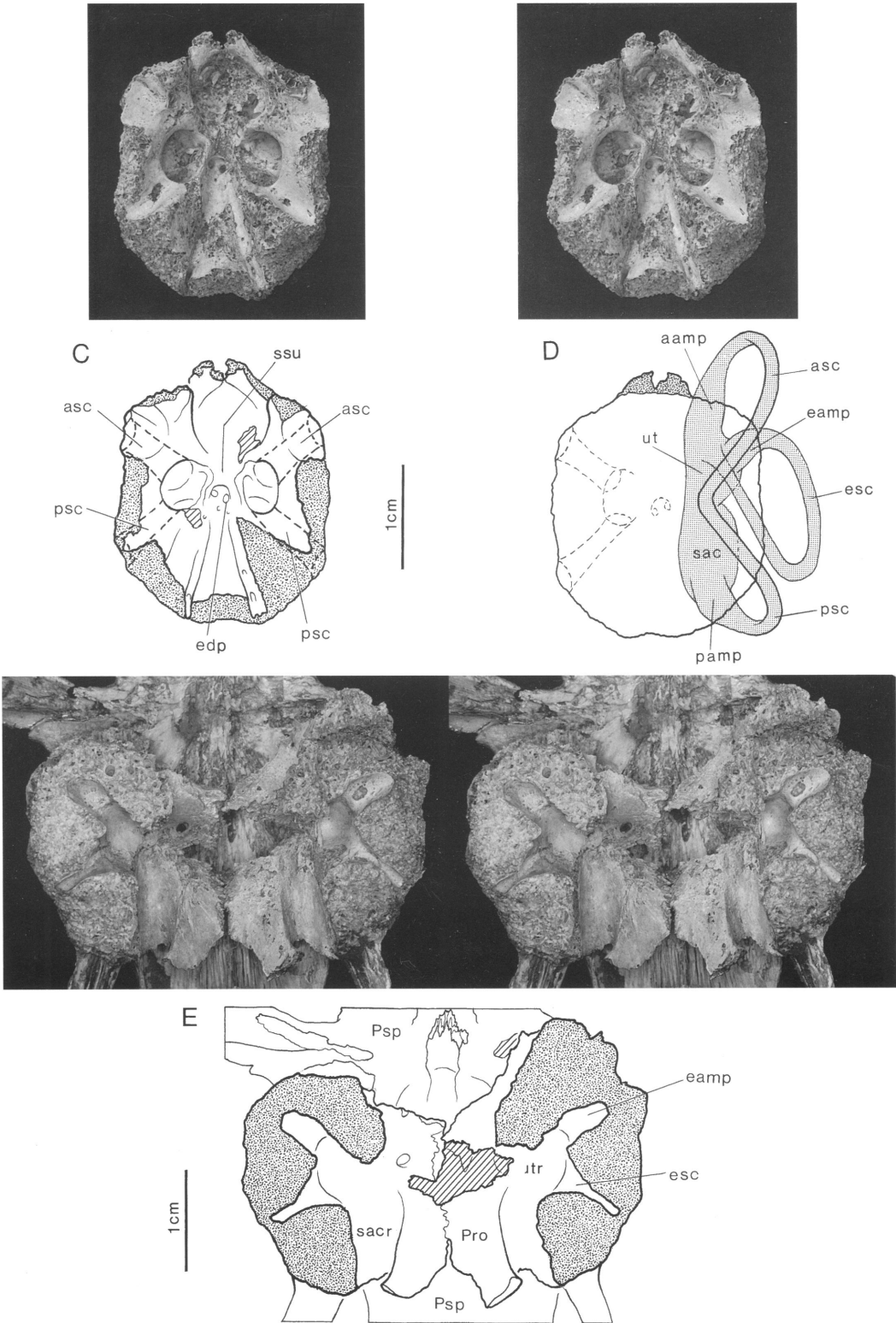
Fig. 6.

Fig. 6. Continued.

epioccipital. The anterior and posterior semicircular canals enter the spongy lateral surfaces of the supraotic and emerge again on its ventral surface within paired chambers (fig. 6D). These represent the dorsal part of the superior utricular sinus, but there is no descending bony support for the sinus as in *Ionoscopus*. There is, however, a small depression just mesial to the entrances to the canals, probably marking the location of the raised apex of the superior utricular sinus as in *Amia* and most teleosts (Retzius, 1881).

Between these paired chambers there is a shallow depression containing two blind pits, probably representing the closed distal extremities of paired endolymphatic ducts (fig. 6C). In *Amia* and gars the ducts extend dorsally almost to the apex of the superior sinus (Retzius, 1881: pl. V). In teleosts, by contrast, the endolymphatic ducts are weakly developed, typically not extending the full height of the superior sinus nor reaching the overlying skull bones. No such pits are present in the supraotic of *Ionoscopus,* suggesting that its endolymphatic ducts did not extend so far dorsally as in *Calamopleurus* and *Amia.*

The supraotic in *Calamopleurus* does not contain a lateral cranial canal (unlike in *Ionoscopus,* described below), although there is a large unossified space between the lateral margin of the supraotic and the upper margin of the prootic; however, this space is probably situated too far dorsally to have contained a lateral cranial canal (fig. 6A). The intercalar in *Calamopleurus* contains some chondral bone (as in AMNH 11829; cf. Patterson, 1975) and possesses a postero-dorsal diverticulum resembling that described in dried *Amia* skulls (Kesteven, 1951). According to Patterson (1975: 414) the diverticulum is not homologous with the lateral cranial canal; thus, *Calamopleurus,* like *Amia,* probably lacks this canal.

A reconstruction of the labyrinth region in *Calamopleurus* was made by mapping the labyrinth of Recent *Amia* onto photographs of a fossil specimen (fig. 7). Slight adjustments were made to the height and shape of the anterior and posterior semicircular canals in *Calamopleurus* where these pass through the supraotic; for example, the position of the saccular-lagenar chamber is shifted farther

beneath the posterior semicircular canal than in *Amia.* The otic region in *Calamopleurus* is more heavily ossified than in *Amia,* especially beneath the saccular recess, although the extent to which the labyrinth is enclosed by the prootic is approximately the same in both taxa. Although *Sinamia* lacks a supraotic, the lateral wall of its otic region is more extensively ossified than in either *Calamopleurus* or *Amia*; for example, the prootic in *Sinamia* extends farther dorsally, almost filling the space between the sphenotic and intercalar (Stensiö, 1935, fig. 2, pl. VI), and the epiotics almost meet at the midline.

Several features of the otico-occipital region in *Calamopleurus* and *Amia* are probably derived, including absence of the pterotic, opisthotic, and lateral cranial canal (fig. 1C, 7). Additionally, the "epiotic" does not contain a supraotic pocket like that found in *Lepidotes* (Patterson, 1975; = "posterior pocket" of Thies, 1989). A corresponding pocket is also present in *Ionoscopus* (discussed below), but the phylogenetic significance (if any) of its absence in *Calamopleurus* and *Amia* is unclear. *Sinamia* agrees in the first two of the above features but is unknown regarding the lateral cranial canal and supraotic pocket. Apomorphic characters of *Amia* not seen in *Calamopleurus* include: (1) absence of the supraotic, (2) absence of chondral bone in the intercalar (cf. Patterson, 1975), and (3) presence of a wide cartilage-filled space between the epioccipitals.

Sinamia agrees with *Amia* in character (1) and disagrees in character (3). Its intercalar is said to be entirely "dermal" (Stensiö, 1935: 15), although this was not verified by Grande and Bemis (1998). The intercalar in *Calamopleurus* is mostly membranous, but it also contains a small amount of chondral bone.

(b) *Ionoscopus* (figs. 1A, 8–10)

The braincase in *I. petraroiae* (type species of *Ionoscopus*; see earlier systematic remarks) is still undescribed. The form studied here is *Ionoscopus cyprinoides,* which is known from complete skeletons from the late Jurassic Solnhofen limestone of Bavaria (Steutzer, 1972; Grande and Bemis, 1998). All the chondral bones present in the brain-
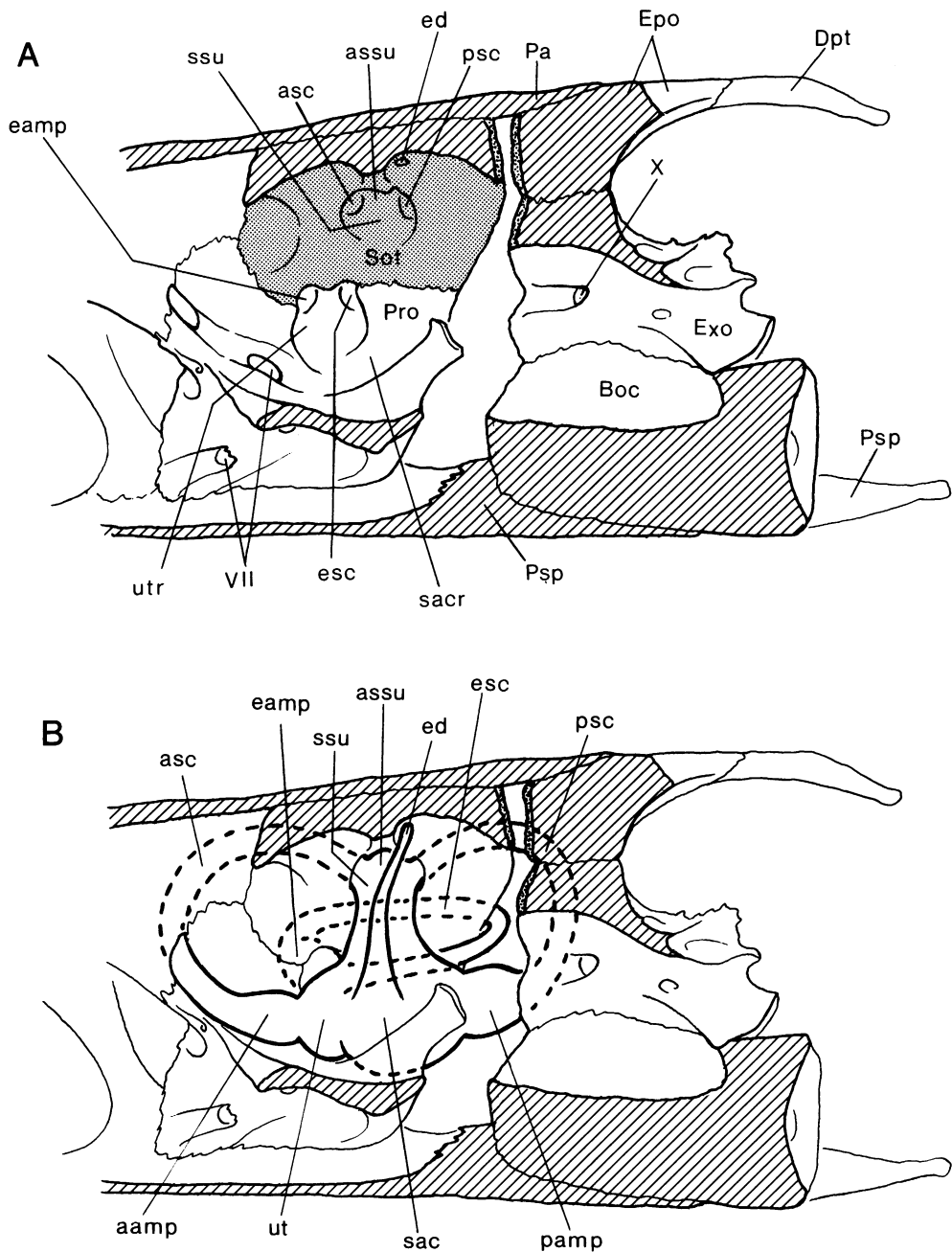
Fig. 7. *Calamopleurus cylindricus:* reconstruction of labyrinth region in sagittal view based on AMNH 11760 & 11840 (anterior to left; diagonal parallel lines indicate sectioned bones). Shapes of bones are simplified, and much of the three-dimensional complexity has been omitted for clarity. (A) Openings in bones for semicircular canals; position of supraotic is defined by a mechanical dot screen pattern; (B) same view with a superimposed outline of the labyrinth in *Amia.* Dashed lines indicate areas where the labyrinth organ is enclosed by bone. The supraotic encloses parts of the anterior and posterior semicircular canals and the tips of the endolymphatic ducts, but there is no lateral cranial canal.

case of *Amia* are also found in *Ionoscopus cyprinoides* (Steutzer, 1972), in addition to which there are (1) small paired opisthotics, only weakly in contact with surrounding bones, (2) pterotics (also small, and wedged between the dermopterotic and epioccipital, within the posttemporal fossa, fig. 8B), and (3) a median supraotic (fig. 1A). The supraotic in *Ionoscopus cyprinoides* is entirely chondral, with perichondrally finished dorsal and ventral surfaces. The bone makes contact with the paired epioccipitals posterolaterally and also meets the very small paired pterotics, which are located beneath the parietals and make contact with the epioccipitals posteriorly (figs. 9, 10). Thus, the general relationship of the supraotic to surrounding bones in *Ionoscopus* agrees closely with Patterson's (1975) original description of the bone in *"Aspidorhynchus,"* suggesting that its internal morphology may also be similar in both taxa.

The internal morphology of the otico-occipital region in *Ionoscopus cyprinoides* has been investigated in a single acid-prepared specimen, BM(NH) 37795a (fig. 9A,B). Here the supraotic reaches the opisthotic ventrolaterally, forming the medial wall of the lateral cranial canal, but the bone fails to meet the prootic even though the latter extends beneath the supraotic posteriorly. As in *Calamopleurus,* the supraotic encloses much of the labyrinth system dorsally, including parts of the anterior and posterior semicircular canals and the superior utricular sinus. Unlike in *Calamopleurus,* however, the supraotic in *Ionoscopus* forms the medial and dorsal parts of the lateral cranial canal, which passes behind the superior utricular sinus and opens anteriorly and posteriorly into the cranial cavity.

The posterior opening of the lateral cranial canal is defined dorsally by the supraotic and ventrally by the opisthotic, although part of this opening is not framed by any bone. Additionally, the ventral part of the anterior opening and the outer (lateral) wall of the lateral cranial canal are not enclosed by bone. By contrast in Rayner's (1948) *"Caturus"* the lateral cranial canal is more completely enclosed by bone (fig. 11), although the relative extent of the supraotic, pterotic, and

prootic in her material is uncertain because sutures are not discernible.

The ventral surface of the supraotic in *Ionoscopus* contains a large median concavity anteriorly, probably for the cerebellum. Another, slightly larger median concavity is also present behind the opening for the posterior semicircular canal. This concavity continues posterolaterally to form a conical hollow within each epioccipital. Patterson (1975: fig. 111) described a similar concavity (the supraotic pocket) within the "epiotic" of *Lepidotes toombsi,* and a similar "posterior pocket" is present in *L. gloriae* (Thies, 1989). The supraotic pocket will be discussed further below.

In comparison with *Amia* and *Calamopleurus,* the labyrinth organ in *Ionoscopus* is tilted upward anteriorly, and the height and curvature of the anterior and posterior semicircular canals are greater in *Ionoscopus* (fig. 10). Relatively more of the saccular chamber is therefore located beneath the superior utricular sinus, which does not rise into a distinct apex as in *Amia.* In *Ionoscopus* the labyrinth region is enclosed by the opisthotic and pterotic laterally and by the supraotic dorsally. In *Ionoscopus* the prootic forms a less extensive floor to the labyrinth region than in *Calamopleurus,* but the extent of the supraotic around the anterior and posterior semicircular canals is similar in these taxa.

The relationship of the supraotic to the lateral cranial canal in *Ionoscopus* is of special interest, as it includes areas occupied by the pterotic in pholidophorids (e.g., "Callovian *Pholidophorus*"; Patterson, 1975: fig. 73; see fig. 22 here). Clearly, the correspondence is not exact, because the supraotic is a median bone whereas the pterotics are paired. Thus, the supraotic in *Ionoscopus* does not enclose any part of the external semicircular canal or the outer wall of the lateral cranial canal, whereas the pterotic in "Callovian *Pholidophorus*" encloses both structures. These differences are essentially topographic; first, the pholidophorid pterotic is located farther dorsolaterally than the supraotic in *Ionoscopus,* and secondly, the pterotic in *Ionoscopus* is much smaller than in pholidophorids and does not reach either the lateral cranial canal or the external semicircular canal (both of which lay mostly in cartilage).
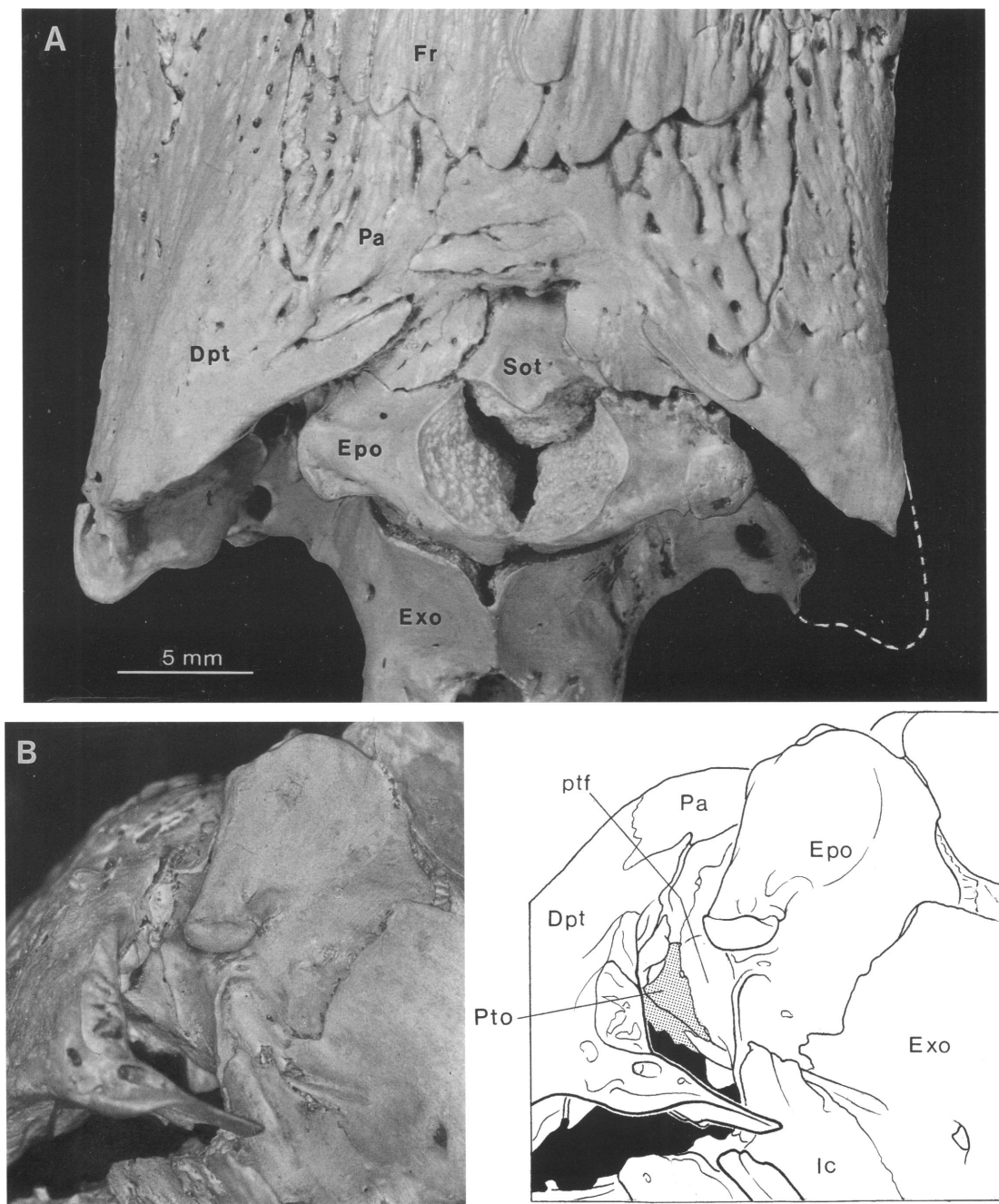
Fig. 8. *Ionoscopus cyprinoides* BM(NH) 37795a. **(A)** Dorsal view of braincase occipital region, showing the median supraotic behind the parietals (the right parietal overlaps the left) and between the epioccipitals; **(B)** oblique posterior view of the posttemporal fossa, showing the position of the small pterotic (indicated by mechanical stipple in line drawing) wedged between the dermopterotic and epioccipital.
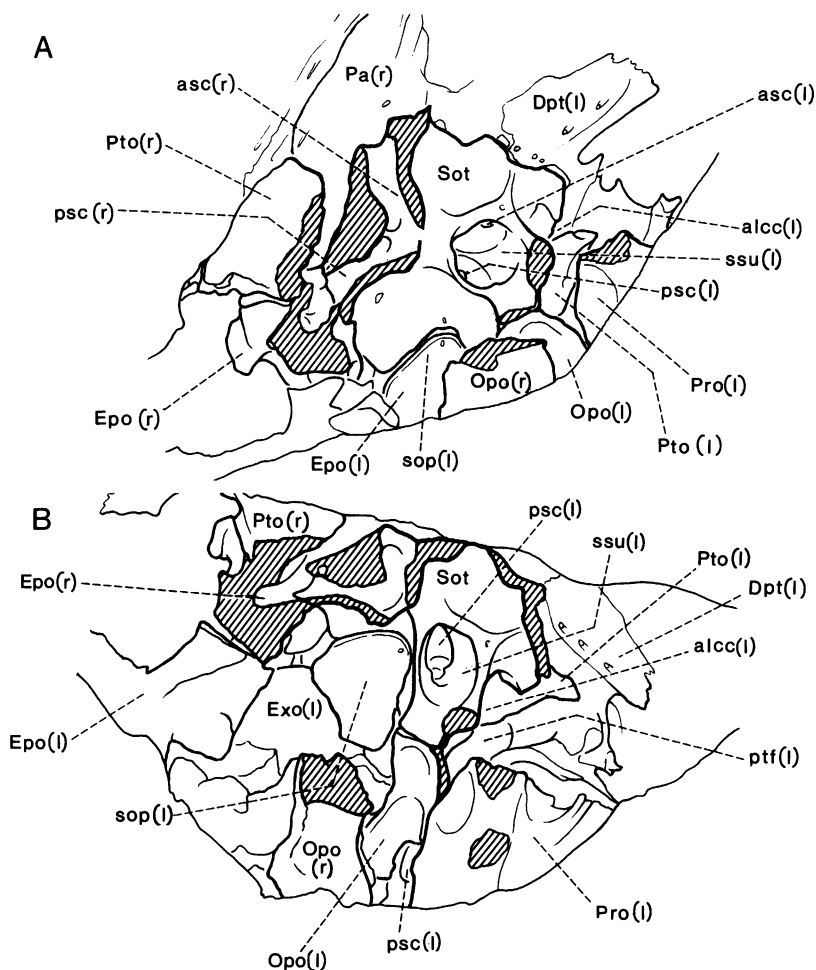
Fig. 9. *Ionoscopus cyprinoides* BM(NH) 37795a: oblique stereopair views of the interior of the otic region, primarily of the left side, showing the extent to which the supraotic encloses the paired semi-circular canals and lateral cranial canal. (A) More dorsally oriented view; (B) more laterally oriented view. The paired epioccipitals contact the posterolateral surface of the supraotic, and each epioccipital contains a deep supraotic pocket. The left side and posterior part of the supraotic is complete but the most anterior part of the right side has been lost. Bone formerly covering the right superior sinus and semicircular canals has been cut through (indicated by diagonal parallel line pattern in drawings), ex-posing more of these canals than on the left side. The anterior opening of the left lateral cranial canal is situated next to the superior utricular sinus (in center of figure A). The posterior opening of this canal is obscured by remnants of the right opisthotic in this view. (B) shows the contact between the supraotic and left opisthotic (containing the ventral part of the posterior semicircular canal). The anterior opening of the left lateral cranial canal and the left supraotic pocket are more clearly observed in this view. No exact scale possible for oblique images; magnification approx. ×2.6.
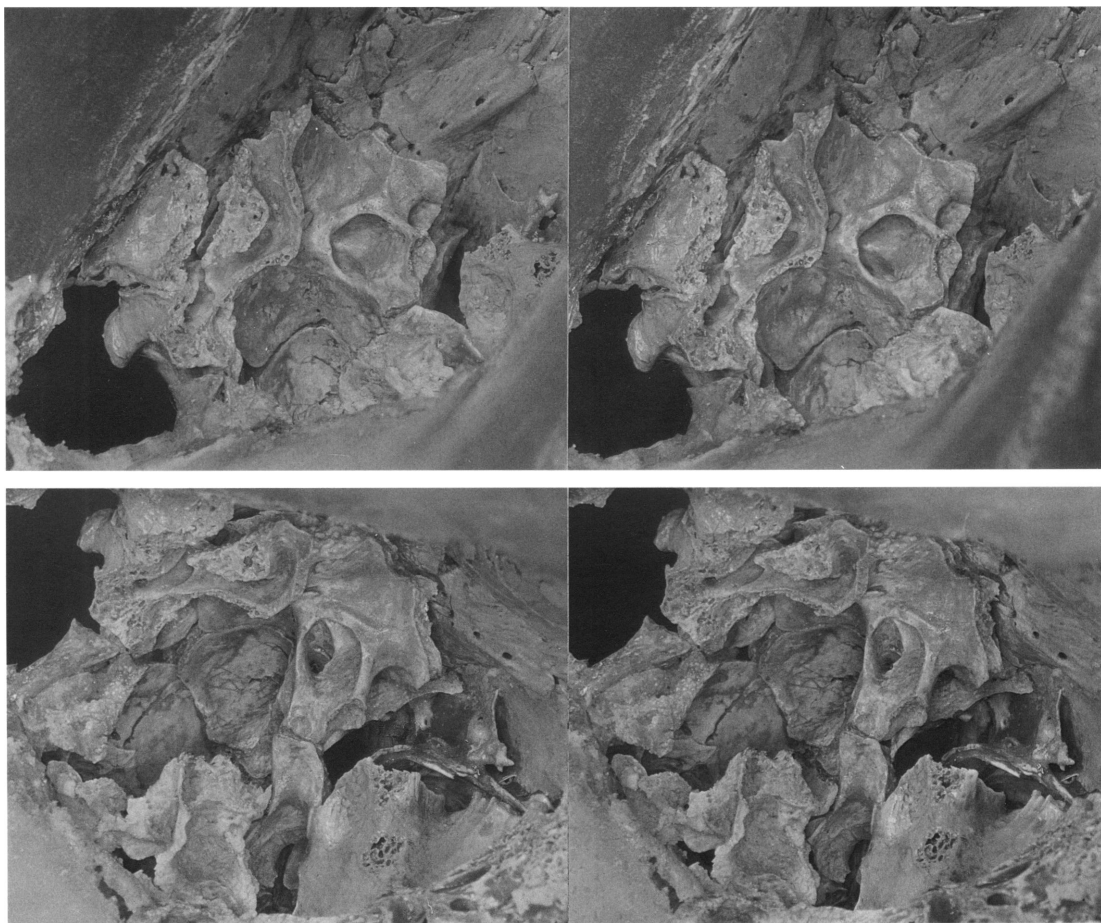
Fig. 9. Continued.

(c) Rayner's "*Caturus*" (fig. 11)

Rayner (1948: 293) described an isolated braincase from the Toarcian (Early Jurassic) of Somerset, England (Bath Museum, catalog number M1288). The specimen was referred to *Caturus* sp., but differs from *C. furcatus* (type species of the genus) in being more heavily ossified and in lacking sutures. These differences could be ontogenetic, although Patterson (1975: 441) suggested that lightly ossified caturids such as *C. furcatus* may be more advanced than more heavily ossified ones. Lambers (1992) characterized *Caturus* by several features including the presence of "supernumerary supraorbitals," small size of the dermosphenotic, preopercle with an expanded ventral limb, and a parasphenoid extending far posteriorly to the basioccipital.

None of these characters can be determined in the Toarcian braincase.

The extent of ossification around the semicircular canals and lateral cranial canal in this braincase is clearly greater than in *Ionoscopus* (Rayner, 1948: fig. 8), although the precise extent of each bone is uncertain in the "*Caturus*" braincase because sutures are absent. Significantly, the extent of ossification in the cranial roof almost exactly matches the region occupied by the supraotic and surrounding bones in *Ionoscopus*. This agreement invites the reconstruction shown in figure 11, and in all probability the "*Caturus*" braincase had a large supraotic.

The superior utricular sinus, together with the medial and dorsal part of the lateral cranial canal, probably lay within the supraotic
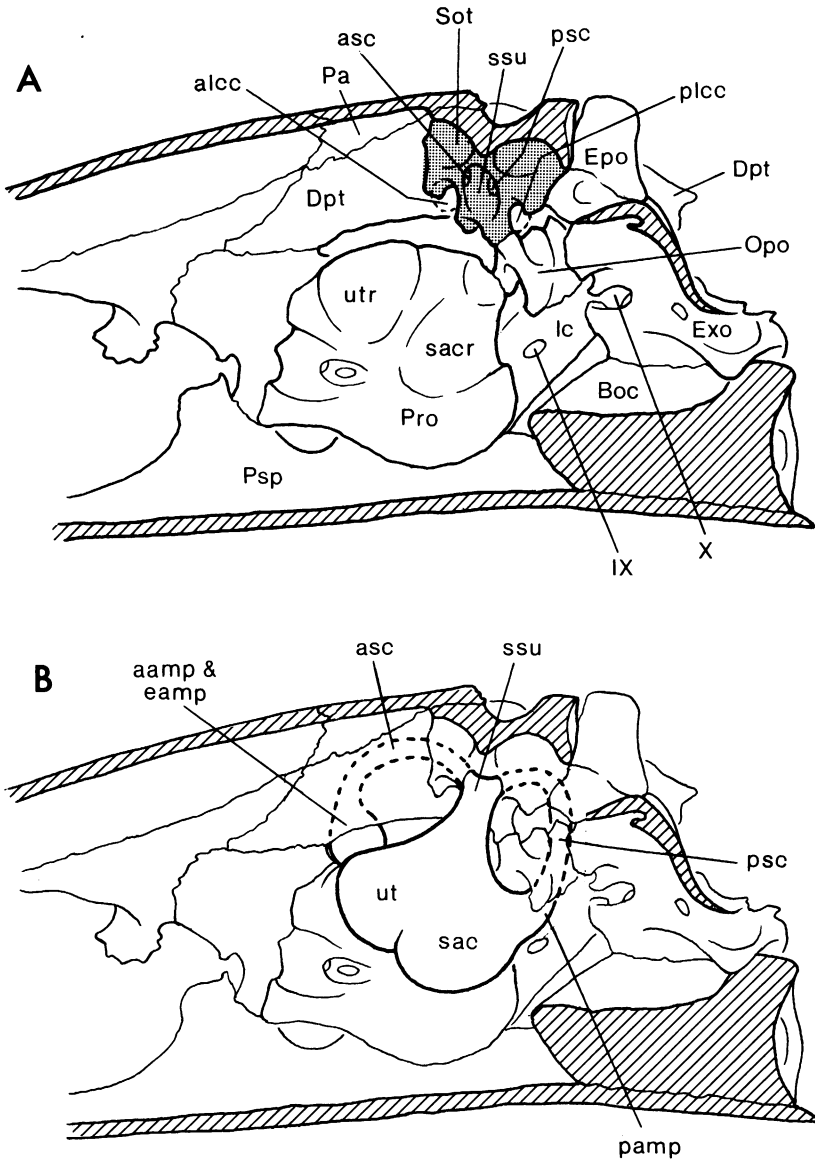
Fig. 10. *Ionoscopus cyprinoides:* reconstruction of labyrinth region in sagittal view based on BM(NH) 37795a (anterior to left; diagonal parallel lines indicate sectioned bones). Shapes of bones are simplified, and the external semicircular canal and much of the three-dimensional complexity has been omitted for clarity. **(A)** Openings in bones for semicircular canals and lateral cranial canal; position of supraotic is defined by a mechanical dot screen pattern; **(B)** same view with superimposed restoration of the labyrinth. Dashed lines indicate areas where the labyrinth organ is enclosed by bone. The supraotic encloses the dorsal parts of the anterior and posterior semicircular canals as well as the upper part of the lateral cranial canal, corresponding in part to that region in pholidophorids occupied by the pterotic. Note that the myodome and other structures in the floor of the braincase are not preserved in this specimen and have not been reconstructed.
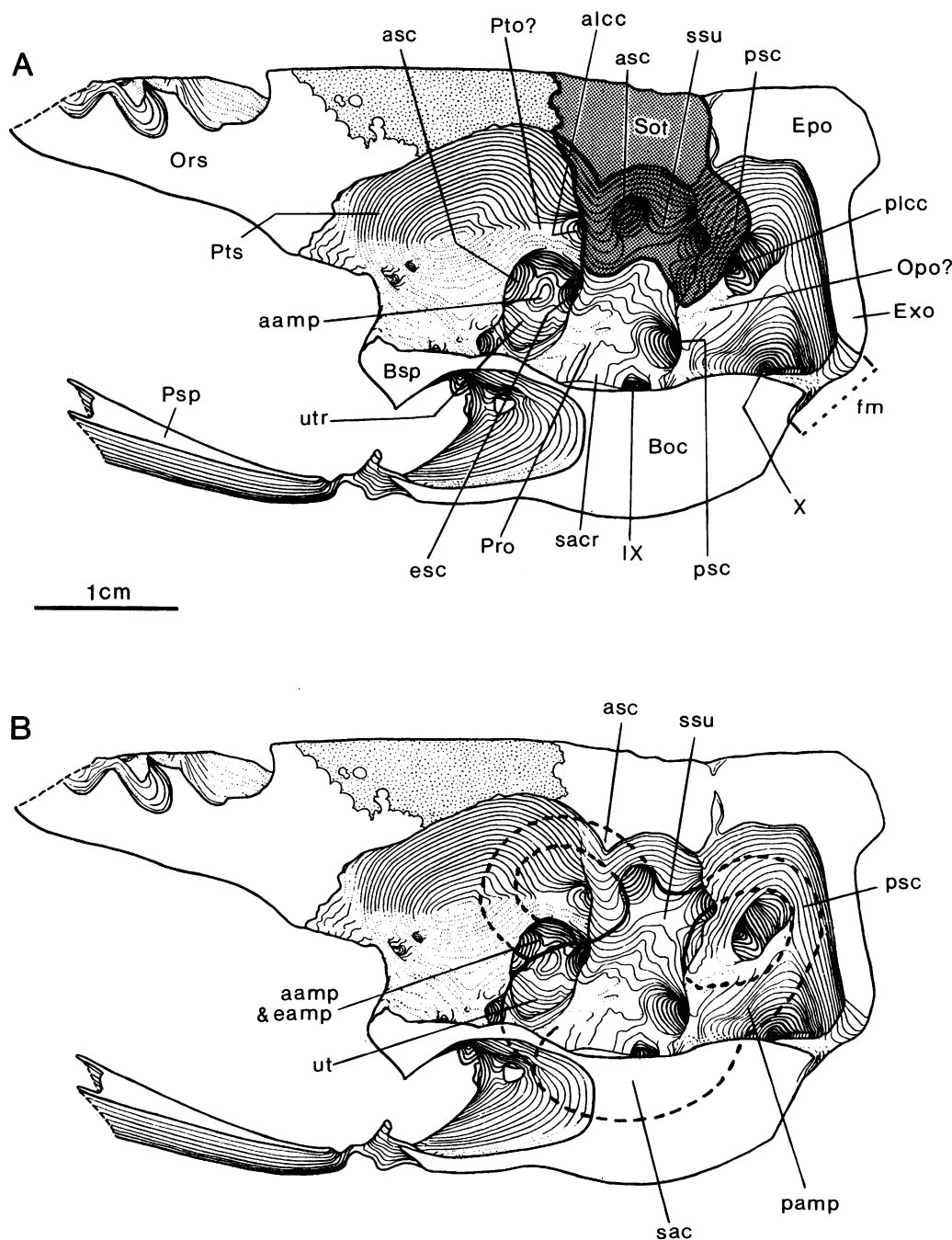
Fig. 11.   Early Jurassic braincase referred to *Caturus* by Rayner (1948). **(A)** Reconstruction of labyrinth region (modified and reversed to facilitate comparison). The inferred extent of the supraotic (indicated by mechanical stipple) corresponds closely to that in *Ionoscopus,* as does the extent of bone surrounding the semicircular canals and lateral cranial canal (see fig. 10). The pterotic and opisthotic probably ossified in the positions indicated (again as in *Ionoscopus*), although no sutures are evident; **(B)** same view with superimposed outline of the labyrinth. The position of the external semicircular canal has been omitted for clarity; the anterior and posterior openings of this canal are indicated in **(A)**.

in "*Caturus*" as in *Ionoscopus,* instead of within the pterotic as in some pholidophorids, but as there are no sutures, the extent of the pterotic in "*Caturus*" is uncertain. Unlike in *Ionoscopus* the outer wall of the lateral cranial canal was fully ossified and the external semicircular canal was largely enclosed by bone. Possibly the pterotic was as extensive in "*Caturus*" as in pholidophorids; alternatively, the supraotic may have been even more extensive than in *Ionoscopus,* and may have enclosed the lateral cranial canal and part of the external semicircular canal. Patterson (1975: 413) noted that in Rayner's "*Caturus*" the posterior opening of the lateral cranial canal is larger than the anterior, unlike in pholidophorids. In *Ionoscopus* the dorsal part of the posterior opening also seems to be the larger.

(d) Rayner's "*Aspidorhynchus*" (fig. 12)

Two isolated braincases, BM(NH) P.9843 and 9844, from the Bathonian of Northamptonshire, England, were originally identified as "*Aspidorhynchus*" (Rayner, 1948), but Patterson (1975) identified tham as "caturid." More recently, Brito (1992; 1997) has described specialized braincases in *Vinctifer, Aspidorhynchus,* and *Belonostomus* that clearly differ profoundly from the "*Aspidorhynchus*" specimens under discussion here. The "*Aspidorhynchus*" braincases are nevertheless remarkably similar to that in *Oshunia,* and may therefore belong to an ionoscopid or some closely related halecomorph.

The "*Aspidorhynchus*" braincases are of historical interest as the first in which the supraotic was recognized, but little can be added to Patterson's (1975: figs. 99, 100) original description, since the internal morphology of the supraotic is still unknown in this material. The supraotic of "*Aspidorhynchus*" is a chondral bone with a finished outer surface, and is exposed on the roof of the braincase between the epioccipitals and parietals, but it does not reach the exoccipitals (Rayner, 1948). The exposed area is much smaller than in *Ionoscopus* and *Oshunia.* It is not known whether a lateral cranial canal is present.

Paired opisthotics are present (Patterson,

1975: figs. 99, 100), with a stronger sutural connection to surrounding bones than in *Ionoscopus.* Small wedge-shaped pterotics are present between the dermopterotic and epioccipital. Judging from their size and extent, the pterotics probably failed to reach the external semicircular canal, as in *Ionoscopus.*

(e) *Oshunia* (figs. 1B, 13, 14)

Oshunia brevis is only the second halecomorph (after *Calamopleurus*) discovered in the Santana Formation (Early Cretaceous, Albian, Brazil). *Oshunia* was originally referred to the Ionoscopidae (Wenz and Kellner, 1986; Maisey, 1991c), although it was subsequently placed in its own family by Grande and Bemis (1998). In either case, phylogenetic analyses support a close relationship between *Oshunia, Ionoscopus* and ophiopsids (Gardiner et al., 1996; Grande and Bemis, 1998).

The braincase in *Oshunia* was first described by Maisey (1991c). It is osteologically very similar to those referred to as "*Aspidorhynchus*" and also agrees with that of *Ionoscopus,* except that pterotics are absent in *Oshunia* and, consequently, the dermopterotic meets the epioccipital along an uninterrupted suture. The braincase in *Oshunia* also differs from that in both *Ionoscopus* and "*Aspidorhynchus*" in having an extensive suture between the epioccipitals below the supraotic. *Ionoscopus* and *Oshunia* both differ from "*Aspidorhynchus*" in having the exoccipital extend anterior to the vagus foramen towards the prootic. The lateral wall of the otic region in *Oshunia* and "*Aspidorhynchus*" is more completely ossified than in *Ionoscopus.* The prootic and opisthotic in *Oshunia* and "*Aspidorhynchus*" together occupy the equivalent area of the prootic in *Caturus furcatus* (discussed below).

The bone located behind the prootic ventral to the dermopterotic in *Oshunia* is identified here as the opisthotic (also see Maisey, 1991c: 159), and the corresponding bone in "*Aspidorhynchus*" was also considered to be an opisthotic by Patterson (1975). Grande and Bemis (1998: fig. 408B) identified this bone in *Oshunia* as the pterotic; interestingly, Schaeffer (1971: fig. 2) also identified the equivalent bone in *Macrepistius* as the pter-
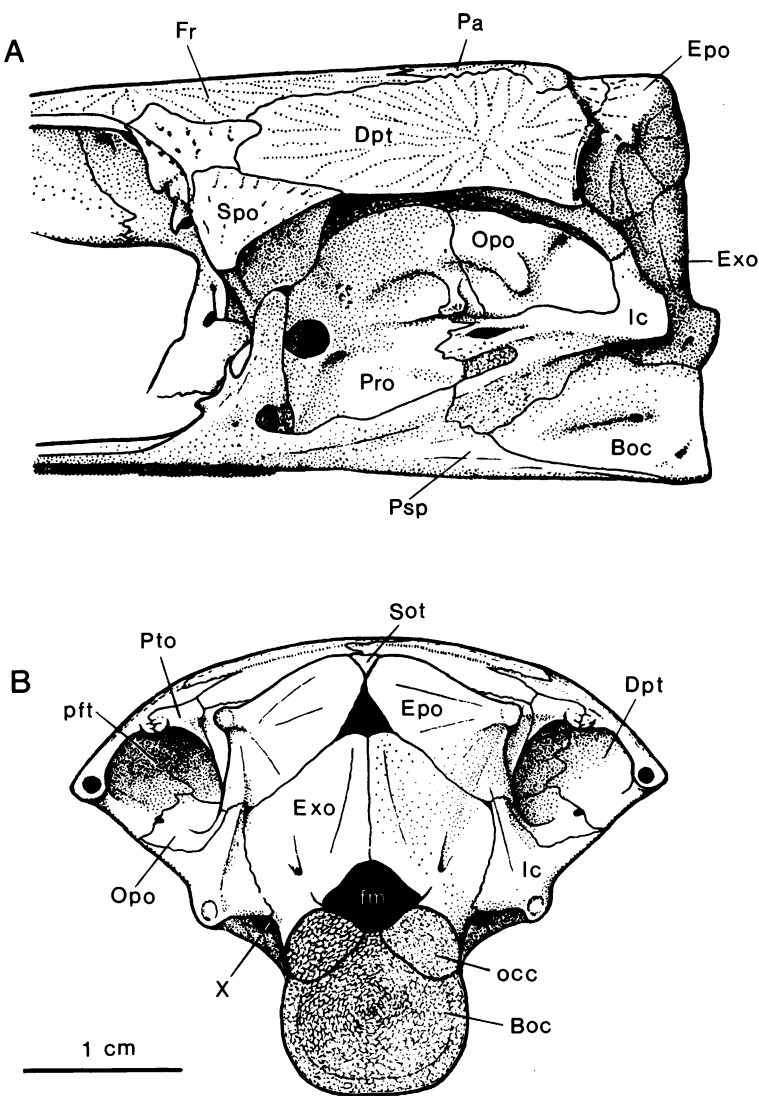
Fig. 12. Jurassic "*Aspidorhynchus*" braincase in (**A**) lateral and (**B**) posterior views (after Patterson, 1975). Note the general morphological similarity between this braincase and that of *Oshunia* depicted in Figure 1B; differences include absence of a pterotic in *Oshunia* and the smaller visible extent of the supraotic in "*Aspidorhynchus*" (compare with figs. 13, 14).
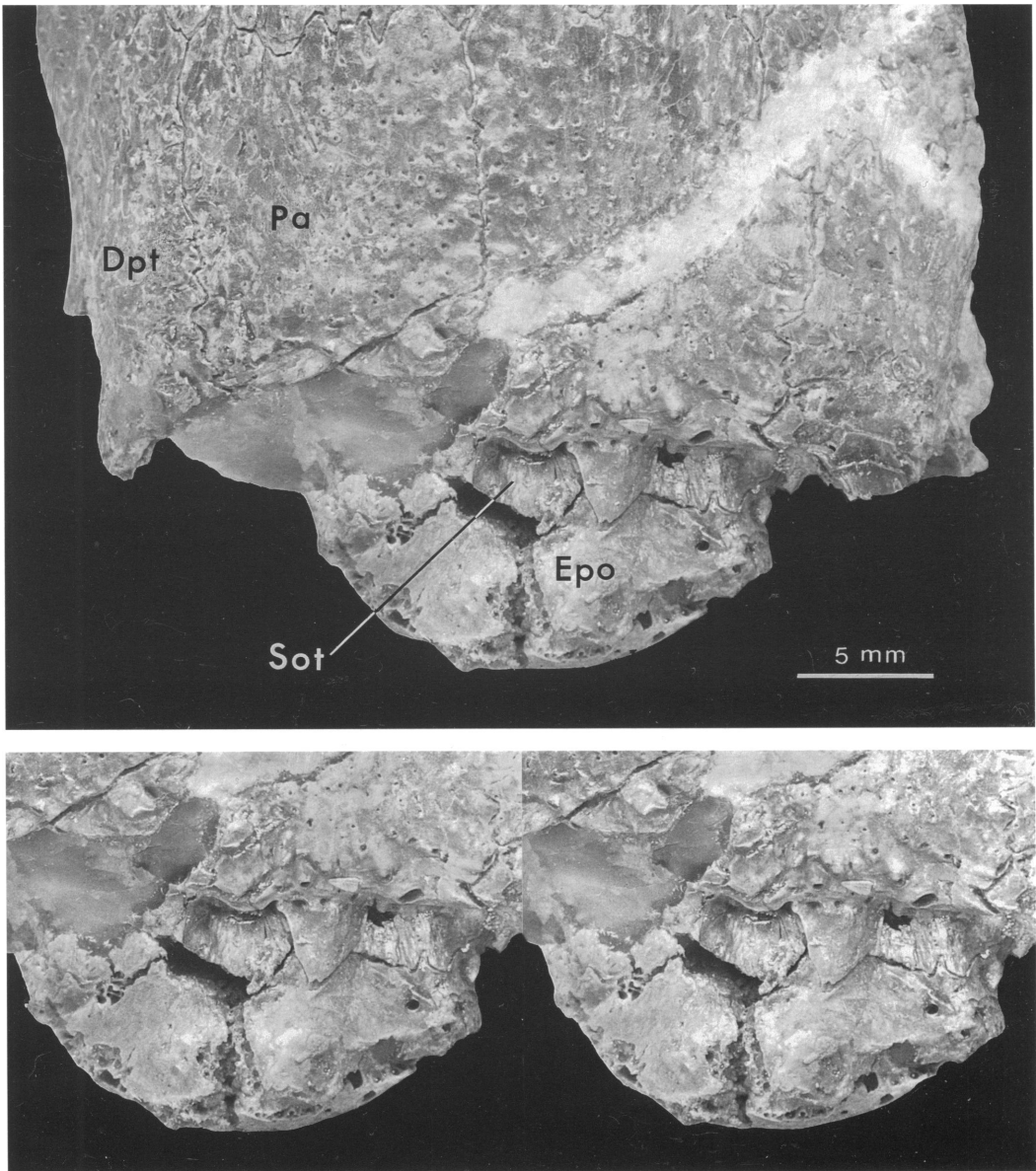
Fig. 13. *Oshunia brevis* AMNH 12000: general dorsal view (above) and stereopair of otico-occipital region in dorsal view (below), showing the supraotic exposed in the skull roof between the epioccipitals and behind parietals.

otic. Although these respective interpretations of an ophisthotic in *Oshunia* and *Macrepistius* seem to agree, the "epiotic" in Schaeffer's (1971) *Macrepistius* reconstruction corresponds to the pterotic in "*Aspidorhynchus*" and *Ionoscopus,* whereas his "supraoccipital" is probably the partly fused epioccipitals (an incomplete median suture is indicated in Schaeffer's original figure). Thus, *Macrepistius* actually agrees with "*Aspidorhynchus*" and *Ionoscopus* in having a small paired bone within the posttemporal fossa (here regarded as the pterotic instead of an epiotic), as well as a larger, more laterally situated bone (here identified as the opisthotic instead of a pterotic). The interpreta-
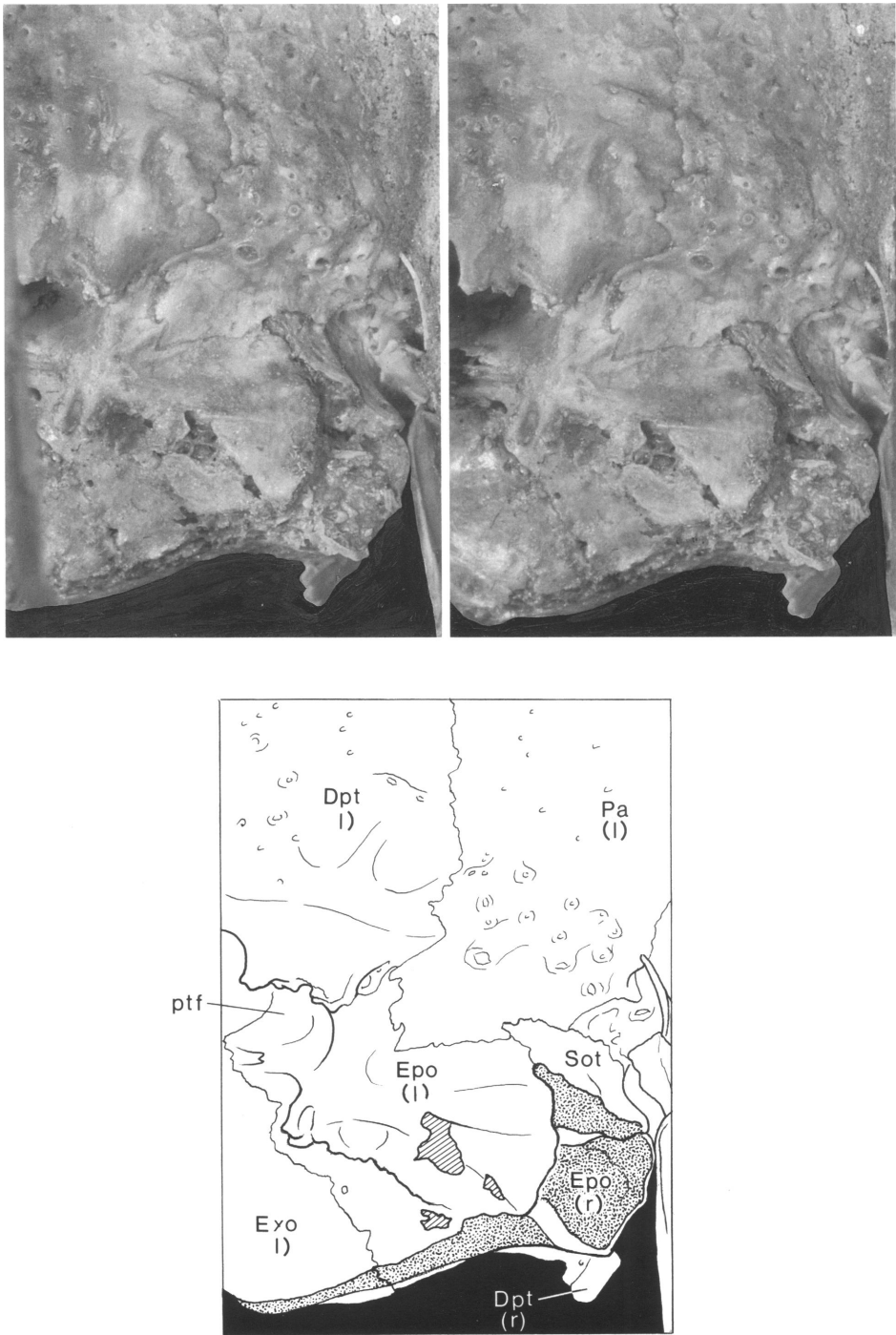
Fig. 14. *Oshunia brevis* AMNH 12793, stereopair of otico-occipital region in oblique view, showing primarily the supraotic and surrounding bones of the left side. Unfinished spongy bone is shown by irregular stipple pattern; broken areas are diagonal parallel line pattern in drawing. Note absence of pterotic between epioccipital and dermopterotic. Process at the lower right is the bony flange of the right dermopterotic. No exact scale possible for oblique image; magnification approx. ×6.

tion of *Oshunia* by Grande and Bemis (1998) leaves the small bone identified here as the pterotic in *Ionoscopus* and *"Aspidorhynchus"* without an identity, and is thus rejected.

The supraotic is visible in two specimens referred by Maisey (1991c) to *Oshunia* (AMNH 12000, 12793), but as in the *"Aspidorhynchus"* braincases, only its external features are known. The exposed part of the supraotic is slightly larger than in *"Aspidorhynchus,"* but the bone is otherwise similar.

(f) The "endochondral supraoccipital" in Pycnodontiformes (figs. 15, 16)

In some (perhaps all) pycnodontiformes there is a median chondral bone located within the otico-occipital region. Although this bone may be very large, it is mostly obscured by the dermal skull roof and has been described only in *Neoproscinetes* from the Santana Formation of Brazil (Nursall and Maisey, 1991). The equivalent bone in some other pycnodontiform fossils has been previously identified as a posttemporal (in *P. platessus*; Blot, 1987) or a supraoccipital (in *Neoproscinetes penalvai, Pycnodus platessus*; Nursall, 1996; *P. nardoensis*; Taverne, 1997). Nursall (1996) regarded presence of the bone (which he termed an "endochondral supraoccipital") as a synapomorphy of pycnodontiforms and teleosts, and suggested that its specialized morphology (including the vertical septum; see below) represents a synapomorphy of the Order Pycnodontiformes. Overlying the chondral bone in *Neoproscinetes* is a median dermal bone (also discussed below); these two bones are unfused even in large (presumably adult) individuals (Nursall and Maisey, 1991; Nursall, 1996).

In acid-prepared specimens of *Neoproscinetes* the median chondral bone usually lies free within the head region making its original position relative to the occipital fissure difficult to assess. Its approximate position within the head is shown by Nursall (1996: fig. 14). Extensive unossified spaces (presumably cartilage-filled in life) separate the bone from the prootics anteriorly and from the occipital complex ventrally. In an undescribed pycnodontiform braincase from the Early Cretaceous of Israel the equivalent

bone seems to lie in front of the occipital fissure, suggesting that it is a supraotic (C. Patterson, personal commun., October 1997). Nursall (1996) has suggested that in *Neoproscinetes* the bone was attached anteriorly to the pterotic, but I have found no evidence of a pterotic in *Neoproscinetes* or any other pycnodontiform. In rare instances (e.g., *Neoproscinetes,* AMNH 11990) the bone identified here as a supraotic is fused to a small posterior extension of the pterosphenoid. In that position the bone presumably extended onto cartilage located anterior to the oticooccipital fissure (synotic tectum or posterior medial tectum, or both). The bone identified by Taverne (1997) as a supraoccipital in *Pycnodus nardoensis* may also meet the pterosphenoid, although these bones are partly overlain by the frontal and parietal in the specimen described and no contact is observable. Interpretation of the bone in pycnodontiforms as a supraotic is founded on rather circumstantial evidence, including: (1) its supposed position relative to the occipital fissure; (2) its position above the anterior semicircular canals; and (3) fusion with the pterosphenoid.

Examples of the supraotic were removed from two acid-prepared specimens of *Neoproscinetes* and are illustrated here (figs. 15, 16). Their most unusual feature is the ascending process, which ends just beneath the median dermal bone forming the posterior part of the skull roof. This ascending process probably lay in the median septum, and the large space on either side of it (posttemporal fossa; Gardiner, 1984: 398; Nursall, 1996: 132) was probably occupied by epaxial musculature although there are no indications of muscle attachment scars on the bone itself. A lateral cranial canal like that in pholidophorids and *Ionoscopus* is absent in *Neoproscinetes,* but there is a perichondrally lined median space located between the anterior semicircular canals, dorsal to most of the labyrinth region and medial to the expected position of a lateral cranial canal.

The perichondral surface of the supraotic in *Neoproscinetes* is pitted by a few small, irregularly distributed openings (presumably for blood vessels) especially at the base of the ascending process and also farther ventrally. The anterior, anterolateral and poste-
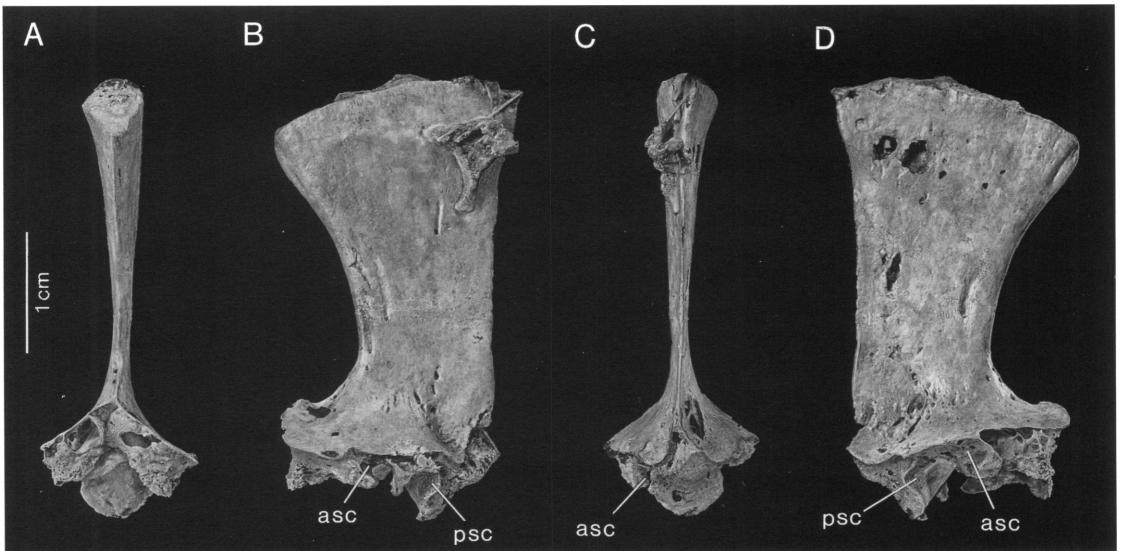
Fig. 15. *Neoproscinetes penalvai* AMNH 11893, a pycnodontiform: median chondral bone (supraotic) removed from a complete acid-prepared skeleton, in **(A)** anterior, **(B)** left lateral, **(C)** posterior, and **(D)** right lateral views. Positions of anterior and posterior semicircular canals are marked by short grooves.

rior surfaces of its expanded basal region are unfinished, as is the extreme apex of the ascending process, and the internal structure of the bone is extremely spongy. The base of the bone is expanded where it overlies the otic region, and the ventral surface is recessed to receive parts of the anterior and posterior semicircular canals as well as the upper extremity of the superior sinus, as in *Calamopleurus* and *Ionoscopus*. Unlike in those taxa, the semicircular canals lay in open grooves rather than being enclosed by bone (fig. 16).

The spinal canal in *Neoproscinetes* passes through the base of the occipital complex, which includes several anterior vertebral segments (as many as five neural arches articulate dorsally with this structure) and the exoccipitals. These are either sutured (in small individuals; e.g., AMNH 11852) or fused (in larger ones; e.g., AMNH 11893) to paired posterior processes of the parasphenoid. The anterior margin of the exoccipital is indented by a deep V-shaped notch for the vagus nerve, and the occipital complex probably lay entirely behind the embryonic occipital fissure. There is no evidence of a basioccipital, but Taverne (1997) identified one in

Pycnodus nardoensis. In *Neoproscinetes* the prootics are separated from the exoccipitals by a wide unossified gap and from the supraotic by an even wider gap.

No attempt has been made here to illustrate the extent of ossification around the labyrinth region in *Neoproscinetes,* but a few observations are appended to illustrate its highly specialized nature. The supraotic encloses only the mesial wall of the anterior and posterior semicircular canals and a small part of the superior utricular sinus. The prootic surrounds much of the labyrinth, including the floor of the sacculus and utriculus, but the entire labyrinth region is tilted through almost 90° relative to the parasphenoid, so that the posterior semicircular canal is much closer to the floor of the braincase. In this configuration of the labyrinth organ, when the external semicircular canal is restored to a horizontal position, the braincase is oriented nose-down. Although it is tempting to suggest that this morphological peculiarity may reflect some behavioral tendency to swim in such an orientation, in specialized modern teleosts, such as flatfishes and tailstanders, the orientation of the labyrinth is not strongly affected by the preferred swim-

ming orientation, and the otic region displays far less asymmetry than the ethmoid and orbital regions (Gregory, 1959: Marler and Hamilton, 1966); furthermore, in flatfishes the left and right otoliths are frequently, but not invariably, asymmetrical (Nolf, 1985: 14).

(g) The "supraotic" in *Lepidotes*

Patterson (1975: 450) reported a "median rod-like bone below the roofing bones in the otic region" of a single specimen of *Lepidotes minor,* and suggested that it may be a supraotic. No comparable ossification has been reported in other semionotid fossils, although the braincase is known in only a few taxa. The bone in question is . . ."a constricted rod, perichondrally lined except at the ends where it passed into cartilage (with) nothing like contact or enclosure of sensory canals, just an ossification in a strip-like taenia tecti medialis". . . (C. Patterson, personal commun., May 1993). It is oriented rostrocaudally and does not enclose any part of the semicircular canal system or lateral cranial canal. As in *Lepisosteus,* the posterior semicircular canal in semionotids is partly enclosed by a paired bone usually identified as the epiotic (e.g., *Lepidotes toombsi, L. gloriae, Araripelepidotes temnurus*; Patterson, 1975: fig. 111; Thies, 1989: fig. 6; Maisey, 1991a; Wenz and Brito, 1996: fig. 3). The bone found by Patterson (1975) in *Lepidotes* represents a median dorsal ossification of the chondrocranium, but probably formed more anteriorly than the supraotic (e.g., on the posterior medial tectum between the epiphyseal bar and synotic tectum rather than only on the latter). Thus, the splintlike median bone in *Lepidotes* probably is not homologous with the supraotic in halecomorphs, nor with the median ossification of pycnodontiforms.

REMARKS ON THE SUPRAOCCIPITAL IN TELEOSTS

DISTRIBUTION OF THE SUPRAOCCIPITAL

In modern teleosts the supraoccipital characteristically separates the epioccipitals and contacts the exoccipitals (Bardack, 1965; Patterson, 1975). A supraoccipital is also present in extinct stem teleosts, such as phol-
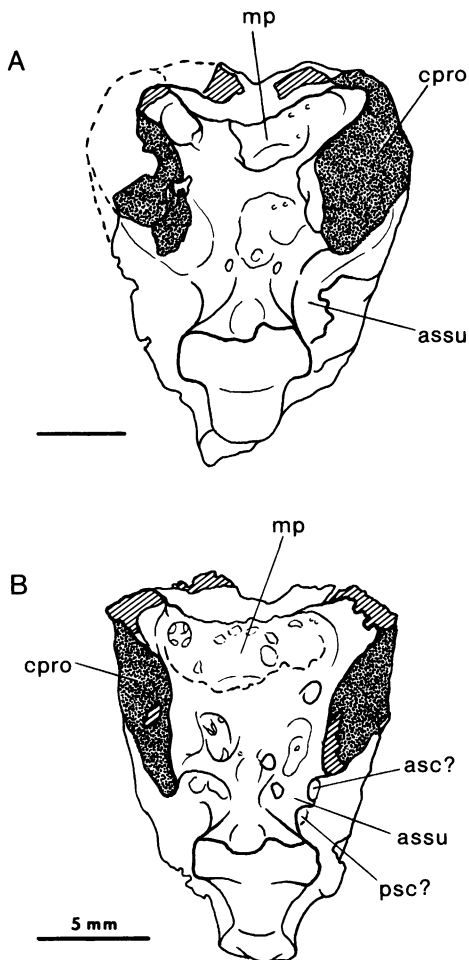
Fig. 16. *Neoproscinetes penalvai:* basal stereopair views of supraotic bones removed from two complete acid-prepared skeletons, anterior is toward top. **(A)** AMNH 11893; **(B)** AMNH 11843. Anterior and posterior semicircular canals lay within grooves in the ventral surface of the bone. Between the anterior semicircular canals there is a median pocket, and between the posterior canals the bone forms a rounded process. Unfinished spongy bone is shown by irregular stipple pattern, broken areas are diagonal parallel line pattern in drawings.

idophorids, leptolepids, and ichthyodectids, in which it has similar relationships to surrounding bones as in Recent forms. A *separate* supraoccipital bone has not been found in pachycormids or aspidorhynchids, although Brito (1992) suggested that this is represented by an area of chondral bone

Fig. 16. Continued.

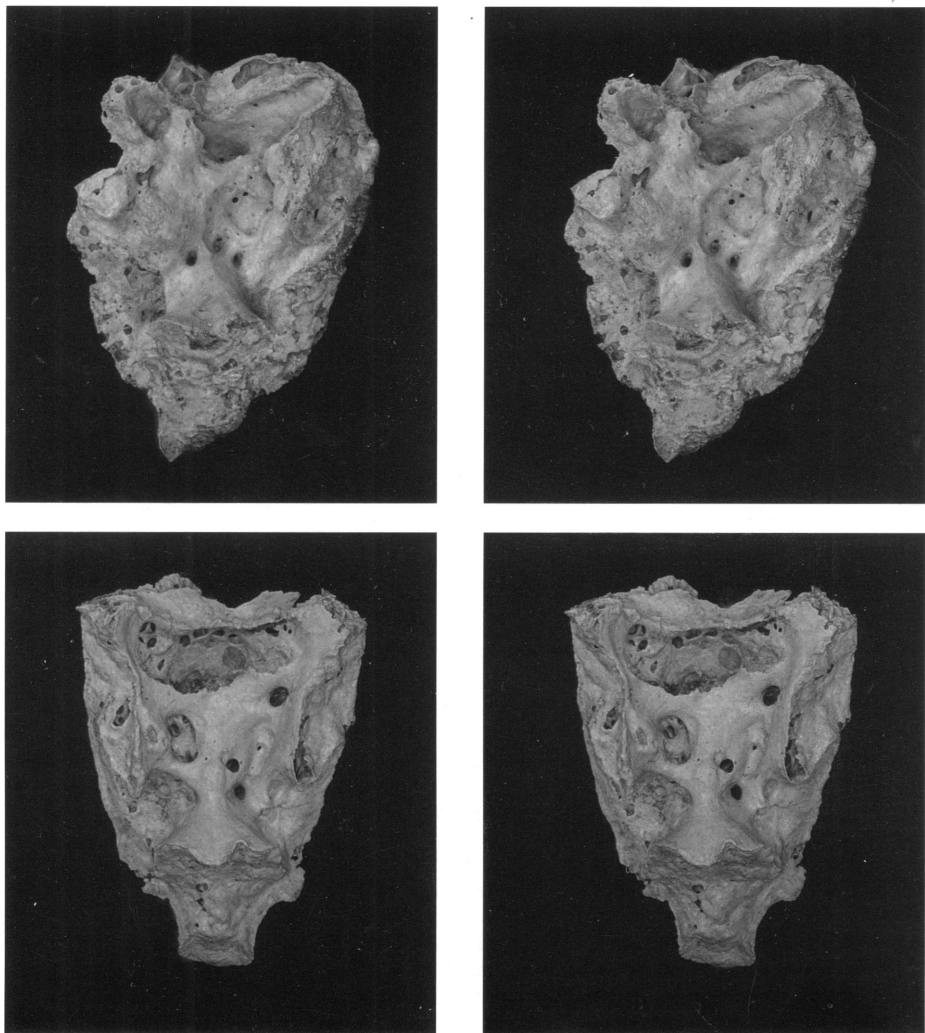above the occiput. Among nonteleostean actinopterygians, Beltan (1963) has identified a median dermal bone in *Saurichthys* from Madagascar as a dermal supraoccipital. In *S. curionii* from Tessin, Switzerland, however, the corresponding bone has been identified as a medial extrascapular (Rieppel, 1985). No median chondral supraoccipital has been described in saurichthyids.

PRIMITIVE AND DERIVED STATES OF THE
SUPRAOCCIPITAL

According to Patterson (1975), the teleost supraoccipital primitively lay posterior to

any contact between the epioccipital and pterotic, and behind the occipital fissure, as for example in *Pholidophoroides*. Several other presumably primitive characteristics of the supraoccipital may also be identified, including the following:

(1) the supraoccipital does not enclose any parts of the semicircular canals or endolymphatic duct, nor does it extend very far anteriorly above the labyrinth region,

(2) a subepiotic fossa (located mesial to the epioccipital) is probably absent,

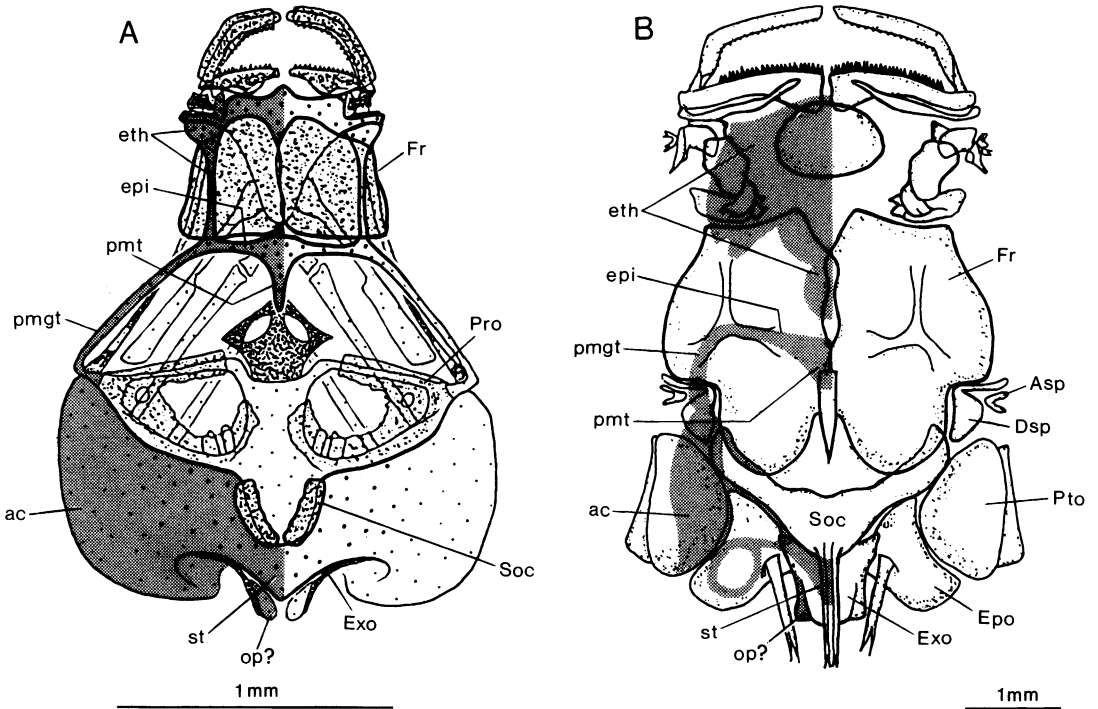(3) the supraoccipital is probably excluded from the posttemporal fossa, it does not oc-

Fig. 17. *Oryzias latipes,* a teleost (modified from Langille and Hall, 1987). **(A)** "Early juvenile" (10–15 mm), dorsal view of the head skeleton, showing the supraoccipital arising as paired ossifications on the anterior edge of the synotic tectum. As originally drawn, there is some doubt as to whether the synotic tectum is fused to the occipital cartilage (op?) more posteriorly; **(B)** "later juvenile" (15–20 mm), dorsal view of the head skeleton showing extent of the cartilaginous braincase and associated bones. There is no anterior medial tectum, but the large ethmoid cartilage extends posteriorly, almost reaching the epiphyseal cartilage. This in turn is connected to the auditory capsule by the posterior marginal tectum (= "orbital cartilage" of Langille and Hall). The large Y-shaped supraoccipital now extends anteriorly beyond the synotic tectum, meeting and underlying the frontals posteriorly. The exoccipitals are also formed on the synotic tectum. The frontals overlie the posterior median tectum and the posterior part of the ethmoid cartilage. Note that parietals are absent in *Oryzias.*

clude the epioccipital from the cranial cavity, and there is probably no pre-epiotic pocket lateral to the epioccipital,

(4) the supraoccipital primitively has only two perichondrally finished surfaces (ventrally and posteriorly),

(5) the bone does not reach the foramen magnum.

According to this scenario, secondarily derived character states of the teleost supraoccipital would include the following:

(1) EXTENSION INTO OTIC REGION

In *Oryzias, Danio,* and *Betta* the supraoccipital bone forms on the anterior rim of the synotic tectum, and also within the ad-

joining wall of the otic cartilage located at the posterior margin of the dorsal fontanelle (fig. 17A; Langille and Hall, 1987; Cubbage and Mabee, 1996; Mabee and Trendler, 1996). Condensation of the supraoccipital may secondarily extend beyond the anterior margin of the roofing cartilage in *Oryzias,* which Langille and Hall (1987: 151) suggested "could be perichondral bone which has spread anteriorly beyond the edge of the cartilage or a mixed bone composed of membrane bone from an anterior ossification center which has fused with the more posterior perichondral bone." As development proceeds further in *Oryzias,* the supraoccipital enlarges posteriorly and laterally over the

otic and occipital regions, and it also spreads anteriorly toward the frontals, meeting and actually passing the (posterior) medial tectum (fig. 17B).

In *Tarpon atlanticus* and other elopomorphs, the supraoccipital forms a roof over the entire labyrinth region anteriorly, contacting the exoccipital, an inturned extension of the pterotic descending lamina and the prootic. Anteriorly the supraoccipital almost reaches the pterosphenoid (figs. 18–20) and, thus, topographically mimics the supraotic in halecomorphs.

(2) CONTRIBUTION TO THE SUBEPIOTIC FOSSA (MESIAL TO EPIOCCIPITAL)

In clupeomorphs and ichthyodectiforms the supraoccipital remains posterior to the contact between the epioccipital and pterotic (its primitive configuration), but part of the supraoccipital is located within a deep subepiotic fossa mesial to the epioccipital. The restricted phylogenetic occurrence of this arrangement suggests it is a derived condition. The lateral surfaces of the supraoccipital are perichondrally lined, but these are simply an extension of its posterior surface. The supraoccipital does not pass in front of the epioccipital or contribute to the pre-epiotic pocket. In ichthyodectiforms the epioccipital separates the posttemporal from the subepiotic fossa. This fossa is small and shallow in *Xiphactinus,* but is much deeper in *Gillicus* and *Cladocyclus* (e.g., Bardack, 1965: figs. 7, 19; Patterson and Rosen, 1977: fig. 4: 96).

The supraotic does not form any part of a subepiotic fossa (this structure is apparently absent in halecomorphs).

(3) CONTRIBUTION TO THE PRE-EPIOTIC POCKET (ANTERIOR AND LATERAL TO EPIOCCIPITAL)

In many elopomorphs and some osteoglossomorphs part of the lateral surface of the supraoccipital intrudes into the posttemporal fossa, between the epioccipital and pterotic, within a pre-epiotic pocket (Allis, 1909; Patterson, 1975), e.g., *Tarpon atlanticus* (figs. 18, 19). This intrusion can be so great that the supraoccipital completely occludes the epioccipital from the cranial cavity (Patterson, 1975: 393; Taverne, 1977). Such

extreme forward development of the supraoccipital may be correlated with increased depth of the occiput and enlargement of the posttemporal fossa (and fossa bridgei), into which extensive epaxial trunk musculature is inserted (and onto which a ligament is attached to the medial surface of the dermosphenotic; Forey, 1973: 52).

Patterson (1975: 392) suggested that presence of the pre-epiotic pocket represents a widespread plesiomorphic feature that was retained by some primitive teleosts, but that view is not supported by the condition found in cladistically primitive stem teleosts such as pholidophorids, leptolepids, and ichthyodectids, in which the pocket is absent. Instead, the pre-epiotic pocket may be an apomorphic feature of modern teleosts that has been secondarily lost in some groups, or it may have been acquired independently within several lineages. Both possibilities are compatible with currently accepted phylogenetic hypotheses for Recent teleosts, despite disagreement over the relative phylogenetic positions of elopomorphs and osteoglossomorphs (e.g., compare Patterson and Rosen, 1977; Lauder and Liem, 1983 with Arratia, 1991, 1995). A third possibility (that presence of the pre-epiotic fossa is apomorphic for a smaller monophyletic group of teleosts including elopomorphs and osteoglossomorphs) is incompatible with current cladistic analyses.

Although there is a deep posttemporal fossa in *Amia* and extinct halecomorphs, a pre-epiotic fossa like that in some teleosts is not developed. In species in which the supraotic is known, it does not extend laterally to reach the posttemporal fossa, and in *Ionoscopus* it is separated from the fossa by the pterotic.

(4) PRESENCE OF PAIRED PERICHONDRAL SURFACES

Where the supraoccipital contributes to the medial wall of the pre-epiotic pocket, the bone has perichondrally finished lateral surfaces that are separated from its posterior surface by the epioccipital (e.g., *Tarpon,* fig. 20). Similar paired lateral surfaces are present on the supraoccipital in the extinct albuloids *Brannerion* (e.g., AMNH 11856) and *Paraelops* (e.g., AMNH 12792) and in gen-

eralized fossil elopocephalans (e.g., *Note-lops, Rhacolepis*). They also occur in the osteoglossomorph *Arapaima* (fig. 21), but in *Scleropages* and *Osteoglossum* the supraoccipital does not contribute to the wall of the posttemporal fossa (Taverne, 1977: figs. 46, 75, 128). No comparable paired perichondral surfaces are known in the supraotic.

(5) SUPRAOCCIPITAL ENCLOSES PARTS OF THE POSTERIOR SEMICIRCULAR CANAL

In *Tarpon,* as in most teleosts, the posterior semicircular canal is located adjacent to the triple contact of the supraoccipital, epioccipital, and exoccipital, and the upper part of this canal lies in a groove in the ventral surface of the supraoccipital (fig. 20A). In some Recent teleosts, e.g., *Arapaima* (fig. 21; see also Taverne, 1977: fig. 132), the dorsolateral part of the posterior canal is completely enclosed by the supraoccipital. Taverne (1977: 212) noted that in a 67 mm juvenile *Arapaima,* the canal did not penetrate the supraoccipital, suggesting that the bone gradually encloses the canal during ontogeny. The posterior semicircular canals are similarly enclosed by the supraoccipital in the extinct chanid *Tharrhias* (e.g., AMNH 11881) and elopocephalans such as *Notelops* (AMNH 11898, 11918) and *Rhacolepis* (AMNH 19153, 19155).

The corresponding part of the anterior semicircular canal is not enclosed by the supraoccipital in any teleost, although its position may be indicated by a groove in the ventral perichondral surface of the bone. The anterior and posterior semicircular canals are completely enclosed dorsally by the supraotic in *Ionoscopus, Calamopleurus,* and perhaps in Rayner's (1948) "*Caturus,*" but lay within open grooves on the ventral surface of the bone in *Neoproscinetes.* Enclosure of the posterior canal by the supraotic in halecomorphs and by the supraoccipital in some teleosts is most parsimoniously interpreted as convergence.

(6) SUPRAOCCIPITAL CONTRIBUTES TO THE MARGIN OF THE FORAMEN MAGNUM

In some osteoglossomorphs (*Hiodon, Heterotis*), many cypriniforms, and all acanthomorphs, the supraoccipital separates the ex-
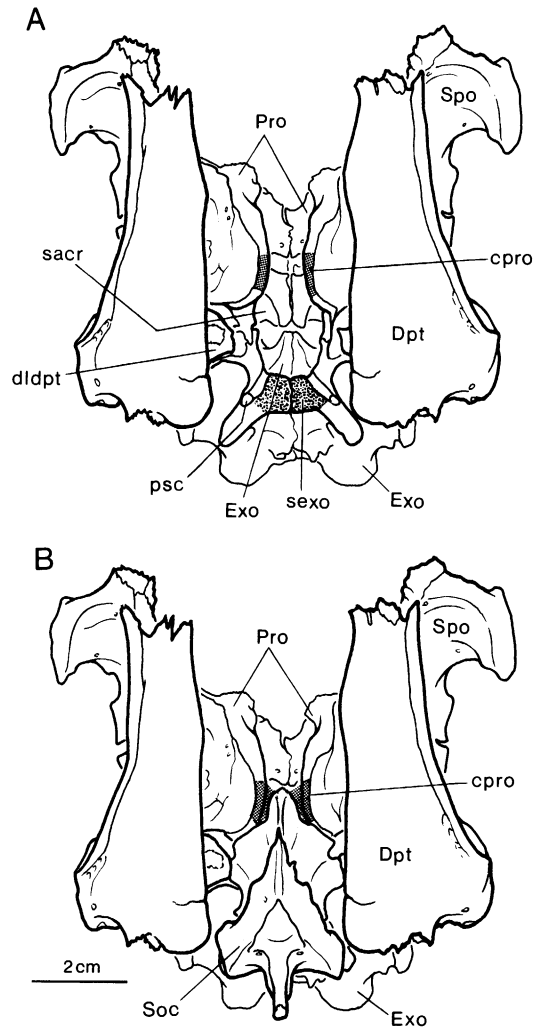
Fig. 18. *Tarpon atlanticus* (Recent). (A) Posterior part of dried braincase in dorsal aspect with supraoccipital removed; (B) same view with supraoccipital in place, showing its successive posterior-to-anterior contact with the exoccipitals, descending lamina of the dermopterotic (inflected inward to form the central part of the floor of the posttemporal fossa), and the prootics (the epioccipitals and pterosphenoids cannot be seen in this view). The supraoccipital forms much of the mesial wall of the posttemporal fossa, an unusual condition (see text for discussion).

occipitals and contributes to the dorsal margin of the foramen. Stiassny (1986: 433) has contended that this condition is derived and arose independently within osteoglossomorphs, ostariophysans, and basal acantho-

Fig. 18. Continued.

morphs. In *Mastacembelus* the supraoccipital separates the exoccipitals and contributes to the margin of the foramen magnum, but the dermal moiety of the supraoccipital does not extend as far posteriorly and is separated from the foramen by the chondral supraoccipital (Taverne, 1973: fig. 1). Posterior extension of the supraoccipital in *Mastacembelus* therefore involves only its chondral part, and this may represent a widespread condition among teleosts whose supraoccipital reaches the foramen magnum.

In halecomorphs the supraotic does not extend onto the occipital segment and the foramen magnum is contained between the exocccipitals and basioccipital. In *Neoproscinetes* the supraotic does not reach the foramen magnum.

DERMAL SUPRAOCCIPITALS AND MEDIAL EXTRASCAPULARS

It has been suggested that the teleost supraoccipital (or at least its dermal component) is of extrascapular derivation (Taverne, 1973: 827; Jollie, 1975: 75; later retracted in Jollie, 1984a: 490). Even if teleosts evolved a medial extrascapular along with the chondral supraoccipital, however, these bones must have coalesced at a very early stage in

teleost evolution, because first, no extinct taxa are known in which the bones are separate, and secondly, this condition is rare (perhaps representing a derived character) even among modern teleosts (e.g., *Mastacambelus*; Taverne, 1973). A separate medial extrascapular is absent in the majority of teleosts and in gars, amiiforms, and *Polypterus,* although a large medial extrascapular is present in *Acipenser.* A dermal supraoccipital is not present in the skull roof of *Dapedium,* but a median canal-bearing bone is present in its extrascapular series (Thies, 1988). No medial extrascapular is associated with the supraotic in *Ionoscopus, Oshunia,* or *Calamopleurus.*

Teleosts are the only actinopterygians in which there is evidence of fusion between medial chondral and dermal bones to form a compound supraoccipital. In *Latimeria* there is a medial canal-bearing extrascapular as well as a chondral supraoccipital, but these bones do not contact each other (Millot and Anthony, 1958). In some extinct actinistians, (e.g., *Mawsonia, Axelrodichthys*; Maisey, 1986) a medial extrascapular, accompanied by a variable number of paired extrascapulars, is incorporated into the posterior margin of the skull roof. At least some of the extrascapulars may make contact with the supraoccipital, but they do not fuse with it. Similarly, in *Eusthenopteron* there is a chondral "supraoccipital plug" situated behind the occipital fissure, within the occipital or posterior tectum (Jarvik, 1980: 132, 1996: 309). The plug makes contact with the ventral surface of the medial extrascapular, but as in *Mawsonia* and *Axelrodichthys,* these bones are not fused. Elsewhere, Jarvik (1996: 309) alluded to similarities between the supraoccipital in humans and *Eusthenopteron,* especially the association of dermal and chondral bones; in humans three dermal bones (a medial interparietal and paired preinterparietal) are fused to the chondral supraoccipital. Thus among sarcopterygians, the dermal bones of the extrascapular series sometimes make contact with the chondral supraoccipital, but fusion between dermal and chondral bone of the supraoccipital is a derived character within tetrapods. Under these circumstances, fusion between chondral and dermal bones to form a compound

supraoccipital is regarded as an apomorphic character of teleosts that was acquired independently of tetrapods.

In pycnodontiforms there is a large ornamented, canal-bearing median "dermal supraoccipital." This bone contributes to the posterior part of the skull roof and is sutured to the frontals and parietals. Its posterior margin contains part of the commissural canal and in some specimens (e.g., AMNH 11852, 11893) the canal can be traced into a splintlike pair of extrascapulars plastered against the posterior margin of the parietal. Accordingly, the median bone is considered a greatly enlarged extrascapular bone that, like the median dermal bone in *Saurichthys,* could also be considered a "dermal supraoccipital."

There is a medial extrascapular in *Dapedium* (a plesiomorphic sister taxon to pycnodontiforms according to Gardiner et al., 1996). There has been some discussion (reviewed by Patterson, 1975: 455) whether a supraoccipital is present in the braincase of *Dapedium.* No such median ossification has been convincingly demonstrated, but if one is present it may have closer morphological similarity with the pycnodontiform supraotic than with the teleost supraoccipital.

COMPARISON OF THE SUPRAOTIC AND SUPRAOCCIPITAL

The presence of a median bone in the otico-occipital region of teleosts and extinct halecomorphs raises the question of homology between these bones. No case of conjunction is known to preclude the possibility, while scenarios of homology and nonhomology between the supraotic and supraoccipital are equally congruent with the phylogenetic hypothesis that halecomorphs and teleosts are sister taxa within the Neopterygii. As the following summary will show, however, morphological support for either hypothesis is weak. The teleostean supraoccipital resembles the halecomorph supraotic in several respects:

(1) Both are primitively chondral bones, with a perichondrally finished internal surface forming part of the braincase vault.

(2) Both lie at the posterior midline of the braincase and may contact the parietals.
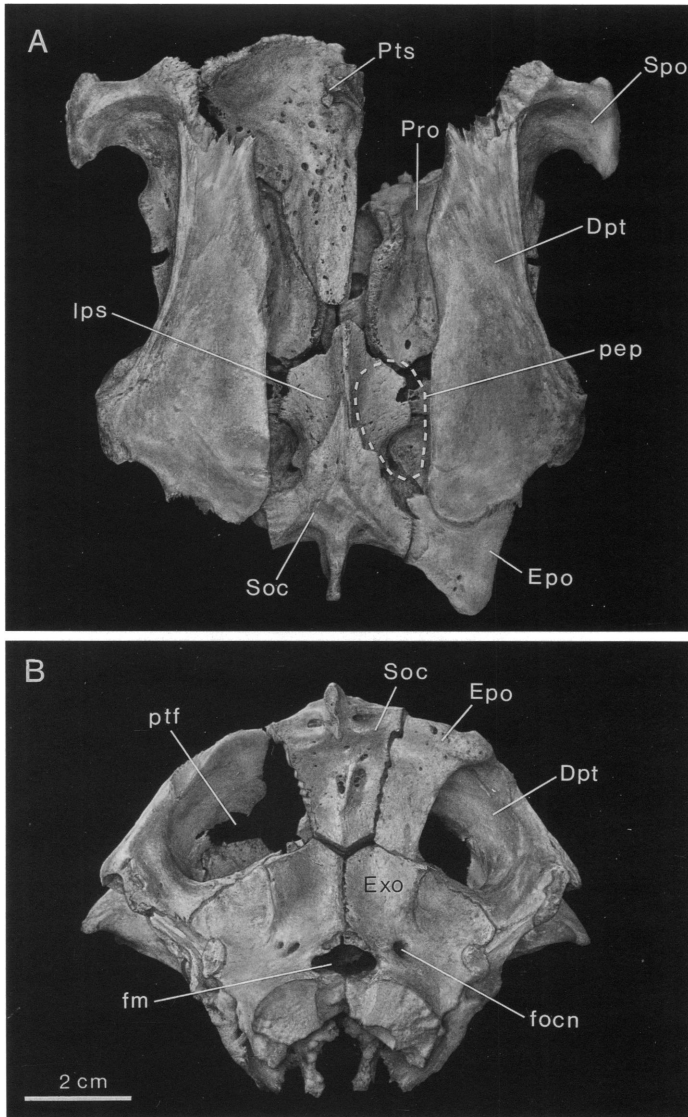
Fig. 19. *Tarpon atlanticus* (same specimen as Fig. 18). Dried braincase in (**A**) dorsal and (**B**) posterior aspect, with the left pterosphenoid and right epioccipital in place, showing their relationships to the supraoccipital. The lateral perichondral surface of the supraoccipital contributes to the mesial wall of the large preepiotic pocket (dotted space shown on right side in A), within the posttemporal fossa. The epioccipital is excluded from the cranial cavity.

(3) Both represent ossification of the mid-dorsal part of the otico-occipital region.

(4) Both overlie the labyrinth region and are closely associated with the semicircular canal system, even to the extent of enclosing parts of the canals by bone.

The pycnodontiform supraotic agrees in features (1–4), but it does not contact the pa-rietals. The chondral supraoccipital in *Latimeria* agrees only in features (1) and (3). In *Latimeria* the supraoccipital does not contact any dermal bones, but in *Mawsonia* (e.g., AMNH 11758) and *Axelrodichthys* (e.g., AMNH 13962) its dorsal surface makes contact with overlying extrascapular bones incorporated into the posterior part of the der-
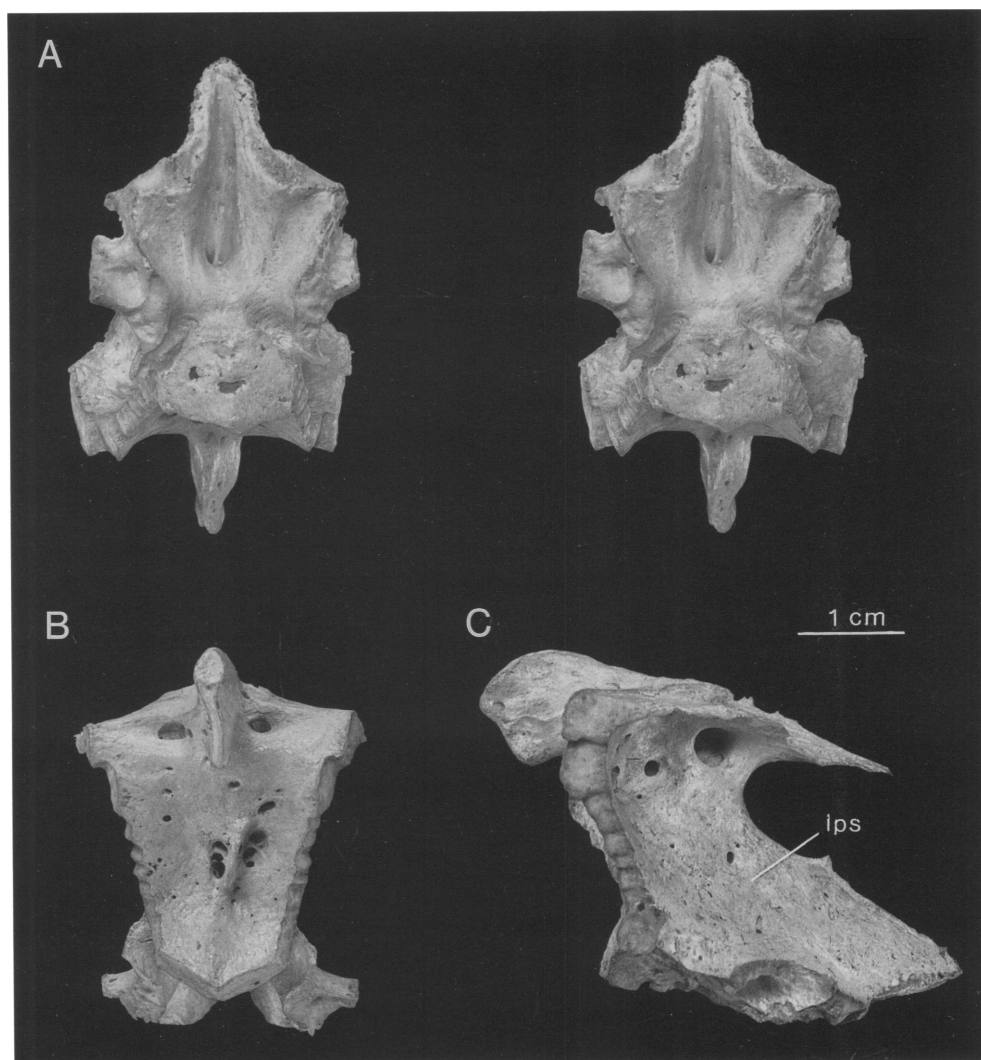
Fig. 20. *Tarpon atlanticus:* isolated supraoccipital from the specimen depicted in Figures 18, 19. **(A)** Ventral view (stereopair); **(B)** posterior view; **(C)** lateral view, right side. There are four perichondrally finished surfaces (posterior, internal, and paired lateral surfaces), separated by sutural contacts with adjacent bones.

mal skull roof (although the bones are not fused together). Cladistic analyses of actinistians suggest that incorporation of extrascapulars into the skull roof represents a derived condition within coelacanths (Forey, 1998), although Wenz (1975) has drawn attention to the similarity between *Mawsonia, Eusthenopteron, Osteolepis,* and tetrapods in this regard. The similarity is further strengthened by the proximity of the chondral supraoccipital to the extrascapulars in all these taxa (for a detailed discussion of the arrange-

ment in *Eusthenopteron,* see Jarvik, 1996). In sarcopterygians (including tetrapods), the supraoccipital is not closely associated with the labyrinth organ.

Morphological differences between the teleost supraoccipital and halecomorph supraotic supposedly include:

(5) The teleost supraoccipital primitively separates the epioccipitals and contacts the exoccipitals (assuming the condition in *Pholidophoroides* is primitive; Patterson, 1975: fig. 82). In *Ionoscopus* the supraotic contacts
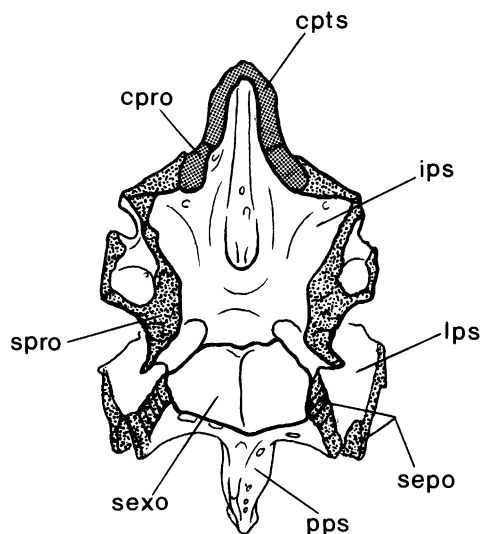
Fig. 20. Continued.

the epioccipitals but not the exoccipitals (possibly a primitive condition within halecomorphs). In some specimens of *Calamopleurus* (e.g., AMNH 12771) the exoccipitals and supraotic just make contact internally (presumably a derived condition). In *Neoproscinetes* there is no contact between the supraotic and epioccipitals or exoccipitals, but in *Pycnodus nardoensis* the equivalent median bone apparently meets the epioccipitals (Taverne, 1997).

(6) The supraotic is an entirely chondral bone (like the supraoccipital in actinistians and the supraoccipital plug in *Eusthenopteron*), whereas the teleost supraoccipital may have an additional (secondary) membranous or dermal component (usually fused to the chondral bone, but rarely separated as in *Mastacambelus*). There is no evidence of comparable fusion between dermal bone and the supraotic in halecomorphs (in which a medial extrascapular is generally absent), nor between the medial extrascapular (= dermal supraoccipital) and the supraotic in *Neoproscinetes*.

(7) The teleost supraoccipital is at least partly exposed on the posterior skull roof. The supraotic may be partly exposed (e.g., *Ionoscopus, Oshunia*) or completely overlain by dermal bones (as by the parietals in *Cal-*

amopleurus and by the "dermal supraoccipital" in *Neoproscinetes*).

(8) The supraotic usually encloses the anterior and posterior semicircular canals. Although the teleost supraoccipital may enclose the posterior canals, the anterior ones are not enclosed by bone. In *Neoproscinetes* the semicircular canals lay within open grooves in the base of the supraotic.

(9) The supraotic is excluded from the posttemporal fossa by the epioccipitals. The supraoccipital is also separated from the posttemporal fossa in extinct stem teleosts such as pholidophorids and leptolepids, but in some teleosts (e.g., elopomorphs) the lateral face of the supraoccipital forms part of the posttemporal fossa, separating the epioccipital and pterotic. The supraotic does not separate the epioccipital and pterotic bones.

(10) The supraotic may enclose part of the lateral cranial canal (as in *Ionoscopus*) unless the canal is absent (e.g., *Calamopleurus, Neoproscinetes*). In extinct stem teleosts in which a lateral cranial canal is present the supraoccipital is situated more posteriorly. In teleosts in which the supraoccipital has moved more anteriorly to form a roof over part of the otic region, there is no lateral cranial canal.

(11) The supraotic encloses the distal extremities of the endolymphatic ducts in *Calamopleurus* but not in *Ionoscopus*. These ducts do not extend into the teleost supraoccipital.

Patterson (1975: 443) distinguished the supraoccipital from the supraotic on purely topographic grounds, maintaining that the former is an ossification behind the dorsal part of the otico-occipital fissure whereas the supraotic was presumably formed anterior to it. Elsewhere in the same work, however, he suggested that teleost "epiotics" may represent epioccipitals that have grown forward across the occipital fissure; thus, the topographic position of a bone relative to the inferred position of the embryonic fissure in fossils may not be a reliable criterion by which to distinguish between bones. In fact, Jollie (1986) questioned Patterson's (1975) interpretation of epiotics as epioccipitals by using essentially the same line of reasoning that Patterson (1975) applied to distinguish between the supraoccipital and supraotic, an

analysis that both highlights and exacerbates the fundamental inconsistency: why would the position of the occipital fissure be crucial in one case but not in the other?

The fact that the supraoccipital sometimes forms exclusively within the synotic tectum (e.g., *Oryzias*; Langille and Hall, 1987) compromises Paterson's (1975) topographic characterization of this bone, suggesting his analysis is applicable only to cladistically primitive teleosts. Even if we were to regard the supraoccipital and supraotic as homologous bones, however, their differing topographic relationship to the otico-occipital fissure would still require an ingenious explanation; we might, for example, invoke different developmental and ossification strategies, involving chondrification and ossification patterns in the occipital and synotic tecta. Unfortunately, the ontogeny of the halecomorph supraotic cannot be investigated, so only cleverly contrived developmental scenarios would provide serious alternatives to Paterson's (1975) assertion that supraotic and supraoccipital ossification centers are not homologous.

OTHER REMARKS

THE LATERAL CRANIAL CANAL

In *Ionoscopus* the supraotic encloses the superior utricular sinus and the medial wall of the lateral cranial canal. In primitive teleosts in which these structures are present, such as pholidophorids and leptolepids, they are enclosed by the paired pterotic bones. *Calamopleurus* differs from *Ionoscopus* in having a completely internal supraotic that houses the distal extremities of the endolymphatic ducts, but the bone did not enclose a lateral cranial canal.

The lateral cranial canal is apparently developed only in actinopterygians. In some primitive extinct neopterygians, such as *Pteronisculus*, it is primitively represented by a posteriorly-situated diverticulum projecting from the cranial cavity through the posterior semicircular canal (Nielsen, 1942; Rayner, 1948; Poplin, 1974; Gardiner, 1984; Coates, 1998). The canal in extinct halecomorphs and stem teleosts (e.g., "*Caturus*," *Ionoscopus*, pholidophorids) invariably passes around the crus commune and reopens

into the cranial cavity anteriorly (Patterson, 1975). This condition could be interpreted as derived relative to that seen in *Pteronisculus*, except that it also occurs occasionally in more primitive actinopterygian taxa (e.g., *Mimia*; Gardiner, 1984), a situation that creates uncertainty as to the primitive condition of the canal in neopterygians.

In *Ionoscopus* the dorsal and medial part of the lateral cranial canal is mostly contained by the supraotic, and its posterior opening is defined by the supraotic and opisthotic (fig. 9). The lateral wall of the canal is contained by the pterotic in pholidophorids but is unossified in *Ionoscopus*. In Rayner's (1948) "*Caturus*," the lateral wall is ossified, but it is not known whether the supraotic and/or pterotic is involved (fig. 11). It is uncertain whether a lateral cranial canal is present in *Oshunia*. In some other fossils there may be a corresponding canal (e.g., *Caturus groenlandicus*; Aldinger, 1932) or an intramural chamber (in parasemionotids, e.g., *Ospia, Watsonulus*; Stensiö, 1932; Lehman, 1952; Patterson, 1975). In *Pteronisculus* a lateral diverticulum projects through the posterior semicircular canal and connects dorsally with a paired space located medial to the posterior semicircular canal. Coates (1998) interpreted this space as the posterior fossa bridgei, but admitted it is a somewhat unusual arrangement, because the posterior fossa bridgei is usually positioned lateral to the posterior semicircular canal. In *Ionoscopus* the posterior opening of the lateral cranial canal is located just anterior to the supraotic pocket within the epioccipital, and it is possible that the two spaces were connected; thus, the supraotic pocket in *Ionoscopus* may be homologous in part with the posterior fossa bridgei in *Pteronisculus*. The same suggestion is made regarding the supraotic pocket in *Lepidotes toombsi* and *L. gloriae*. In these taxa the lateral cranial canal and supraotic pocket are separated by the posterior semicircular canal, part of which lay within the "epiotic" (Patterson, 1975: fig. 111: Thies, 1989: figs. 3, 6). According to Wenz and Brito (1996: fig. 3), the epiotic in *Araripelepidotes temnurus* differs from that of *L. toombsi* and *L. gloriae* in lacking the supraotic pocket and lateral cranial canal,
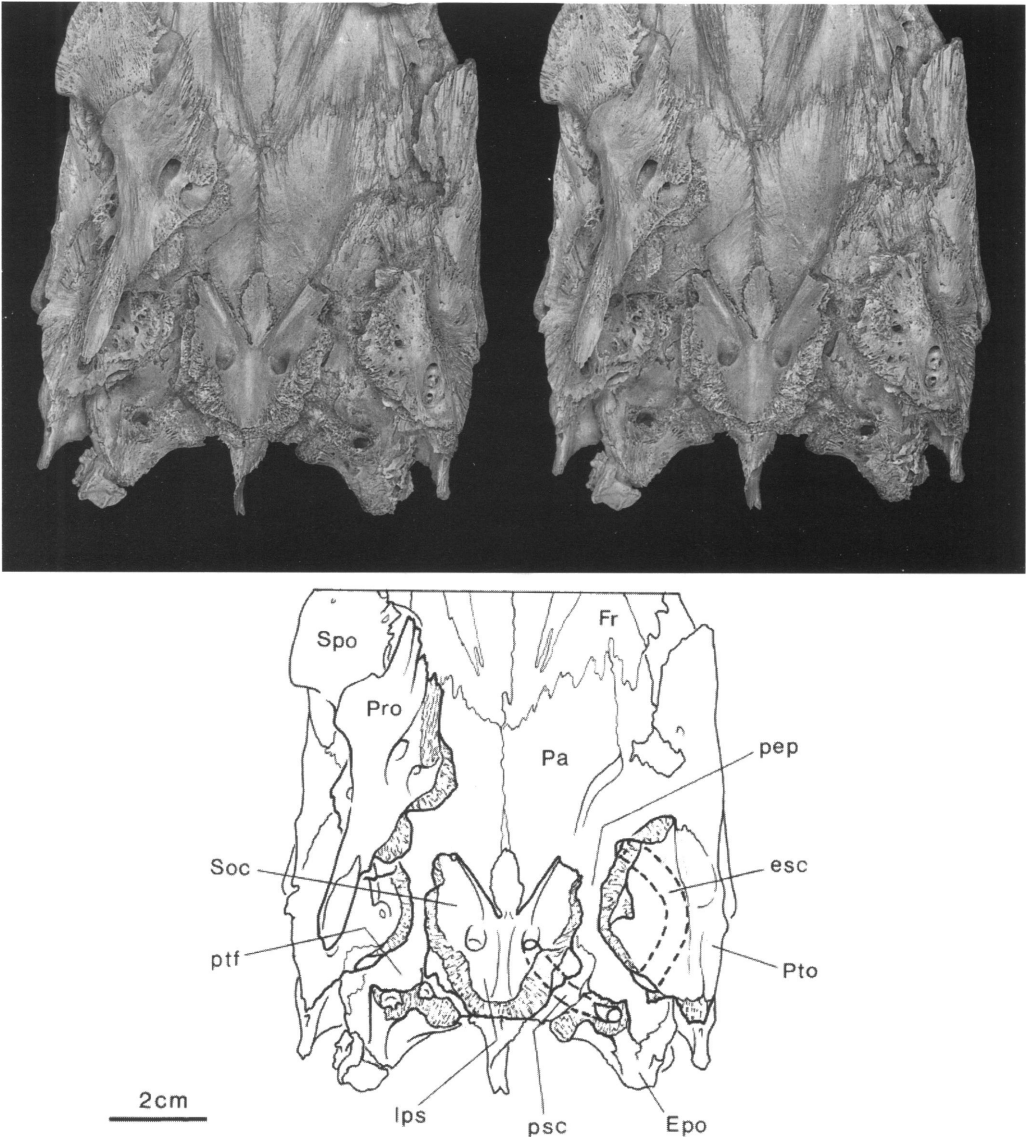
Fig. 21. *Arapaima gigas* (Recent): ventral view of skull roof (stereopair). The internal perichondral surface of the supraoccipital contains a pair of openings for the posterior semicircular canals. Note the contribution made by the supraoccipital to the mesial wall of the preepiotic pocket and posttemporal fossa. The positions of the posterior semicircular canal (within the supraoccipital and epioccipital) and external semicircular canal (within the pterotic) are indicated by dashed lines. Both of these semicircular canals pass into the exoccipital (not seen here).

although a small part of the posterior semi-circular canal is present within the bone.

Absence of the lateral cranial canal in amiids and modern teleosts is most parsi-moniously interpreted as an independent loss rather than a synapomorphy. A lateral cranial canal is not known in any amiid, but *Cala-*

mopleurus demonstrates that the supraotic may be present even when the lateral cranial canal is absent. It is unlikely that the medial pocket in the base of the supraotic of *Neo-proscinetes* represents any part of a lateral cranial canal.

In pholidophorids the bony strut of the

pterotic supporting the superior utricular sinus is slender and the lateral cranial canal is correspondingly short (fig. 22). The superior utricular sinus in many Recent teleosts is also long and slender in comparison with other gnathostomes (Retzius, 1881). In pholidophorids the superior utricular sinus rests on the medial surface of the strut of bone and is not enclosed by a canal like that found in the supraotic. In *Ionoscopus* and Rayner's (1948) "*Caturus*" braincase, the bone supporting the sinus is comparatively broad and forms a complete canal, while the lateral cranial canal is comparatively longer than in pholidophorids. The broad sinus and elongate lateral cranial canal in *Ionoscopus* and "*Caturus*" may represent a primitive halecostome condition, and the presence of a narrow sinus in pholidophorids may represent a synapomorphy with modern teleosts.

EXTENT OF ENDOLYMPHATIC DUCTS

The endolymphatic ducts are primitively open in gnathostomes, and their closure in actinopterygians is considered derived (Gardiner, 1984: 247). In *Mimia* and *Moythomasia* part of the endolymphatic duct ran within a gutter in bone; according to Gardiner (1984) the duct was probably open in *Moythomasia* and closed in *Mimia*. In *Mimia* the ducts are positioned directly above the lateral cranial canal, whereas in *Moythomasia* they are located slightly farther laterally (Gardiner, 1984: figs. 11, 27). In teleosts the endolymphatic ducts are reduced and no part is enclosed by bone. In *Calamopleurus* the endolymphatic ducts were probably confined to the otic capsule as in *Amia*, gars, *Polypterus*, and teleosts, and did not extend into the cranial cavity as in *Acipenser*.

The area containing the endolymphatic ducts in *Mimia* and *Moythomasia* probably represents the same part of the braincase as the supraotic in *Calamopleurus*, in which small pits for the distal extremities of the endolymphatic ducts are present. There is no evidence of a separate supraotic bone in the Paleozoic taxa, however, and the lateral cranial canal in *Mimia* and *Moythomasia* may have lain within the pterotic as in primitive teleosts.

EPIOCCIPITALS AND "EPIOTICS"

In teleosts the dorsal part of the occipital segment includes a pair of chondral bones, originally called epiotics by Huxley (1858). Patterson (1973: 257; 1975: 425) suggested that in modern teleosts these were actually epioccipitals that had extended forward and invaded the otic region, to enclose parts of the posterior semicircular canal following closure of the dorsolateral part of the occipital fissure. In primitive fossil stem teleosts the equivalent bones lay mainly or even entirely behind the occipital fissure, not enclosing any parts of the semicircular canals, and the occipital fissure was perichondrally lined. In modern teleosts the occipital fissure is obliterated and the epioccipitals form the posterior wall of the otic cartilage (e.g., *Oryzias, Danio*; Langille and Hall, 1987; Cubbage and Mabee, 1996).

The paired bones occupying the posterodorsal part of the otic capsule in gars have been identified as pterotics (e.g., *Lepisosteus*; Patterson, 1973: fig. 11A; Wiley, 1976: fig. 8; *Obaichthys*; Wenz and Brito, 1996). Patterson (1975) termed these bones "epiotics" (his quotations), but suggested they represent pterotics that have extended posteriorly (in an evolutionary sense) to replace the epioccipitals. According to that evolutionary scenario, absence of epioccipitals may be an apomorphic feature of gars (Wiley, 1976: 24; Wenz and Brito, 1992: 1519; 1996: 163) or of gars and semionotids (Olsen, 1984; Olsen and McCune, 1991). *Amia* also possesses a pair of "epiotic" bones, although Patterson (1975: 443) suggested that these represent epioccipitals that have extended anteriorly (in an evolutionary sense) following loss of the pterotics, but he cautioned that they could also be pterotics that have extended posteriorly. To Jollie (1986) the principal weakness in all these scenarios is the supposition, which he regarded as developmentally insupportable, that an ossification center can move evolutionarily and traverse the occipital fissure; as an alternative he suggested that the gar "epiotic" is actually the undifferentiated equivalent of both the pterotic and epiotic in teleosts. Thus, there are two important unresolved questions regarding the "epiotics" of gars and *Amia*: (1) are they homologous
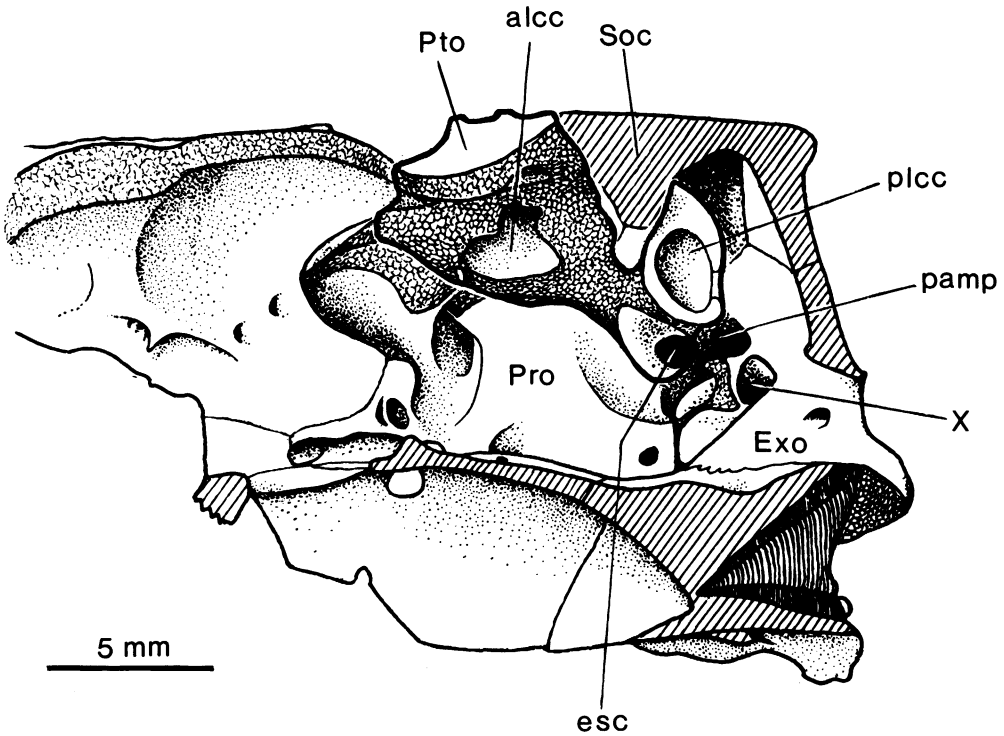
Fig. 22. "Callovian *Pholidophorus* sp." (modified from Patterson, 1975): internal (sagittal) view of neurocranium, anterior to left. In this pholidophorid the lateral cranial canal and parts of all three semicircular canals are contained by the pterotic, whereas the supraoccipital does not contain any of these structures. The pterotic thus occupies part of the braincase formed by the supraotic in *Ionoscopus* (compare with fig. 10).

with each other? and (2) do they correspond with a particular bone in teleosts?

In *Ionoscopus* the perichondrally lined internal surface of the epioccipital contains a deep conical supraotic pocket (fig. 9), located mesial to the posterior semicircular canal, but does not contain the lateral cranial canal (which is contained mostly within the supraotic). A supraotic pocket is present in the "epiotic" of *Lepidotes toombsi* and *L. gloriae,* behind the position of the posterior semicircular canal and lateral cranial canal (Patterson, 1975: Thies, 1989). In *Araripelepidotes* the "epiotic" ("...which may be homologue of the pterotic or the epioccipital"; Wenz and Brito, 1996: 155, fig. 3) differs from that of *Lepidotes* in containing neither a supraotic pocket nor a lateral cranial canal. A supraotic pocket is absent from the corresponding bone in *Lepisosteus,* although a pit for the posterior part of the lateral cra-

nial canal is present (Patterson, 1975: fig. 111). The internal features of this bone have not yet been described in the cladistically primitive extinct gar *Obaichthys.* According to Rayner's (1948: fig. 8) reconstruction of "*Caturus,*" there is no supraotic pocket comparable to that in *Ionoscopus.* The lateral cranial canal and supraotic pocket are both absent in *Amia* and *Calamopleurus.* There is clearly some variation in the presence or absence of these structures among semionotids and extinct halecomorphs. Absence of the supraotic pocket may represent a synapomorphy of "*Caturus*" and amiids, whereas absence of the lateral cranial canal in *Amia* and *Calamopleurus* may be an amiid synapomorphy and an independent loss from teleosts.

These observations provide no compelling evidence that the "epiotic" in *Amia* and *Calamopleurus* is a different bone from that

called the epioccipital in *Ionoscopus*. Furthermore, the presence of a supraotic pocket in *Ionoscopus* suggests that this bone is homologous with the "epiotic" in *Lepidotes*; thus, the semionotid "epiotic" may also represent the epioccipital. On the other hand, Wenz and Brito (1996: 158, 161) remarked that the "epiotic" of *Obaichthys* has a pteroticlike anterior position relative to the exoccipital and is linked to the descending lamina of the dermopterotic. They concluded that the gar "epiotic" is really a pterotic, despite the general morphological similarity of the "epiotics" of gars and *Lepidotes* (Patterson, 1975: fig. 111). These "epiotics" may therefore represent different ossifications (a pterotic or "pterotic-epiotic" in gars, an epioccipital in *Lepidotes* and halecomorphs), although the most widespread view (e.g., Patterson, 1975; Olsen, 1984: fig. 19; Olsen and McCune, 1991: fig. 16; Wenz and Brito, 1996) is that the "epiotics" in both semionotids and gars are modified pterotics. In gars the pterotic supposedly became highly modified to form the "epiotic" while the epioccipitals were lost (Wiley, 1976). Similarities between the epioccipitals of semionotids and primitive halecomorphs (e.g., presence of the supraotic pocket, posterolateral position of the bone in the braincase) probably represent primitive conditions.

Conjunction of an epioccipital (= "epiotic") and pterotic (as in "*Aspidorhynchus*," *Ionoscopus*, macrosemiids, and primitive teleosts) precludes hypotheses of bone-for-bone homology between them. It is nevertheless important to note that (1) no such conjunction between the pterotic and "epiotic" has been found in gars, and (2) such a conjunction is fully compatible with Jollie's (1984b; 1984c; 1986) alternative scenario in which neopterygians primitively possessed a "pterotic-epiotic" that subsequently evolved into two separate bones without evolutionary migration of ossification centers across the occipital fissure (cf. Patterson, 1975).

In *Amia* the epioccipitals are widely separated by cartilage. There is a similar gap between the epioccipitals in *Sinamia* (Stensiö, 1935). In some specimens of *Amia* there is a cartilage-filled space between the epioccipitals and exoccipitals, as depicted by Allis (1897) and Patterson (1973), but in other in-dividuals these bones contact each other (seen in several dried skulls in the AMNH collection; see fig. 2; also Grande and Bemis, 1998: figs. 35, 36). In *Calamopleurus* the exoccipitals meet the epioccipitals and the gap between the epioccipitals is smaller than in *Amia*, although the latter still do not make contact with each other medially. In *Calamopleurus* the supraotic is occluded from the posterior surface of the cranium by the epioccipitals. In *Ionoscopus* and *Oshunia* the supraotic is visible on the posterior surface of the braincase, even though there is an extensive vertical sutural contact between the epioccipitals. The supraotic is also visible externally in "*Aspidorhynchus*," in which the epioccipitals only just make contact dorsally. In all these taxa there is a pronounced hump, formed by the epioccipitals and supraotic, that is lacking in both *Calamopleurus* and *Amia*, and the supraotic is exposed dorsally in the midregion of this hump. A similar hump occurs elsewhere among extinct neopterygians (e.g., *Dapedium*; Patterson, 1975: fig. 112) and may represent a primitive feature, and its absence in amiids (along with occlusion or loss of the supraotic) is probably derived. In *Calamopleurus* it is the topographic shape of the epioccipitals, rather than the distance between them, that is responsible for occlusion of the supraotic from the posterior surface of the braincase. Separation of the epioccipitals in amiids may represent an apomorphic state within halecomorphs, and the amiid otico-occipital arrangement may thus include at least three apomorphic features.

An extensive vertical sutural contact between the epioccipitals occurs in some halecomorphs including *Ionoscopus*, *Oshunia*, and *Macrepistius* (in which the epioccipitals may be partly fused; Schaeffer, 1971: fig. 2), although this contact is not developed in "*Aspidorhynchus*" and the condition is unknown in *Ophiopsis* and *Caturus*. There may be similar contact between the epioccipitals in *Watsonulus* although no sutures are visible (Olsen, 1984). In *Lepidotes* the epioccipitals have a lengthy medial margin, although the bones do not meet at the midline (Patterson, 1975: fig. 110), and in *Lepisosteus* and *Perleidus* cf. *stochiensis,* the corresponding bones are widely separated by the exoccipi-

tals (Patterson, 1973: fig. 11; 1975: figs. 115).

Two different morphological patterns are therefore discernible in the dorsal part of the otico-occipital region in halecomorphs. One of these patterns is apparently restricted to amiids, involving increased separation of the epioccipitals, absence of the posterodorsal hump, and occlusion or absence of the supraotic. The other pattern is more widespread among extinct halecomorphs (e.g., in ionoscopids, *Macrepistius,* and perhaps *Watsonulus*), involving extensive vertical sutural contact between the epioccipitals. The first of these patterns is probably apomorphic for amiids. Depending on how one interprets *Watsonulus,* the second pattern may be an apomorphic character of halecomorphs (sensu Gardiner et al., 1996: fig. 3), or it may represent a synapomorphy of ionoscopids and ophiopsids (ibid.: fig. 4).

THE PTEROTIC AND OPISTHOTIC

Absence of the pterotic in *Caturus* is cited as a synapomorphy with amiids (Patterson, 1973; Lambers, 1992; Gardiner et al., 1996). Grande and Bemis (1998: 678) listed absence of the pterotic and opisthotic as two of three supposedly nonhomoplaseous characters supporting monophyly of their Amiiformes (a group including amioids plus *Caturus* and *Liodesmus*). Their characterization of the pterotic is inaccurate, however, because the bone is also absent in *Oshunia* (which falls outside their Amiiformes), although the opisthotic is retained. Thus, there is some homoplasy in the distribution of the pterotic, and according to the phylogeny presented by Grande and Bemis (1998), it would presumably have been lost at least twice (in Amiiformes and Ionoscopiformes).

The history of bone reduction and loss within halecomorphs is probably far more complex than presently realized. Pterotics and opisthotics are present in "*Aspidorhynchus,*" *Ionoscopus,* and *Macrepistius,* whereas in *Oshunia* the pterotic is absent and the opisthotic is present. Both these bones are absent in the amioid group recognized by Grande and Bemis (1998), but the situation in *Caturus* and *Liodesmus* still needs clarification. The braincase is unknown in *Lio-*

desmus, and in *Caturus furcatus* the pterotic and opisthotic are often said to be absent, but the detailed morphology of the posttemporal fossa has never been described and it is consequently uncertain whether the pterotic is absent or merely concealed from view within the fossa.

In some *Caturus* material a single large bone occupies the equivalent position of the combined prootic and opisthotic in *Oshunia* and "*Aspidorhynchus,*" suggesting that the opisthotic may be fused with the prootic in *Caturus* rather than absent (e.g., BMNH P. 20578; Lambers, 1992, p. 126, fig. 14; Grande and Bemis, 1998: fig. 404C: BMNH P. 20577; Grande and Bemis, 1998: figs. 402, 403).

RELATIVE OTOLITH SIZE IN NEOPTERYGIANS

In *Amia,* as in other actinopterygians, there are three paired otoliths (Grande and Bemis, 1998: fig. 26C,D): the lapillus (utricular otolith), sagitta (saccular otolith), and astericus (lagenar otolith). In *Amia* the lagenar otolith is the largest (correctly indicated in Grande and Bemis, 1998: fig. 26C–H; not the saccular otolith as stated in their text, p. 20), while the utricular otolith is the smallest. The same size relationship has been found among the otoliths of the Eocene amiid *Cyclurus kehreri* (Jermańska, 1977: table IV), but otoliths have not been documented from other extinct amiids. By contrast, the largest otolith in many teleosts is the saccular one, except in ostariophysans (e.g., *Cyprinus*) where the lagenar otolith is largest and has a characteristic morphology (Popper and Coombs, 1982: 316 and fig. 1).

Having the saccular otolith greatly enlarged may represent a derived condition for teleosts (M. Coates, personal commun., 1998), although according to Retzius (1881: pl. V, fig. 8), the largest otolith in *Lepisosteus* is also the saccular one; thus, otolith size alone is an inadequate distinguishing feature of teleosts unless it is supplemented by morphological criteria. Some general trends in otolith size are nevertheless discernible in actinopterygians. For example, in the Pennsylvanian actinopterygian described by Gottfried (1993; see also Coates, 1998: fig. 12A,C), the lagenar otolith is by far the

smallest, as in *Lepisosteus* (Retzius, 1881) and most teleosts. In *Polypterus bichir* and *Erpetoichthys* (*Calamoichthys*) *calabaricus* the lagenar otolith is the largest and the utricular otolith the smallest, as in *Amia* and *Cyclurus* (Popper, 1978: fig. 1; Coates, 1998: fig. 12B). The greater size of the saccular otolith in teleosts and of the lagenar otolith in cladistians, ostariophysans, and amiids may therefore represent independently acquired derived states within these phylogenetically disjunct taxa. The increased size and elaboration of the lagenar otolith in ostariophysans is perhaps functionally associated with other modifications to the ear region (e.g., otophysic connections; posterior position of the saccular and lagenar chambers and their proximity to the midline; Rosen and Greenwood, 1970). Popper and Coombs (1982: 323) found striking similarities between the saccular and lagenar chambers in ostariophysans and mormyrids, concluding that the swimbladder–inner ear complex "...has evolved as a functional unit in a number of taxonomically unrelated species in response to similar acoustic environments." Perhaps enlargement of the lagenar otolith in groups other than ostariophysans is also related to some shared functional adaptation to the same acoustic environment.

DISCUSSION

PHYLOGENETIC DISTRIBUTION OF THE SUPRAOTIC

The supraotic is known only in fossils, where no ontogenetic investigation is possible. It has been recognized in comparatively few fossils, including some ionoscopids, amiids, and pycnodontiforms, but the bone identified as a supraotic in pycnodontiforms is highly specialized. There is no evidence of a separate supraotic bone in cladistically primitive halecomorphs such as *Ospia*, *Watsonulus*, and *Caturus groenlandicus*. Neither the topographic relationships of the bone nor its phylogenetic congruence with other features provide much information about its evolutionary history. Patterson's (1975) interpretation of the supraotic as an evolutionary novelty in halecomorphs is supported circumstantially by its restricted geological occurrence (halecomorphs with a supraotic

range in age from the Toarcian to at least the Albian), but presence of a supraotic in pycnodontiforms (which range from the Triassic to the Eocene; Gardiner, 1993) suggests that the bone has a longer history. The supraotic could be interpreted as a synapomorphy of a more inclusive group that includes both halecomorphs and pycnodontiforms (e.g., halecostomes or even neopterygians), although this supposes that the absence of a supraotic in some groups (e.g., within teleosts and *Amia* among halecostomes; or within gars, *Amia,* and teleosts among neopterygians) represents an early and complete loss. The splintlike bone in the posterior medial tectum of *Lepidotes* is probably not a supraotic or a supraoccipital. Absence of a median chondral bone (supraoccipital or supraotic) in the otico-occipital region of gars is probably more parsimoniously regarded as a primitive condition among neopterygians.

A supraotic is present in the extinct amiid *Calamopleurus,* and its absence in *Amia* probably represents a previously unsuspected apomorphic character within the Amiidae. It is not clear exactly where this character falls within amiid phylogeny because the morphology of the braincase is unknown in most extinct members of the group. Thus, in the phylogeny of Grande and Bemis (1998) the supraotic may have been lost in the amiine sister group to the Vidalamiinae, or perhaps it disappeared earlier in amiid evolution and reappeared as a homoplaseous feature in *Calamopleurus.*

HOMOLOGY BETWEEN THE SUPRAOTIC AND SUPRAOCCIPITAL: THE IMPORTANCE OF FOSSILS

The three tests of homology (conjunction, similarity, congruence) outlined by Patterson (1982) yield varying and largely unsatisfactory results where the supraoccipital and supraotic of neopterygians are concerned. No case of conjunction has been found that would refute homology between these bones. Their topographic (and, by inference, ontogenetic) dissimilarity is not universal, as the teleost supraoccipital may be formed entirely anterior to the occipital region, and both bones may dorsally enclose parts of the otic region. The test of congruence gives ambiguous results, depending on which phyloge-

netic level is considered; the presence of a middorsal ossification in halecomorphs and teleosts is certainly consistent with their putative sister group relationship (there is no evidence of a supraoccipital or supraotic center of ossification in "preneopterygian" or basal neopterygian actinopterygians), but the ossification may not be present in cladistically primitive members of either group.

The topographic distinction drawn by Patterson (1975) between the supraotic and supraoccipital has not been refuted by new evidence from fossil halecomorphs. Of course, since the supraotic is known only in extinct taxa, it can be studied only in fossils. But what if a supraotic was discovered in *Amia,* so that its development could be studied? Ontogenetic data alone might lead us to conclude that the supraotic is homologous with the teleost supraoccipital, since both may be formed on the synotic tectum. The distinction between these bones noted by Patterson (1975) is apparent only in fossils because the ontogeny of the supraoccipital in many (perhaps all) Recent teleosts is secondarily specialized to resemble the supraotic in extinct halecomorphs. The supraoccipital is restricted to the occipital arch only in a few stem teleosts such as *Pholidophoroides,* whereas both the supraotic (primitively) and the supraoccipital (secondarily) may ossify on the synotic tectum. The two bones are distinguishable topographically only where the dorsal part of the cranial fissure is retained. There is no further paleontological evidence (such as conjunction of a supraoccipital and supraotic) that these bones are *not* homologous with each other. Patterson's (1975) fossil-based assertion that the teleost supraoccipital is primitively of occipital-arch derivation would be strengthened by finding a modern teleost in which the supraoccipital develops entirely on the occipital arch, but I know of no such example.

The actinistian supraoccipital differs in many respects from both the supraotic and the teleost supraoccipital (especially in its relationships to surrounding bones), and the presence of a separate supraoccipital in sarcopterygians is most parsimoniously considered an independent apomorphic character. Cladistically primitive coelacanths, such as *Sassenia* and *Laugia,* do not appear to have a supraoccipital, and the condition in *Rhabdoderma* is doubtful; according to the phylogeny presented by Forey (1998: fig. 9.7), presence of a supraoccipital represents a synapomorphy of a monophyletic group within coelacanths. Thus, the coelacanth supraoccipital may have evolved independently from that in extinct stem tetrapods such as *Eusthenopteron.*

OSSIFICATION PATTERNS IN THE HALECOMORPH OTICO-OCCIPITAL REGION

In primitive halecomorphs the otico-occipital region was well ossified, with large parts of the labyrinth enclosed by bone, although it is uncertain whether a supraotic was primitively present. In ionoscopids the prootic, opisthotic, and supraotic all enclose parts of the labyrinth, and in the "*Caturus*" braincase described by Rayner (1948), the pterotic may also make a contribution. In amiids, first the opisthotic and pterotic were probably lost (e.g., in *Calamopleurus*), followed by the supraotic (in cladistically advanced taxa, including *Amia*). Having the supraotic bone exposed in the posterior skull table is interpreted as a primitive condition, and the completely internal supraotic in *Calamopleurus* (and *Neoproscinetes*?) is regarded as an alternative (or intermediate) derived condition for amiids (and perhaps for pycnodontiforms).

Loss of the opisthotic in amiids and teleosts probably occurred independently, and loss of the pterotic in *Oshunia* and amiids may also have occurred independently. No amiid is known with either bone, but the braincase in *Oshunia* demonstrates that some halecomorphs lost the pterotic and retained the opisthotic. From the shape and extent of the "prootic" in *Caturus furcatus,* it is possible to conclude that the bone represents a fusion of the prootic and opisthotic, and that the latter is not really absent in caturids. Thus, the opisthotic may be more widely distributed among primitive halecomorphs than is generally supposed.

The bone identified as an epioccipital in *Ionoscopus* is probably homologous with the "epiotic" in *Amia, Calamopleurus,* and *Lepidotes.* Recent interpretation of the braincase in *Obaichthys* (Wenz and Brito,

1996) suggests that the gar "epiotic" is really the pterotic and therefore not homologous with the epioccipital/epiotic in teleosts, halecomorphs and *Lepidotes*. Thus the "epiotics" of gars and *Amia* may represent different bones. Jollie's (1986) proposal that the bone in gars represents a primitive "pterotic-epiotic" is neither confirmed nor denied, but is consistent with the present findings and avoids the difficulty of migrating ossification centers inherent in Patterson's (1975) hypothesis.

CONCLUSIONS

1. The supraotic is known only in some extinct neopterygians, in which its distribution is disjunct and poorly resolved. The supraotic is probably restricted to the synotic tectum. In the extinct stem teleost *Pholidophoroides*, the supraoccipital is restricted to the occipital arch. In both cases this restriction may be correlated with a failure of the occipital and synotic tectum to fuse dorsally during development. In many modern teleosts the synotic tectum and occipital pila are fused at an early developmental stage, and the supraoccipital may extend secondarily across cartilage of both the otic and occipital regions. In some Recent teleosts the supraoccipital forms entirely on the synotic tectum.

2. Even if a supraotic were to be found in a Recent fish (e.g., *Amia*), it is unlikely that ontogenetic data alone would permit us to distinguish it from the supraoccipital, since both bones may form entirely on the synotic tectum. The supraoccipital can be distinguished topographically from the supraotic only in cladistically primitive stem teleosts, such as *Pholidophoroides*. Thus, fossils can provide important information about homology questions that may not be answerable with ontogenetic data by revealing differences in the plesiomorphic condition that have become masked by subsequent evolutionary convergence.

3. The supraoccipital appears to have evolved independently in at least three osteichthyan lineages (coelacanths, tetrapods, and teleosts). The supraotic probably represents a different bone, which evolved once or perhaps twice within neopterygians (depending on the phylogenetic relationship of

pycnodontiforms to halecomorphs). The supraotic has no known occurrence outside neopterygians.

4. Improved sampling of different ossification patterns in extinct halecomorph braincases offers considerable potential for future phylogenetic analysis. As an example, the presence of a supraotic in *Calamopleurus* shows that the bone was present in some early amiids, and suggests that its absence in *Amia* represents a previously unsuspected loss at a presently unresolved level within amiid phylogeny.

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