THE BRAINCASE IN PALEOZOIC SYMMORIIFORM AND CLADOSELACHIAN SHARKS

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ABSTRACT

The concepts of platytrabia/platybasia and tropibasia/tropitrabia in gnathostomes are reviewed. The terms platytrabia and tropitrabia refer to *developmental* states of the embryonic trabecular cartilages that can be determined only by ontogenetic studies. The terms *platybasia* and *tropibasia* originally had this meaning, but have subsequently taken on additional descriptive connotations involving *morphological* features in the prechordal part of the adult chondrocranium. However, *platybasia* and *tropibasia* are *not* synonymous with *platytrabia* and *tropitrabia*. In gnathostomes, platytrabia *usually* gives rise to a platybasic adult condition (but not invariably; e.g., *Lepisosteus*), and tropitrabia *usually* gives rise to the tropibasic condition (modern elasmobranchs may be an exception). Thus, ontogeny does not provide an absolute guide to the adult condition, nor does adult morphology provide an accurate means to assess the prior ontogenetic condition in gnathostomes. *Platybasia* and *tropibasia* are regarded here as useful morphological terms that can be applied to fossils or to extant forms for which ontogenetic data are not available (although it may still be possible to reach some ontogenetic conclusions, based on morphological observations).

A well-preserved but disarticulated fossil symmoriiform shark braincase from the Pennsylvanian of Arkansas is described under the informal generic designation "*Cobelodus*", using digital reconstructions made from a high-resolution computerized-tomography (CT) scan. The braincase is morphologically tropibasic and clearly represents a departure from the common platybasic pattern found in elasmobranchs (e.g., *Tamiobatis*, *Cladodoides*, *Orthacanthus*).

The contribution made by the embryonic polar cartilage in "*Cobelodus*" was probably extensive (unlike in modern gnathostomes), as in the platybasic Paleozoic shark *Cladodoides*. Thus, tropibasia in "*Cobelodus*" seems to be superimposed on an already-specialized pattern of cranial morphology found in some early platybasic elasmobranchs. The basicranial arterial circuit in "*Cobelodus*" was highly modified, and its internal carotids could not have communicated with the cranial cavity via the bucco-hypophyseal chamber as in other elasmobranchs. Internal carotids either were absent or met the efferent pseudobranchials within the orbit before the combined vessel entered the cranial cavity via the orbital cartilage, but the arrangement was certainly not osteichthyan-like (where the combined internal carotid/efferent pseudobranchial arteries pass through the basisphenoid pillar).

"*Cobelodus*" and many other Paleozoic sharks possessed a postorbital palatoquadrate articulation (possibly strengthened by ligaments above the articulation in "*Cobelodus*"), on cartilage presumably formed in the embryonic lateral commissure. This arrangement differs from that in amphistylic hexanchiform sharks, where the lateral commissure is absent and there is no postorbital arcade; the postorbital articulation is located instead on the primary postorbital process (an outgrowth of the supraorbital shelf). Hexanchiforms are the only extant elasmobranchs with a postorbital articulation, but do not occupy a basal position in modern morphological and molecular phylogenetic analyses. Amphistyly in hexanchiforms is therefore viewed as a derived state rather than a highly conserved feature.

No hyomandibular facet has been identified in "*Cobelodus*", suggesting that its epihyal had only a ligamentous connection to the braincase. However, previous suggestions that symmoriiforms were aphetohyoidean (with a complete hyoidean gill slit and "unmodified" hyoid arch) are not supported by morphological evidence.

The systematic classification of symmoriiform sharks is in disarray. Symmoriiforms collectively are probably monophyletic, but within them only the family Falcatidae is characterized convincingly by synapomorphies. Remaining symmoriiforms have been traditionally classified as "stethacanthids" and "symmoriids", based respectively on the presence or absence of a spine-brush complex, but that distinction seems artificial because no undisputable "brushless male symmoriids" or "brushed female stethacanthids" have been documented and because sex-linked dimorphism of the spine-brush complex has been demonstrated only in falcatids. The braincase in *Cladoselache* shares some unusual features with "*Cobelodus*", suggesting that *Cladoselache* and symmoriiforms are closely related, but it has yet to be determined whether *Cladoselache* was morphologically platybasic or tropibasic.

INTRODUCTION

Fossil remains of chondrichthyan skeletons are extremely rare, and three-dimensionally preserved specimens are truly exceptional. Consequently, new discoveries may have considerable impact on previously entrenched views on the anatomy, diversity, and phylogenetic relationships of early shark-like fishes, and even have the potential to affect the deeper phylogenetic significance of certain features within gnathostomes (e.g., *Pucapampella*; Maisey, 2001a; Maisey and Anderson, 2001). In this work, new observations are presented that will challenge previous interpretations of cranial morphology in extinct sharks (e.g., Zangerl and Case, 1976; Zangerl, 1981; Williams, 1985; Coates and Sequeira, 1998).

New fossil discoveries have also revealed previously unsuspected patterns of structural complexity among early chondrichthyans, for example, the recent revelation that the braincase is morphologically tropibasic in some Paleozoic sharks (including at least some of the forms described in this work), i.e., with an interorbital septum separating the prechordal part of the cranial cavity from the basicranium, as in many actinopterygians and tetrapods (Maisey, 2004a). Prior to this discovery, chondrichthyans had all been considered morphologically platybasic (with the orbits completely separated by the cranial cavity). A brief review of the criteria by which tropibasia and platybasia have been recognized will be presented below.

The main purpose of this paper is to present detailed descriptions of cranial morphology in extinct sharks belonging to the order Symmoriiformes. Zangerl (1981) regarded these sharks as forming a monophyletic group, which has customarily been defined using a combination of conserved elasmobranch characters (e.g., fusiform body, heterocercal tail) plus several presumably apomorphic features having a more restricted systematic distribution (e.g, spine-brush complex, features of the postcranial endoskeleton, lack of body squamation). Zangerl (1981) erected the Order Symmoriida (= Aphetohyoidea of Zangerl and Case, 1976) to include two extinct families, the Symmoriidae Dean 1909 and the Stethacanthidae Lund 1974. However, the informal term "symmoriid" is ambiguous, since it may refer to the order or to the family. To avoid confusion and to bring ordinal-level terminology into line with that of other elasmobranchs, Zangerl's (1981) Order Symmoriida is here renamed the Order Symmoriiformes. Thus, in the present work, symmoriiforms include "stethacanthids" (i.e., those Paleozoic sharks in which a distinctive "spine-brush" complex is present, but whose monophyly is still in some doubt), "symmoriids" (a poorly resolved and potentially artificial assemblage of stethacanthid-like sharks thought to lack the "spine-brush" complex, but otherwise indistinguishable from "stethacanthids"), and falcatids (regarded as monophyletic on the basis of several apomorphic characters; Zangerl, 1990).

Although symmoriiforms are morphologically distinctive and probably form a monophyletic group, it is far from clear whether "symmoriids" and "stethacanthids" are monophyletic sister groups, or alternatively that one is paraphyletic without the other. This systematic uncertainty is exacerbated by cases of apparent synonymy between taxa supposedly lacking a spine-brush complex and others that possess one (e.g., *Denaea meccaensis*, *Stethacanthulus longipeniculus*). For these reasons, most of the taxa described below will not be assigned to a family, and are considered Symmoriiformes *incertae sedis* pending future phylogenetic analysis of the entire group. The only exceptions are *Falcatus* and *Damocles*, highly specialized forms that together are sufficiently distinct from all other symmoriiforms to merit inclusion in a separate family (Family Falcatidae Zangerl, 1990).

Coates and Sequeira (2001a, 2001b) identified one unambiguous symmoriiform synapomorphy (posterior dorsal fin with delta-shaped cartilage) and several other synapomorphies of some but not all symmoriiforms (e.g., "physonemid" dorsal spine shape in *Akmonistion*, *Falcatus*, and *Damocles*; procoracoid directed posteriorly, pelvic plate semicircular with anterior concavity, clasper with clawed terminus in *Cobelodus* and *Denaea*). They also identified two characters shared by *Cobelodus*, *Denaea*, and *Cladoselache* (caudal axis upturned steeply, supporting high aspect-ratio lunate fin; eurybasal pectoral articular surface), one character shared only by symmoriiforms and *Cladoselache* (laterally directed otic fossa on the palatoquadrate), plus one character shared by symmoriiforms, *Cladoselache*, and *Acanthodes* (semicrescent-shaped hyomandibula). Lund and Grogan (2004) also presented a phylogenetic analysis (primarily intended to resolve interrelationships among holocephalimorphs), in which *Stethacanthus*, *Falcatus*, and *Damocles* were united (as "stethacanthids") by three characters (dorsal fin squamation on crest of fin only; anterior dorsal spine develops at puberty; anterior dorsal spine enameloid absent) plus one character shared with *Echinochimaera meltoni* (sexually dimorphic anterior dorsal fin, resolved as an independently acquired feature). However, their analysis omitted supposedly anacanthous (lacking a fin spine) "symmoriids", so the phylogenetic significance of features shared only by "stethacanthids" and holocephalimorphs in their analysis is unclear.

Articulated "stethacanthids" occur from the Upper Famennian to the Upper Pennsylvanian Zangerl, 1981; Williams, 1985). No "symmoriids" are known from the Devonian, although several Mississippian and Pennsylvanian forms have been described. Falcatids are apparently restricted to the Mississippian. No Mesozoic or younger symmoriiforms have been recognized; the last known records are from the Lower Permian, including isolated teeth from the Russian Arctic ("*Denaea*" *decora* Ivanov, 1999; see discussion of *Stethacanthulus* below) and possibly the braincase of *Dwykaselache oosthuiseni* Oelofsen, 1986 (also discussed below).

ABBREVIATIONS

Institutional

AMNH	American Museum of Natural History, New York
CM	Carnegie Museum, Pittsburgh
CMNH	Cleveland Museum of Natural History, Cleveland
FMNH	Field Museum of Natural History, Chicago
MV	University of Montana Paleontology Museum, Missoula
NMNH	New Mexico Museum of Natural History, Albuquerque
OUZC	Ohio University Zoology Collection, Athens
SAM	South African Museum, Cape Town

Anatomical

aa	anterior ampulla
acv	anterior cerebral vein
add γ	adductor γ muscle and tendon
add md	mandibular adductor muscle
adll	foramen for anterodorsal lateral line ramus
af	aortic fenestra
art n	articular notch of postorbital articulation
art pr	articular process of postorbital articulation
asc	anterior semicircular canal
ba	basal angle
basa	basilar artery
bas f	basicranial fenestra
bf	basal foramen (*Acanthodes*)
bpt pr	basipterygoid process
br	cartilage bridge between abducent and facial foramina
cc	crus commune
c cav	cranial cavity
cer	cerebellar chamber
ch	ceratohyal
cra	wall of cranial chamber
da	foramen or course of median dorsal aorta
dc 1,2	dorsal constrictor 1, 2
dlof	dorsolateral otic fossa
dor	dorsal otic ridge
dppr	dorsal paroccipital process
ds	dorsum sellae
ea	external ampulla
ect pr	ectethmoid process
ehy	efferent hyoidean artery
epsa	efferent pseudobranchial foramen
esc	external semicircular canal
eth os	ethmoid ossification
fm	foramen magnum
gc	glossopharyngeal canal

gr epsa	groove for efferent pseudobranchial artery
gr VII hy	groove for hyomandibular trunk of facial nerve
hl	hypotic lamina
hmf	hyomandibular facet
hy	hyomandibula
hyp ch	hypophyseal chamber
hypth	region occupied by hypothalamus
ica	foramen or course of internal carotid artery
inf l	infundibular lobe
inp	internasal plate
iof	interorbital fenestra
ios	interorbital septum
jc	jugular canal
kp	ventral keel-process of basicranium (*Centroscyllium*)
lda	course of lateral dorsal aorta
lg	lateral groove (for efferent pseudobranchial?)
lof	lateral otic fossa
lor	lateral otic ridge
Mc	Meckel's cartilage
med	medullary chamber
mes	mesencephalic chamber
mx lev	maxillary levator muscle
nas os	nasal ossification
n epsa	notch for efferent pseudobranchial artery
oca	occipital arch
oc cot	occipital cotylus
oc os	occipital ossification
olf cap	olfactory capsule
olln	foramen of otic lateral line nerve (= "otic ramus of trigeminal")
onc	orbitonasal canal
oof	otico-occipital fissure
opa	course of optic retinal artery
opha	foramen for ophthalmic artery
or	orbit
ora	course of orbital artery
or art	orbital articulation for palatoquadrate
or os	orbital ossification
pa	posterior ampulla
pbc	posterior basicapsular commissure
pdf	posterior dorsal fontanelle
ped	attachment area of optic pedicel
pepr	periotic process
pf	pineal foramen
pit v	foramen for pituitary vein
plg	posterolateral groove (for internal carotid/lateral dorsal aorta?)
pnw	postnasal wall
po art	postorbital articulation for palatoquadrate
po art gr	postorbital articular groove
po art r	postorbital articular ridge
po lig	postorbital ligament
popr	postorbital process
pq	palatoquadrate
prcf	precerebral fontanelle
pre	preorbital muscle
prfc	prefacial commissure
prof	foramen for profundal nerve
prsl	presphenoid ledge
psc	posterior semicircular canal
pt	posterior tectum
re	pit for origin of external rectus muscle
rec	recess in posterior part of orbit (*Trigonognathus*)
rhy	rays of hyoid arch
sac	saccular chamber
scr	sclerotic ring
sls	sensory line scales
sof	spino-occipital nerve foramina
son	spino-occipital nerve (endocast)
soph	course of superficial ophthalmic complex
spir	spiracle
ss	sinus superior
sub s	suborbital shelf
sup n	notch in supraorbital shelf
sup s	supraorbital shelf
sv	region occupied by saccus vasculosus
t add γ	attachment area of adductor γ tendon
tel	telencephalic chamber
unc	uncalcified area of interorbital septum
ur	utricular recess
vc 2	ventral constrictor muscle 2
vlc	vestibulolateral chamber
vppr	ventral paroccipital process
II	optic nerve
III	oculomotor nerve
IV	trochlear nerve
V	trigeminal nerve
V md	mandibular ramus of trigeminal nerve
VI	abducent nerve
VII	facial nerve (undifferentiated)

VII ar	anterior palatine ramule of facial nerve
VII h	hyomandibular trunk of facial nerve
VII hy	hyoid ramus of facial nerve
VII pal	palatine ramus of facial nerve (undivided)
VII pr	posterior palatine ramule of facial nerve
IX	glossopharyngeal nerve
X	vagal nerve
1–5	spino-occipital nerve canals
?	indicates uncertain identification
(L), (R)	left and right, respectively

PLATYBASIC AND TROPIBASIC BRAINCASES

The terms "platybasic" and "tropibasic" refer to the general topology of the gnathostome basicranium (*platys*, Gr. "broad, wide, level, flat"; *tropis*, Gr. "keel, ridge"; *basis*, Gr. "pedestal, foundation"; Brown, 1965). These terms have both morphological and ontogenetic connotations, although they were originally coined in order to distinguish between two extremes of *ontogenetic* patterning found in the trabeculae of the developing chondrocranium in gnathostomes (see De Beer, 1937: 377). As originally intended, the difference between a tropibasic and platybasic braincase is one of degree; the embryonic chondrocranium was said to be platybasic where the paired trabeculae are wide apart, and tropibasic when they are close together and fused extensively at the midline, forming a trabecula communis below the brain (De Beer, 1937; Daget, 1964). Unconventional criteria for these concepts can be also found in the literature, for example, using cranial proportions (Martin, 1972), or presence/absence of a hypophyseal stalk (Rizkalla, 1976).

The terms "platytrabic" and "tropitrabic" have also been advocated for these two ontogenetic conditions, emphasizing the crucial role played by the embryonic trabeculae in determining which adult condition will develop (Van Wijhe, 1922; De Beer, 1937). Although those terms have not met with widespread acceptance, they provide a useful means to distinguish between the ontogenetic and morphological aspects of the two extremes. This distinction is valuable because tropibasia and platybasia have occasionally been characterized using purely adult morphological criteria when the ontogeny is unknown or cannot be investigated (as in fossils; e.g., Watson, 1937; Stensiö, 1948, 1963a, 1963b; Maisey, 2004a).

Such a distinction between ontogeny- and morphology-based criteria might seem unnecessary, since in many extant gnathostomes there is congruence between tropitrabia or platytrabia in the embryo and platybasia or tropibasia in the adult. For example, in many actinopterygians, the embryonic chondrocranium is tropitrabic and the adult braincase is morphologically tropibasic (e.g., *Salmo*; De Beer, 1937; Ristovska et al., 2006). In others, the embryonic chondrocranium is platytrabic and the adult skull is platybasic (e.g., cypriniforms; Vandewalle et al., 2005; catfishes, some clupeomorphs; De Beer, 1937; Vandewalle et al., 1999, and references therein; Geerincks et al., 2005). In squamates other than snakes, the embryonic chondrocranium is tropitrabic, with a trabecula communis extending throughout the length of the orbit, and the adult skull is morphologically tropibasic. However, snakes are ontogenetically platytrabic in that the embryonic trabeculae are fused only anteriorly, forming a short trabecula communis that does not extend through the entire orbit; consequently, there is no roof or side wall to the chondrocranium and an interorbital septum is absent (De Beer, 1937; Rieppel and Zaher, 2000). In modern urodeles and salamanders, however, the chondrocranium is platytrabic and the adult skull is platybasic (usually regarded as a phylogenetically secondary condition, because early tetrapods are morphologically platybasic; Watson, 1926; Case, 1933).

Nevertheless, it is not possible to view the platytrabic and tropitrabic conditions simply as the respective ontogenetic precursors to morphologically platybasic and tropibasic adult conditions, and there are important exceptions. For example, according to Pehrson (1922), in *Amia* the embryonic chondrocranium is platytrabic and the adult braincase is platybasic, but in *Lepisosteus* an interorbital septum develops very late in ontogeny (after Pehrson's 70 mm stage); however, the trabeculae do not form a trabecula communis and are separate (though slightly convergent anteriorly), contributing to the orbitonasal wall as in *Amia*. Pehrson (1922: 33) concluded that in *Lepisosteus* "the cranium is thus during its embryonic development platy- rather than tropibasic, which was hardly to be expected with regard to the fairly pronounced tropibasia in the adult." In modern elasmobranchs, Holmgren (1942) was reluctant to categorize modern elasmobranchs as either tropibasic or platybasic, because he had previously discovered (Holmgren, 1940) that the embryonic trabeculae are initially separate but become fused anteriorly in front of the bucco-hypophyseal fenestra at a comparatively early stage during ontogeny (as in some tropitrabic actinopterygians; e.g., *Salmo*; De Beer, 1937). Moreover, this early fusion occurs whether the prechordal part of the basicranium subsequently becomes broad (e.g., *Scyliorhinus*, *Raja*, *Torpedo*) or it remains comparatively narrow (e.g., *Squalus*, *Etmopterus*). In addition, Holmgren (1940) noted an extensive "medial area" (initially narrow and blastemic, but becoming wider as it chondrifies) forming much of the rostrum and anterior part of the cranial floor, supposedly anterior to the trabeculae and connected to them via blastemic tissue. According to other investigators (e.g., De Beer, 1931; El-Toubi, 1949; Jollie, 1971), this "medial area" represents an anterior extension of the trabeculae (apparently an apomorphic character of elasmobranchs), although Holmgren (1940) found the connection between them to be rather tenuous at the earliest stages he investigated. The "medial area" may nevertheless represent the anterior extension of a trabecula communis into the ethmoid region, even though no interorbital septum is developed in the floor of the cranial cavity. On the basis of these observations, the chondrocranium of modern elasmobranchs could be characterized as tropitrabic in the embryo and platybasic in the adult.

Holmgren (1942: 135) summarized the situation succinctly: "no conclusion as to tropibasia or platybasia may be drawn from the features of an adult skull" (but for "tropibasia" and "platybasia" read "tropitrabia" and "platytrabia", because he was referring to the condition of the trabeculae in the embryo). This dilemma arises both from the absence of ontogenetic data for extinct organisms, as well as from exceptions such as those noted above. Under these circumstances it becomes problematic to infer the precursor ontogenetic condition using only adult morphological characteristics, as Holmgren (1942: fig. 4) illustrated by superimposing the outline of an *Acanthodes* basisphenoid on a ventral view of an adult *Oxynotus* chondrocranium. He observed that "if the skull of *Acanthodes* is a tropibasic skull, that of this modern shark is at least equally tropibasic". Although ontogeny is unknown (for different reasons) in both *Oxynotus* and *Acanthodes*, his fundamental point (that appearances may be deceptive) is well taken.

The most widely cited *morphological* characteristic of tropibasia in extinct gnathostomes is the presence of an interorbital septum formed in a trabecula communis extending the length of the orbits. Stensiö (1963b) distinguished between morphologically platybasic and tropibasic braincases on the basis of several adult features involving the relationship of the cranial cavity to surrounding structures. For example, the platybasic braincase has a cranial cavity extending anteroposteriorly throughout the length of the interorbital wall as far as or beyond the postnasal wall and extending ventrally to the basis cranii forming the ventral endocranial wall; by contrast, the tropibasic braincase has a thin median bony or membranous interorbital septum, the interorbital part of the cranial cavity is confined to the upper half of the interorbital wall (also frequently restricted to its posterior portion) far above the basis cranii, and the bucco-hypophyseal fossa is deep. Stensiö (1963b) correlated these features in tropibasic forms with upward and/or posterior displacement of the telencephalon and the upper parts of the diencephalon, along with increased depth of the hypothalamus and hypophysis.

Purely on the basis of morphological evidence, it has been suggested that some acanthodians were tropibasic. In fact, Watson (1937: 117) stated emphatically that in

Acanthodes and perhaps in *Cheiracanthus* "the skull is tropibasic, there being a narrow inter-orbital septum with a brain cavity contained within its dorsal part", unlike elasmobranchs (including extinct forms such as *Cladodoides*), which he regarded as platybasic. The median basicranial ossification in *Acanthodes* resembles the basisphenoid of osteichthyans and probably contained arterial vessels supplying the brain (Miles, 1973: figs. 8, 9).

It has also been claimed on morphological grounds that some placoderms were tropibasic (e.g., antiarchs, some arthrodires, ptyctodontids; Stensiö, 1948, 1963a, 1963b). However, the evidence in antiarchs is very weak and was mostly inferred from the position of the eyes close to the dorsal midline. Young's (1984: fig. 9) more recent reconstruction of the braincase in *Bothriolepis* suggests that it was much deeper than Stensiö (1948) supposed, and instead resembled that of other placoderms with a broad basicranium (based on several proposed homologies in the skull roof). Accordingly, the basicranium in *Bothriolepis* was broad and flat or concave, with a narrow interocular region dorsally behind the rhinocapsular region. It is possible that antiarchs possessed an interorbital septum above the brain (analogous to that of modern chimaeroids, although there is no evidence of a chimaeroid-like ethmoidal canal passing through this region). Among arthrodires, Stensiö (1963a) proposed that certain coccosteomorphs and pachyosteomorphs had a tropibasic braincase (especially forms with large orbits; e.g., *Pholidosteus*, *Trematosteus*). His suggestion is certainly plausible, but the evidence is equivocal and was inferred from his hypothetical reconstructions of the neurocranium rather than from actual specimens. In ptyctodontids, there are large paired chondral ossifications within in the floor of the neurocranium (Ørvig, 1962; Miles, 1967; Miles and Young, 1977; Long, 1997). Their arrangement is unique among gnathostomes, since the ossifications form a paired series on either side of the midline that correspond only loosely to the embryonic basicranial cartilages in modern gnathostomes. These ossifications are best known in *Austroptyctodus gardineri* (Miles and Young, 1977; Long, 1997), although corresponding ossifications are also known to be present in other ptyctodontids (e.g., *Ctenurella*, *Chelyophorus*). Behind the olfactory capsules there are paired nasal ossifications, followed successively by paired ethmoidal, orbital, and occipital ossifications, collectively forming a semicontinuous pavement below the neurocranium (Long, 1997: fig. 34). However, the relationship of these ossifications to the neurocranium is controversial and there are radically different interpretations of their orientation in the orbit. In *Austroptyctodus*, the orbital ossification met a mesial process of the marginal plate, but opinions differ as to whether it contributed to the side wall of the cranial cavity or to the floor of the orbit (cf. Miles and Young, 1977; Long, 1997). However, there is agreement that the orbital ossification provided an attachment area for the optic pedicel (known to be present in various placoderms; e.g., *Radotina*, *Romundina*, *Brindabellaspis*, *Buchanosteus*; Ørvig, 1975; Young, 1979, 1980, 1986; Gardiner, 1984b). Furthermore, the internal surfaces of the orbital ossifications are perichondrally lined and were therefore separated by an intracranial space (i.e., they did not form the opposing sides of an interorbital septum). In modern elasmobranch embryos, the optic pedicel is secondarily fused to the base of the antotic pila just above the polar cartilage, suggesting that the orbital ossification in *Austroptyctodus* also includes the embryonic antotic pila and perhaps the polar cartilage (indirect support for this comes from the inferred position of the pituitary vein in *Chelyophorus*; Long, 1997: fig. 33D). Thus, no evidence of an interorbital septum is provided by the orbital ossifications in *Austroptyctodus*. However, the suggestion by Miles and Young (1977: 170) that the ethmoidal ossifications farther anteriorly "enclosed a high, narrow median space representing the anterior continuation of the cranial cavity" suggests that they formed within a preorbital extension of a trabecula communis (perhaps corresponding to the rostrum in modern squaloids) and/or that they contributed to the orbitonasal wall (as in *Lepisosteus*). Thus, *Austroptyctodus* may have been ontogenetically tropitrabic, with fused trabeculae anterior to the hypophysis, but it apparently did not possess an interorbital septum in the adult (i.e., it was morphologically platybasic).

Holmgren (1942: 135) observed that the basicranium in the Devonian shark *Cladodoides wildungensis* (“*Cladodus*”) is much wider than in *Acanthodes*, but in the shark more than two-thirds of this surface is formed in the suborbital shelves. He reached no definite conclusion as to its “platybasia” in the absence of ontogenetic evidence for platytrabia or tropitrabia, but inferred that *Cladodoides* was no more “platybasic” than *Acanthodes*. Now that cranial morphology (including the endocast) of *C. wildungensis* is known in detail from CT scanning (Maisey, 2005), it can be established that the section through its cranium depicted by Holmgren (1942: fig. 5) in fact passes below the main cranial cavity and through the hypophyseal chamber (cf. Maisey, 2005: fig. 12B, C), the side walls of which presumably formed in the polar cartilages as in modern gnathostomes. Farther anteriorly, the cranial cavity has a flat floor that separates the orbits completely. Thus, there is no interorbital septum in *C. wildungensis* and its chondrocranium is morphologically platybasic. By contrast, in *Acanthodes* an interorbital septum was probably present and the cranial cavity did not extend fully between the orbits (Watson, 1937). We will probably never know for sure whether the developing chondrocranium of *C. wildungensis* was platytrabic or if that of *Acanthodes* was tropitrabic, but we can nevertheless characterize them respectively as platybasic and tropibasic on the basis of adult morphology.

A correlation has long been noted between the platybasic and tropibasic conditions and the relative size of the eyeballs and the extent of the brain between the eyes (De Beer, 1937). For Stensiö (1963b: 10), “the shape and position of the cranial cavity and brain in lower vertebrates are…strongly influenced by the general, structural type of the endocranium and the position and size of the eyes”. Such a “skeleton first” interpretational bias has unfortunately pervaded vertebrate paleontology for generations, despite the fact that the soft tissues surrounding the skeleton that are responsible for its existence (as well as for its growth, maintenance, and form) are themselves the products of highly conserved developmental pathways (e.g., neural crest, the brain, dorsal nerve cord, myotomes, etc.) whose evolutionary ancestry is far older than the skeleton. The formation of the prechordal part of the braincase is highly constrained by surrounding soft tissues, reflecting differential growth trajectories in the developing head (in particular, the brain exerts a powerful inductive influence on the final form of the skull; Carlson, 1981). Many surrounding soft tissues undoubtedly help specify the existence, spatial patterning, maintenance, and form of the endoskeleton and dermal bones (Wolpert, 1983; Wedden et al., 1988; Hall, 1988; Witmer, 1995).

In cyclostomes, the basicranium is essentially flat below the brain, but most of the basicranium is formed from the parachordal cartilages. There is a long-standing controversy whether cyclostomes possess trabeculae (discussed by De Beer, 1937; Janvier, 1996), but they certainly do not make a significant prechordal contribution to the braincase. Ontogenetically based definitions of platytrabia and tropitrabia are therefore inappropriate for modern agnathans (and probably for some extinct agnathans as well), since they are applicable only to craniates in which the trabecular-polar cartilage makes a significant contribution to the prechordal basicranium (e.g., crown-group gnathostomes). From a cladistic perspective, therefore, cyclostomes are uninformative as to whether platytrabia or tropitrabia is primitive for gnathostomes. Whenever suitably early ontogenetic stages in gnathostomes have been investigated, however, the prechordal part of the chondrocranium is initially platytrabic and becomes tropitrabic only secondarily (Marinelli, 1936; Holmgren, 1942). Furthermore, in *Petromyzon*, the paired cartilages thought to be homologous to the orbital cartilage in gnathostomes are completely separated by the brain and cranial cavity (De Beer, 1937: 46, pl. 10). The cranial cavity also completely separates the orbits in osteostracans (e.g., *Norselaspis*, *Benneviaspis*; Janvier, 1981, 1985), galeaspids (e.g., *Duyunolepis*; Janvier, 1984) and *Pituriaspis* (Young, 1991), which seem to be closely related to gnathostomes and perhaps even possessed embryonic trabeculae. These observations suggest that the brain primitively separated the orbital cartilages in craniates and that this arrangement was conserved in gnathostomes following the acquisition of an extensive trabecular basicranial component. Thus, we may postulate the following developmental evolutionary scenario: a cladistically primitive craniate condition (trabeculae absent/vestigial, orbital cartilages separated by the cranial cavity) gave rise to a primitive platytrabic gnathostome condition (including the acquisition of extensive trabecular cartilages, but conserving the craniate arrangement of the orbital cartilages), from which a derived tropitrabic gnathostome condition (involving trabecular fusion at the midline, forming a trabecula communis below the brain) probably arose in several lineages (e.g., actinopterygians, stem tetrapods, symmoriiform chondrichthyans).

Besides the morphological criteria distinguishing between platybasia and tropibasia, it is well known that other topographical landmarks mark the former boundaries between various embryonic cartilages of the chondrocranium in extant gnathostomes. These landmarks are frequently conserved into adulthood and are recognizable both in fossils and in extant forms for which ontogenetic data are unavailable. Such features provide useful clues (by the ontogenetic equivalent of "reverse engineering") about certain aspects of cranial structure and development (thereby extending classical comparative anatomical observations inferentially into progressively earlier ontogenetic stages).

In gnathostomes, the orbital cartilage becomes attached to the basicranium at several roots. According to De Beer (1937: 387), there are typically three such roots: the preoptic pila (anterior to the optic foramen), the metoptic pila (behind the optic foramen and anterior to the metoptic foramen, enclosing the oculomotor nerve, ophthalmic artery, and pituitary vein), and the antotic pila (anterior to the prootic foramen). The ontogenetically earliest and most important basicranial connection is formed by the antotic pila, whereas the preoptic and metoptic pilae represent secondary connections that form as chondrification extends farther anteriorly and ventrally into the orbit. De Beer (1931, 1937) and El-Toubi (1949) concluded that the antotic pila in modern elasmobranchs becomes attached to the anterior part of the parachordal, but Holmgren (1940) argued that it fuses with the dorsolateral surface of the acrochordal (a secondary transverse condensation above the anterior ends of the parachordals, to which the polar cartilages and optic pedicel also become fused). In either case, however, the orbital cartilage in gnathostomes is first attached to the chordal part of the braincase, not to the (prechordal) trabeculae. In *Petromyzon*, the orbital cartilage is attached to the "anterior parachordal" by two pillars, the posteriormost of which may be homologous to the antotic pila of gnathostomes (De Beer, 1937). Attachment of the orbital cartilage to the trabeculae in gnathostomes is therefore derived (in both a developmental and phylogenetic sense) in comparison with cyclostomes. In many actinopterygians, the antotic pila and pedicel are lost (and the polar cartilage is lost or reduced) in conjunction with development of a posterior myodome, and the orbital cartilage retains only its secondary connections with the trabeculae (via the metoptic and/or preoptic pilae). However, the arrangement of features in the orbit of the early actinopterygian *Ligulalepis* (Basden and Young, 2001) suggests that the antotic pila and polar cartilage were both present.

In modern elasmobranchs, the efferent pseudobranchial artery passes between the anterior border of the polar cartilage and the posterior end of the trabecula, while the pituitary vein lies between the posterior border of the polar cartilage and the acrochordal or parachordal (De Beer, 1931, 1937; Holmgren, 1940; El-Toubi, 1949). Their foramina are therefore useful markers that respectively help delimit the anterior and posterior borders of the polar cartilage. Furthermore, according to El-Toubi (1949: 242), the optic pedicel in *Squalus* becomes attached secondarily to the base of the antotic pila just above its contact with the polar cartilage. Thus, at least three features in the orbit of an adult elasmobranch braincase help define the former extent of the embryonic polar cartilage: pituitary foramen posteriorly, optic pedicel dorsally, and efferent pseudobranchial foramen anteriorly. Additionally, according to Sewertzoff (1899) the optic foramen marks the approximate line of fusion anteriorly between the embryonic trabeculae and orbital cartilages. However, his proposal that the oculomotor foramen also lies along the contact between these cartilages is less clear-cut, since it lies above the optic pedicel and is enclosed secondarily between the antotic and metoptic pilae as the orbital cartilage becomes expanded above the polar cartilage.

Other utilitarian landmarks include: the row of superficial ophthalmic foramina above the orbit, formed along the contact between the supraorbital shelf and orbital cartilage (typically at a late stage of development; Holmgren, 1940); the orbitonasal canal, which probably lies at the junction of the orbital cartilage and nasal lamina (forming the postnasal wall behind the olfactory capsule, but not contributing to the side wall of the cranium proper; Sewertzoff, 1899; De Beer, 1931, 1937; Holmgren, 1940; El-Toubi, 1949), and the bucco-hypophyseal fenestra and internal carotid foramina below the orbit (both representing parts of an originally continuous polar fenestra, whose posterior border is defined by the postpituitary commissure below the level of the parachordals and behind the internal carotids; Holmgren, 1940).

Using such topographic landmarks, it is possible to map the hypothetical extent to which various embryonic cartilages contributed to the adult chondrocranium. Examples are presented here of four elasmobranch braincases (figs. 1, 2), two of which are modern (*Squalus acanthias*, *Chlamydoselachus anguineus*) and two are Paleozoic fossils (*Cladodoides wildungensis*, "*Cobelodus*"). In all cases, the contributions made by various embryonic cartilages indicated should be considered very approximate, because they chondrify and grow within blastemic tissues that are interconnected and relatively continuous, and in practice their precise limits are somewhat nebulous. Moreover, ontogenetic data for the head are available only for one of these examples (*S. acanthias*; e.g., De Beer, 1937; Holmgren, 1940; El-Toubi, 1949; Jollie, 1971). The extent to which embryonic cartilages contributed to the adult chondrocranium in *Chlamydoselachus* is completely inferential as its ontogeny has never been described. Ontogenetic data are also unavailable for the two fossil examples, but their chondrocranial morphology is now known in considerable detail (for *Cladodoides*, see Gross, 1937; Maisey, 2005, and below). The "*Cobelodus*" reconstruction shown here is based mainly on a three-dimensional Pennsylvanian braincase described later in this work, with additional details of the ethmoidal region and olfactory capsules based on information obtained from other symmoriiforms that are also described below. "*Cobelodus*" differs from the three other examples shown here in having a deep interorbital septum below the cranial cavity. *Cladodoides* and "*Cobelodus*" both have an extensive postorbital arcade that is hypothesized to include at least two components of the embryonic chondrocranium: the primary postorbital process (sensu Holmgren, 1940) and the lateral commissure (which encloses the lateral head vein as in *Oxynotus* and *Squatina*; in other squaloids it encloses only the hyomandibular trunk of the facial nerve; Holmgren, 1941). Another feature of interest is the much greater extensive contribution to the orbital wall apparently made by the polar cartilage in *Cladodoides* and "*Cobelodus*" (see below and Maisey, 2005: figs 10, 11).

Some modern squaloids in which cranial ontogeny is unknown have an extremely bizarre adult cranial morphology, with a deep basal angle resulting in a marked ventral prolongation of the orbital articulation and the bucco-hypophyseal chamber (e.g., *Trigonognathus kabeyi*; fig. 3E, F). This extreme basal angle probably formed as in other squaloids (e.g., *Squalus*, *Etmopterus*; Holmgren 1940; El-Toubi, 1949), in which the polar cartilages apparently become fused to the anterior ends of the parachordals before the trabeculae have finished migrating from their embryonic to adult positions, creating a hump ventrally between the trabeculae and polar cartilages. A basal angle is developed only in some elasmobranchs with an orbital articulation for the palatoquadrate on the posterior end of the embryonic trabeculae (Maisey, 1980, 2005). The deep basal angle in dalatiiforms is probably related to specializations of the feeding mechanism, enabling the jaws to be protracted extensively at the orbital

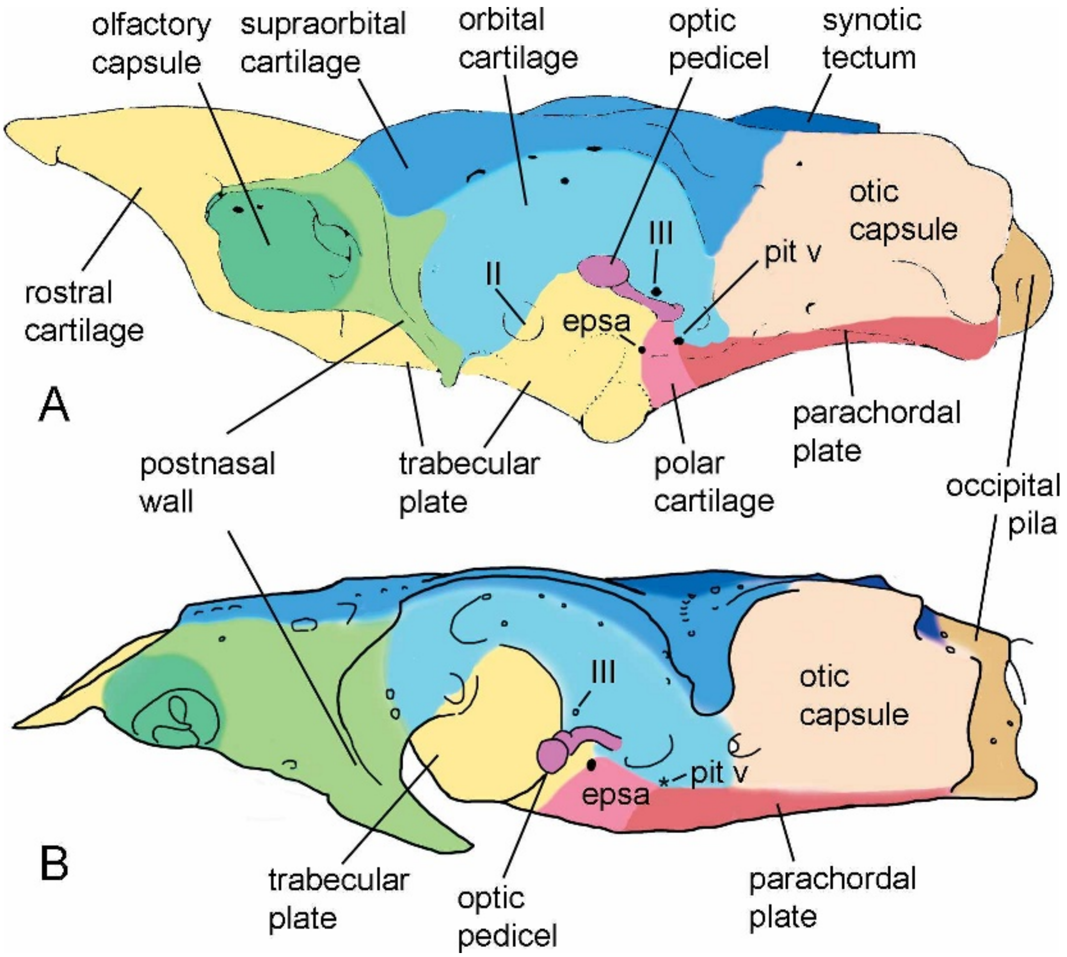

Fig. 1. Approximate extent of contributions made by major embryonic cartilages in the adult chondrocranium of two modern sharks. **A**, *Squalus acanthias* (based on ontogenetic data); **B**, *Chlamydoselachus anguineus* (hypothesized). Not to scale.

articulation during prey capture (*T. kabeyi* has a clutching-type dentition with extremely long teeth instead of the usual squaloid cutting-type dentition, and is suspected of being a ram-feeder; Shirai and Okamura, 1992; Yano et al., 2002).

The region inferred to have formed in the trabeculae in *Trigonognathus kabeyi* is arched and elevated with respect to the parachordal region, although it still forms the floor of the cranial cavity. There is no interorbital septum anterior to the basal angle, but in other etmopterids there is a narrow median interorbital process ventrally on the basicranium (the keel process; Holmgren, 1940; e.g., *Etmopterus*, *Aculeola*, *Centroscyllium*, *Miroscyllium*; Shirai and Nakaya, 1990; see fig. 3A, B). The keel process is probably not homologous to an interorbital septum, because (according to Holmgren, 1940) in *Etmopterus* it forms comparatively late in ontogeny, chondrifying only at a comparatively late stage (55 mm), and it is located on the ventral rather than the dorsal surface of a narrow median "trabecular commissure" (a late-forming structure, possibly arising from the trabecula communis and resulting from secondary growth of the trabeculae as the hypophyseal fenestra begins to close late in ontogeny). The keel process in etmopterids (e.g., *Etmopterus*, *Centroscyllium*; fig. 4A, B) is located anterior to the palatoquadrate

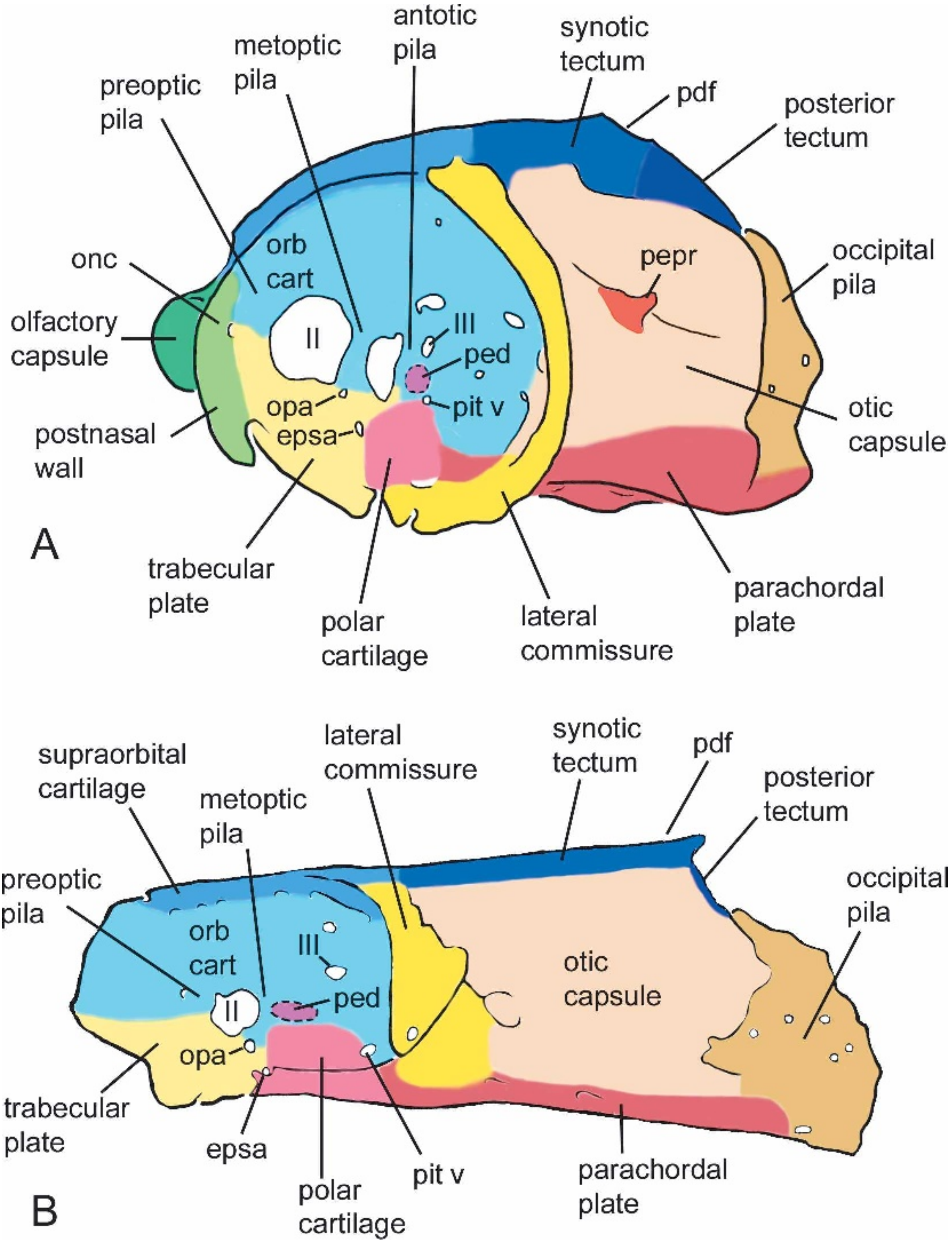

Fig. 2. Hypothetical contributions made by major embryonic cartilages in the chondrocranium of two Paleozoic sharks. **A**, an idealized symmoriiform (mainly based on "*Cobelodus*", but with ethmoid region after *Stethacanthulus* and *Falcatus*); **B**, *Cladodoides wildungensis*. Colors correspond to features in fig. 1. Not to scale.

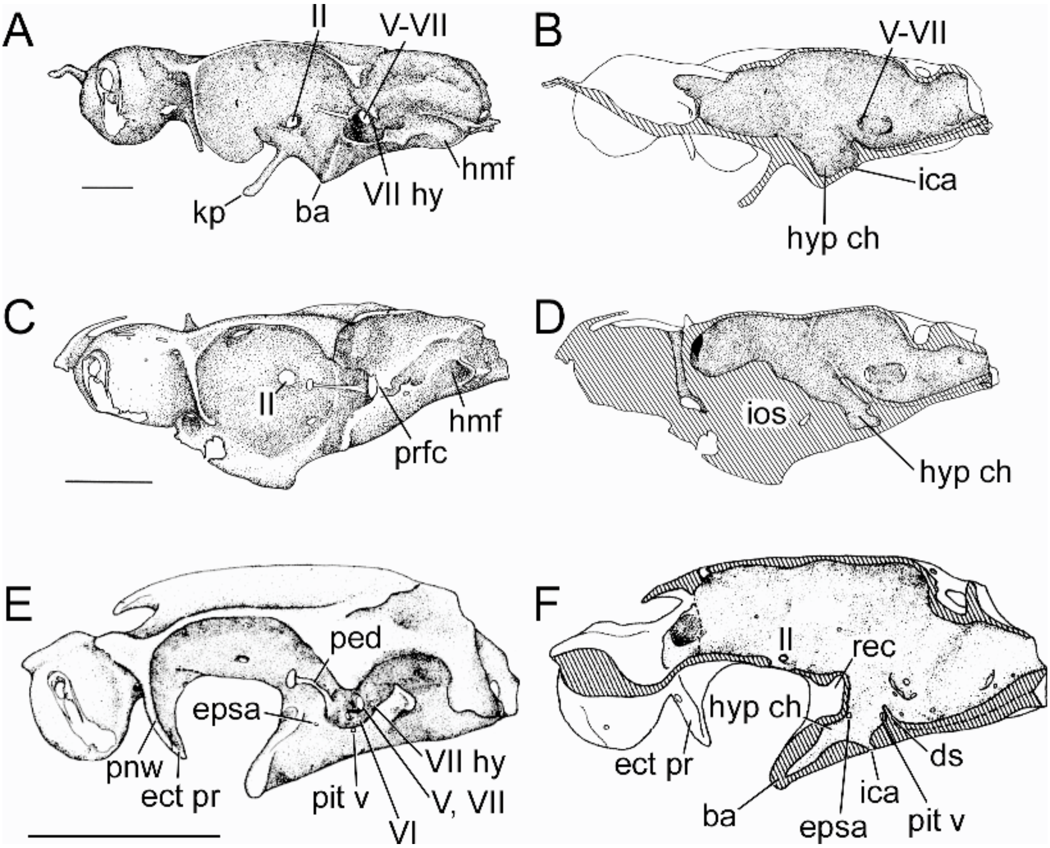

Fig. 3. Left lateral and sagittal views of three modern dalatiiform elasmobranch braincases. **A**, **B**, *Centroscyllium excelsum*; **C**, **D**, *Squaliolus laticaudus*; **E**, **F**, *Trigonognathus kabeyai*. After Shirai (1992), Shirai and Okamura (1992). Scale bars = 10 mm.

symphysis and extends anteroventrally in front of the jaws, whereas the preorbital muscle (= suborbitalis of Shirai, 1992) arises on the interorbital wall at the base of the keel process and inserts on the anterior border of the mandibular adductor muscle. The keel process and the preorbital muscle are both absent in *Trigonognathus* (figs. 3E, F; 4C), and a keel process is also absent in modern elasmobranchs, in which the preorbital muscle arises on the antorbital wall or ectethmoid process (e.g., *Heptranchias*, *Echinorhinus*, *Zameus*). The internal carotids in *T. kabeyi* enter the hypophyseal chamber via basicranial foramina (the usual arrangement in modern elasmobranchs), and the efferent pseudobranchial foramen is located in the ventral process forming the side wall of the hypophyseal chamber and inferred to have formed between the dorsal margin of the polar cartilage and the posterior end of the trabecular cartilage. Thus, the basicranial circuit in *T. kabeyi* has the usual elasmobranch arrangement, including a union between the internal carotids and efferent pseudobranchials dorsal to the trabecular cartilage. The region presumably derived from the antotic pila is well developed in *Trigonognathus*, which has a deep recess between the paired dorsal ends of the orbital articulation in the back of the orbit (Shirai and Okamura, 1992). This recess is superficially similar to the posterior myodome in osteichthyans, but does not contain the eye musculature (instead, the pedicel and the ocular muscles originate on the lateral surface of the cranium farther posteriorly, where they are associated with the trigemino-

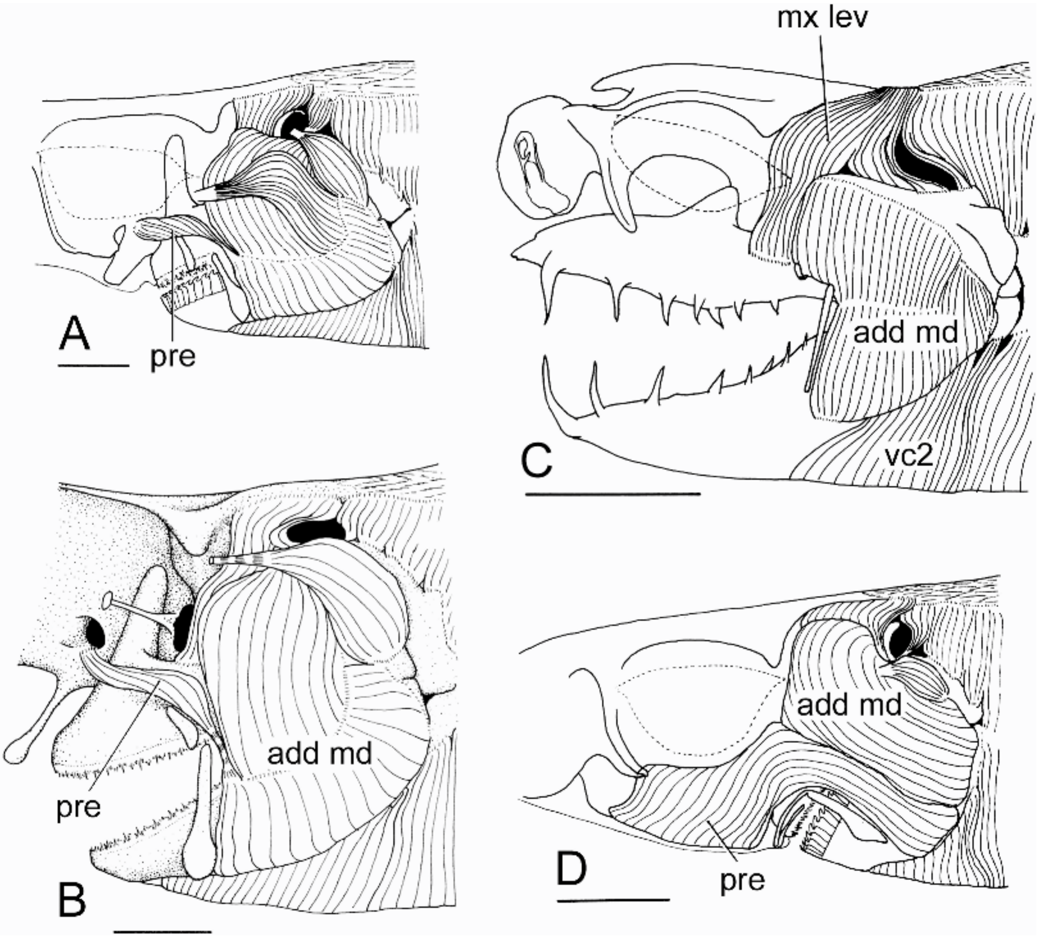

Fig. 4. Left lateral views of the mandibular musculature in four modern dalatiiform sharks to show variation in the origin and extent of the preorbital (suborbital) muscle. **A**, *Etmopterus spinax*; **B**, *Centroscyllium excelsum* (preorbital muscle originates above ventral keel process in A and B); **C**, *Trigonognathus kabeyai* (preorbital muscle absent); **D**, *Squaliolus laticaudus* (preorbital muscle originates on interorbital septum). After shirai (1992), Shirai and Okamura (1992). Scale bar = 10 mm.

facialis recess as in other modern elasmobranchs).

The floor of the braincase is comparatively flat in *Dalatias* (Shirai, 1992: pl. 8), but in other dalatiids there may be a very deep interorbital septum below the cranial cavity (e.g., *Squaliolus*; fig. 3C, D). In this form, the preorbital muscle has an extensive origin along the entire ventral part of the septum and is inserted on the lower jaw anterior to the mandibular adductor (fig. 4D). However, the ontogeny of the braincase has not been described, and it is therefore uncertain whether the interorbital septum in *Squaliolus* represents a ventral extension of the embryonic trabeculae (like the keel process in *Etmopterus*; Holmgren 1940) or a dorsal extension arising from a trabecula communis (analogous to the situation in many actinopterygians).

To summarize, platytrabia in embryonic gnathostomes *usually* gives rise to an adult platybasic condition (but not invariably; e.g., *Lepisosteus*, ophidians), and tropitrabia *usually* gives rise to the tropibasic condition (although modern elasmobranchs may be an exception, if the “medial area” represents a trabecula communis anterior to the orbit).

Thus, ontogeny does not provide an absolute guide as to what the adult condition will be, nor does adult morphology provide an accurate means to assess the prior ontogentic condition (although there are certainly many cases of congruence among extant gnathostomes). On the other hand, the terms "platybasic" and "tropibasic" can be applied to fossils and extant forms in a purely morphological descriptive context, even where ontogenetic data are not available and without making any ontogenetic implications (although it may still be possible to draw some inferences about ontogeny, based on particular morphological observations). A platybasic braincase may be defined morphologically as one with no interorbital septum in the floor of the cranial cavity, and in which the side walls completely separate the left and right orbits. By contrast, an interorbital septum is present in a tropibasic braincase, and the cranial cavity separates the orbits only dorsally and posteriorly, while the basicranial fenestra may not even communicate with the overlying hypophyseal chamber (as in "*Cobelodus*"; see below). Unless stated otherwise, the terms platybasic and tropibasic will be used throughout this work in a purely morphological context.

Finally, it is important to recognize a distinction between tropibasia and the mere presence of an interorbital septum. For example, the interorbital septum in *Squaliolus* may or may not be homologous with the keel-process in etmopterids (i.e., a ventral rather than dorsal extension of the trabecula communis). Although the septum undoubtedly includes cartilage of trabecular origin and extends below the floor of the cranial cavity, ontogenetic studies are needed to determine whether the orbital cartilages are also involved in its formation. In chimaeroids, the orbital cartilages form a septum only *above* the brain and cranial cavity, while the side walls of the cranium arise from the ventral part of the orbital cartilages on either side of the cranial cavity and meet paired upgrowths of a broad basicranial plate (probably formed in the trabeculae; De Beer and Moy-Thomas, 1935; Holmgren, 1942; but cf. Allis, 1917). The interorbital septum in chimaeroids therefore probably arises from the orbital cartilages and does not include the trabeculae. Unfortunately, the trabeculae are already fused into a continuous plate in the earliest ontogenetic stages of chimaeroids investigated thus far and their original arrangement is unknown, although there is no evidence of a trabecula communis below the cranial cavity and the morphological relationship of the brain to the prechordal part of the braincase is therefore identical to that in modern platybasic sharks.

CLASS CHONDRICHTHYES HUXLEY 1880
ORDER SYMMORIIFORMES
(= ORDER SYMMORIIDA ZANGERL 1981; APHETOHYOIDEA ZANGERL AND CASE 1976)

"COBELODUS"

MATERIAL EXAMINED: FMNH PF 13242: an isolated three-dimensional braincase of a symmoriiform shark in a pyritized concretion, Fayetteville Formation (Chesterian, Upper Pennsylvanian), Town Branch outcrops, Fayetteville, Arkansas (fig. 5). Scanned at the University of Texas at Austin by Richard Ketcham and Matthew Colbert on 3/6/99. Scan data: P250D, 420 kV, 1.8 mA, 2 brass plate filters (1/8 inch total), translate-rotate, integration time 16 ms, slice thickness 0.25 mm, S.O.D. 752 mm, 1 ray averaged per view, 1 sample per view, oversampling ratio 2.0, interslice spacing 0.25 mm, field of reconstruction 56.5 mm, reconstruction offset 450, reconstruction scale 120. Sample scanned in air. 8-bit and 16-bit scan files; 8-bit export parameters: level 2047, width 4095.

GENERAL REMARKS: This unique specimen was collected many years ago by Dr. Harold E. Ewald (Geology Department, University of Arkansas) from a streambed that cuts through the Town Branch outcrops of the Fayetteville Black Shale (Chesterian Stage) in Fayetteville, Arkansas. This braincase came to the attention of Dr. Rainer Zangerl, who first recognized that it came from a symmoriiform shark and informally referred it to the genus *Cobelodus*. He prepared parts of the specimen by grinding away areas of pyritic matrix, although this exposed only a few external morphological features on one side and revealed nothing of its internal structure. He did not publish his findings and no further progress was made on the specimen until the advent of reliable high-resolution CT-scanning technology. In 1999, the braincase was scanned on behalf of the author at the Geology Department of the University of Texas at Austin (UTA). Three-dimensional digital reconstructions of the braincase were generated in Imaris/Surpass as contour-based isosurface renderings made from the 8-bit CT scan at the American Museum of Natural History (for details of this procedure see Maisey, 2005). The specimen provided the first unequivocal evidence of tropibasia in an extinct elasmobranch (Maisey, 2004a).

Despite the unusual morphology of this braincase, it shares many similarities with other symmoriiforms such as *Cobelodus aculeatus* (Zangerl and Case, 1976). FMNH PF 13242 is therefore identified with some confidence as having come from a symmoriiform shark, and the specimen provides a wealth of information about symmoriiform cranial morphology, despite the uncertainty surrounding its identity at genus or species level. The same taxon may nevertheless be represented by more complete but less well-preserved symmoriiforms from the Fayetteville Shale of Arkansas (OUZC 5300–5305; see below). That material is not yet described, but will be discussed later in this work. FMNH PF 13242 will be left in open nomenclature and is referred to as "*Cobelodus*" simply for convenience. It should be emphasized that there is no evidence that this form was (or was not) more closely related to *Cobelodus aculeatus* than to other symmoriiforms.

At some time in the past, the right side of the braincase was prepared mechanically using a small grinding wheel. That preparation exposed some features in the orbit, but also caused damage to surrounding structures (especially the right postorbital arcade, which superficially appears intact but has in fact suffered extensive damage and repair). In places, mechanical preparation has also created a misleading appearance; for example, the specimen seems to have an extensive supraorbital shelf, but scanning reveals that most of this is really matrix. Fortunately, the left side is unprepared and almost intact, providing more reliable data concerning the original morphology of the braincase.

The braincase is remarkably well preserved, and there is an extremely high contrast in density between the calcified cartilage and pyritized matrix as revealed by X-rays. In order to reduce "flares" in the scan caused by deflection of lower-energy X-rays hitting the pyritized specimen, the object was shielded in a cast-iron cylinder that only higher energy X-rays could penetrate. This necessitated an exceptionally long scan time (approx. 20 hours), but in all other respects the much lower density of fossilized cartilage provided optimum conditions for CT-scanning. Pyritized matrix uniformly fills the braincase and no voids or areas of secondary crystallization were encountered. No evidence of bioturbation, diagenetic compression, or other distortion was noted, but small isolated fragments and flakes of calcified cartilage were observed in the matrix filling the orbit and cranial cavity.

GENERAL MORPHOLOGY: The specimen is almost complete except for the ethmoid region, which probably consisted originally of membranous or uncalcified tissues (fig. 5). No teeth or denticles are associated with the braincase, which appears to be completely isolated. However, the delicate nature of this specimen suggests it underwent very little postmortem disturbance or transportation. Several other articulated symmoriiform skeletons have been recovered from the same horizon at a nearby locality (see below), suggesting *Lagerstätten*-like conditions.

Only a few general features can be discerned on the dorsal, ventral, and posterior surfaces of the braincase. Additionally, a few large foramina are evident within its partially excavated right orbit, but many of the smaller ones are obscured by matrix and could be observed only in the scan. On the dorsal surface, the broad and slightly domed braincase roof is visible. It is continuous with the prominent postorbital arcade laterally and is tapered both anteriorly and posteriorly. Its pointed anterior margin includes a small precerebral fontanelle dorsally. The orbits are roofed by cartilage although its original extent is uncertain. The right orbit has been partially excavated to reveal a large uncalcified region centrally (which presum-

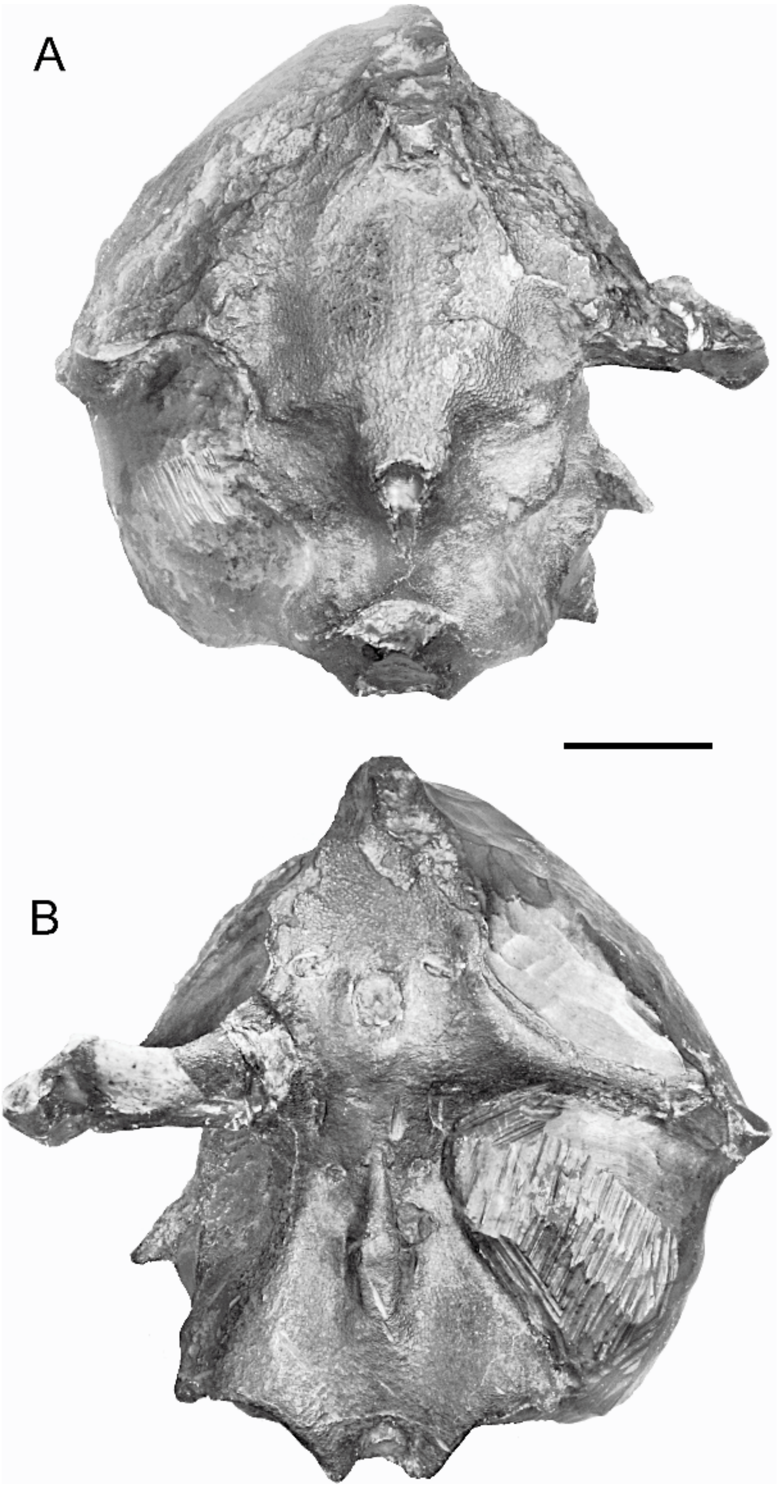

Fig. 5. Arkansas symmoriiform braincase FMNH PF 13242 ("*Cobelodus*"). **A**, dorsal view; **B**, ventral view; **C**, lateral view, right side. Scale bar = 10 mm.

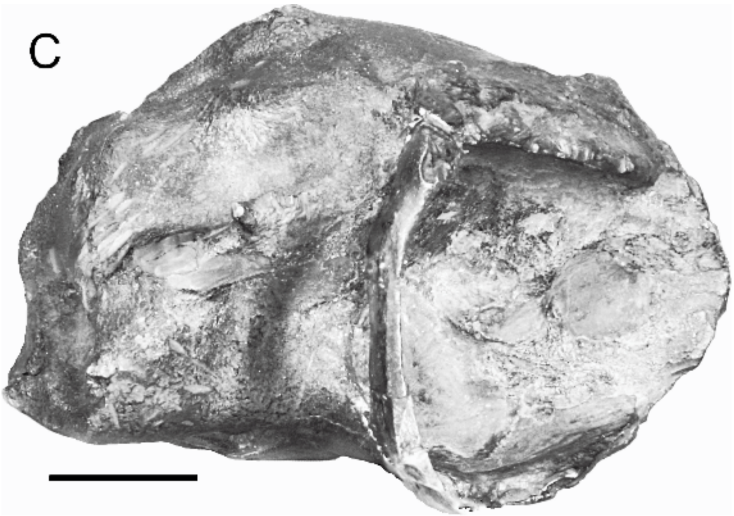

Fig. 5. Continued.

ably enclosed the optic nerve in life), behind which the orbital wall forms a low, anteroposteriorly oriented bulge similar to the pedicel attachment area in *Cladodoides* (Maisey, 2005). Posteriorly, the braincase roof is raised at the midline where it meets a small posterior dorsal fontanelle, behind which is a short posterior tectum. The wall of the right otic capsule has been prepared, revealing several features including a lateral otic ridge that bears a short process midway along its length, and a weak dorsal otic ridge extending posteromedially from the level of the postorbital process. The occipital arch is separated from the otic region dorsally and dorsolaterally by an otico-occipital fissure, although only parts of it can be observed directly on the specimen. The entire braincase is remarkably well preserved, but because so few external features can be seen on the specimen it is not particularly informative from an anatomical or phylogenetic point of view without CT scanning.

Scanning reveals that the cartilage is perichondrally mineralized throughout most of the braincase, apart from a few areas such as the medial capsular walls of the otic region, the ethmoid region, and the anterior parts of the orbital walls. Where calcification is present it is tesselated as in modern chondrichthyans, and as far as can be determined only a single continuous layer of tesserae is present throughout the braincase. No evidence was found for multiple layering of the tesserae, nor for internal calcified struts like those occasionally found in modern elasmobranchs (Summers, 2000).

The following remarks are almost entirely based on observations made from digitally generated contour-based surface reconstructions (figs. 6–11, 13). While these reconstructions are considered accurate, the contour plotting is necessarily subjective. Wherever possible, therefore, morphological features identified in contour-based surface reconstructions were checked repeatedly against individual CT scan slices and volume renderings created from the raw image data (e.g., figs. 12A, 17, 18, 20B). Relatively few morphological features can be directly observed on the specimen.

In lateral view (fig. 6), the suborbital shelf extends farther ventrally than the rest of the braincase, and the large orbit forms approximately half the preserved length of the braincase. The interorbital septum is deep but narrow from side to side, and contains several uncalcified or unchondrified areas, especially anteriorly. A single layer of tesserae covers each external surface of the septum, but there is no evidence of deeper calcified layers, suggesting that the entire thickness of the septum was cartilaginous and that the orbital cartilages were fused medially (if

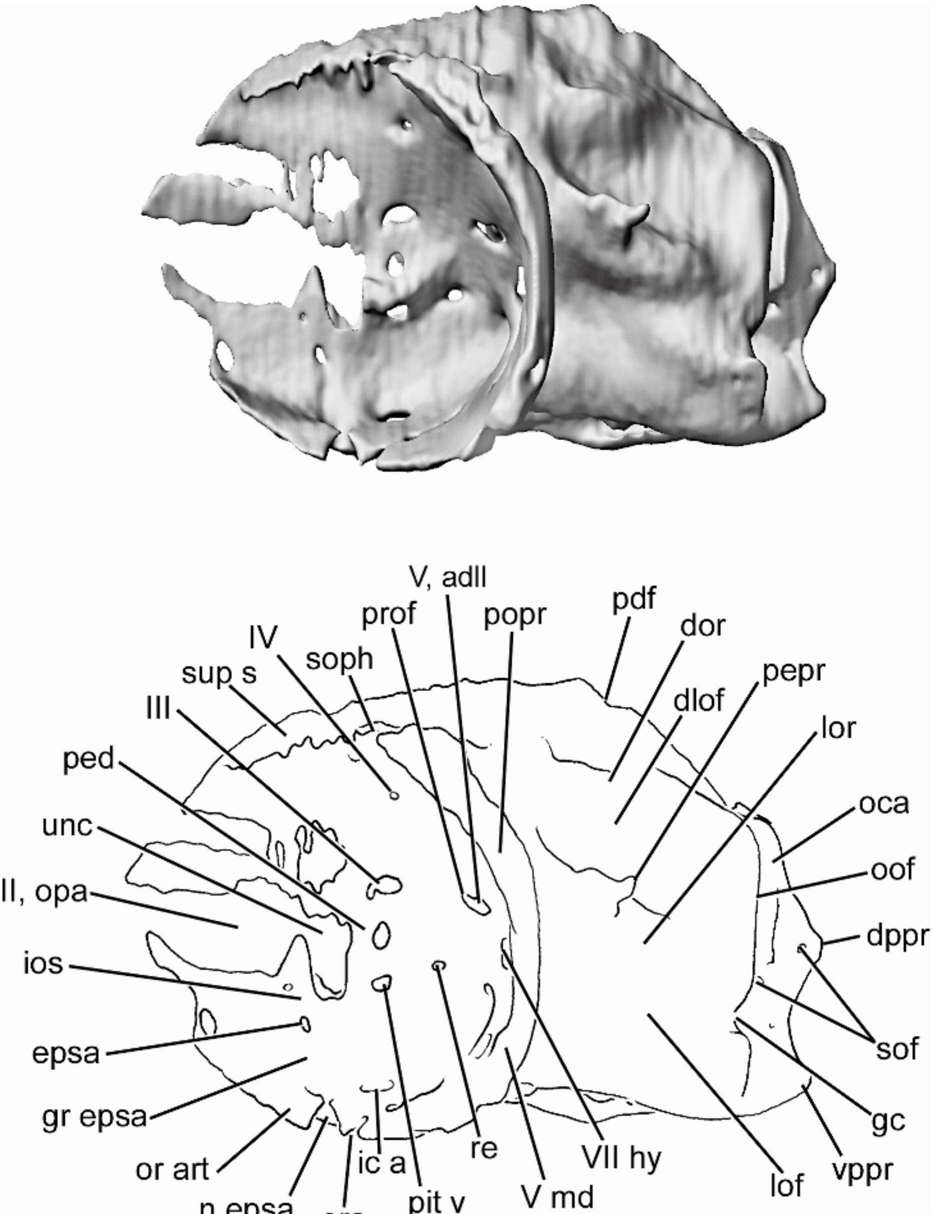

Fig. 6. FMNH PF 13242 ("*Cobelodus*"). Lateral view of contour-based surface rendering generated from CT-scan slices.

these had been separate, another calcified layer would be expected over their inner surfaces). Thus, there is no evidence that the cranial cavity extended between the orbits ventrally; instead, the interorbital septum supports the floor of the cranial cavity and separates it from the basicranium (as in many actinopterygians). There is a deep recess for the efferent pseudobranchial artery in the suborbital shelf, immediately in front of which is an articular surface for the palatoquadrate. A similar relationship seems to exist between the middle palatoquadrate articulation and the efferent pseudobranchial

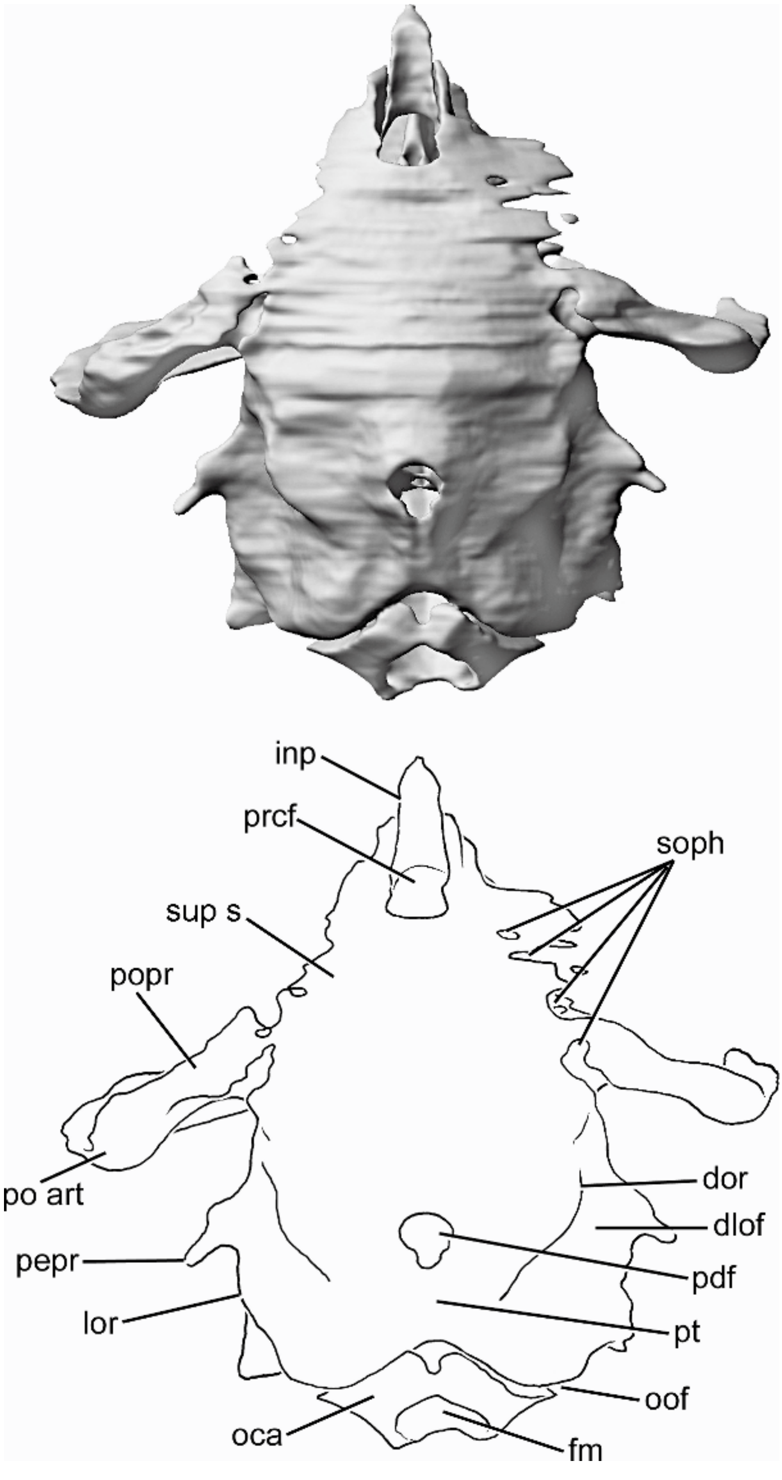

Fig. 7. FMNH PF 13242 ("*Cobelodus*"). Dorsal view of contour-based surface rendering generated from CT-scan slices.

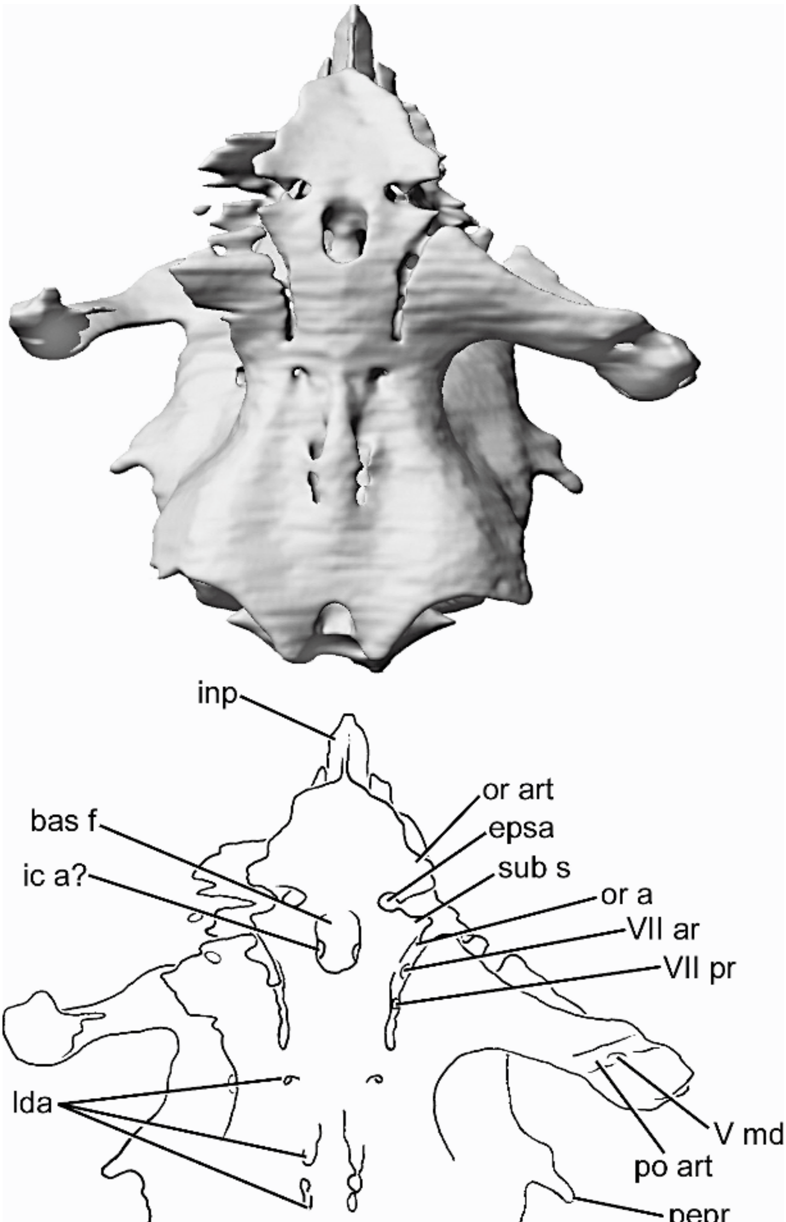

Fig. 8. FMNH PF 13242 ("*Cobelodus*"). Ventral view of contour-based surface rendering generated from CT-scan slices.

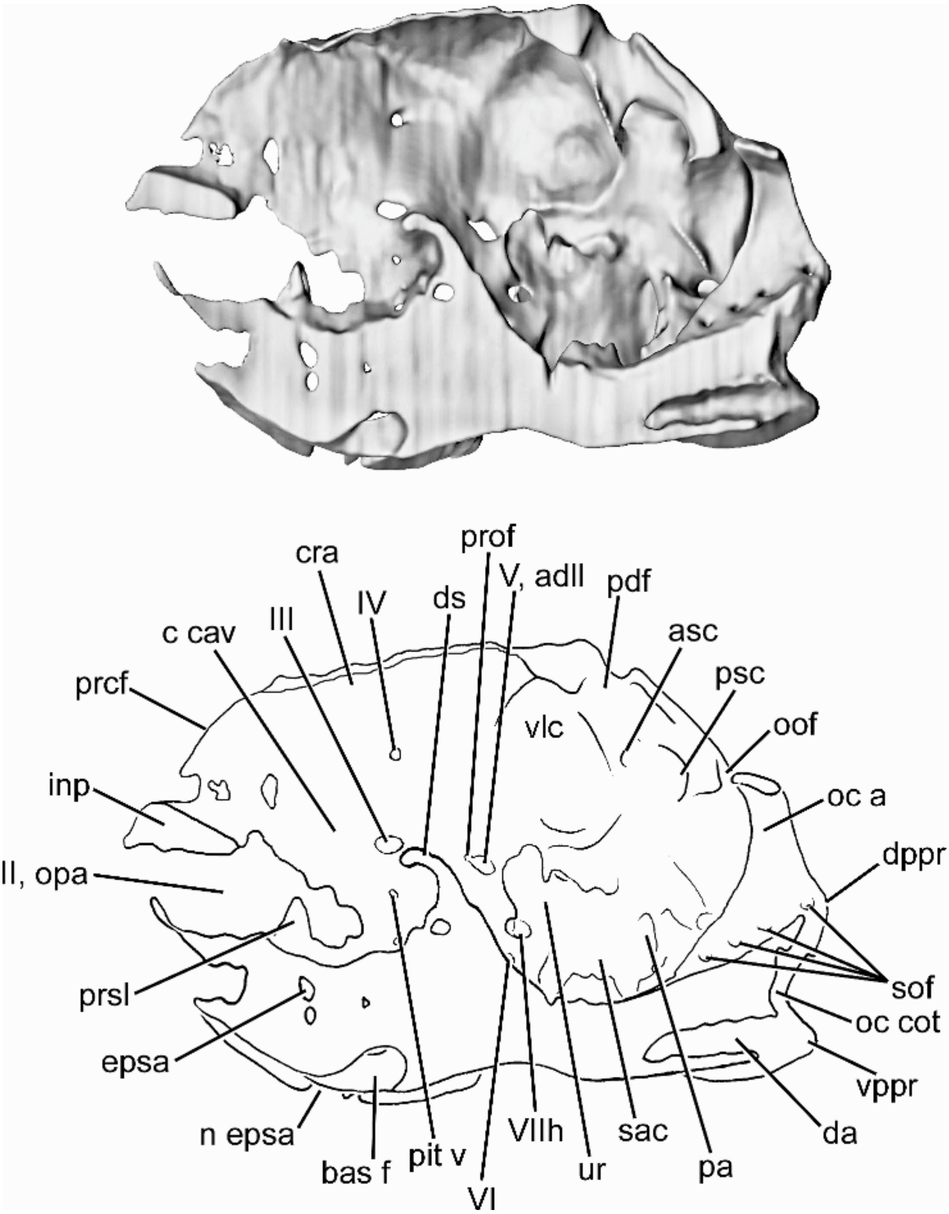

Fig. 9. FMNH PF 13242 (“*Cobelodus*”). Medial view made from sagittal section of contour-based surface rendering generated from CT-scan slices.

foramen in *Buchanosteus* (Young, 1986: fig. 9A,B).

The postorbital arcade in “*Cobelodus*” is extremely short anteroposteriorly, forming a wide rim surrounding the large jugular canal. In the floor of the orbit there is a small opening that connects ventrally with the basicranial fenestra. The otic and occipital regions are both short, unlike in *Cladodoides*, *Tamiobatis*, and *Orthacanthus*. Other symmoriiform sharks also seem to have comparatively short otic and occipital regions (Zangerl and Case, 1976; Williams, 1985; Coates and Sequeira, 1998). In “*Cobelodus*”, the lateral part of the otico-occipital fissure is directed ventrally toward the opening of the

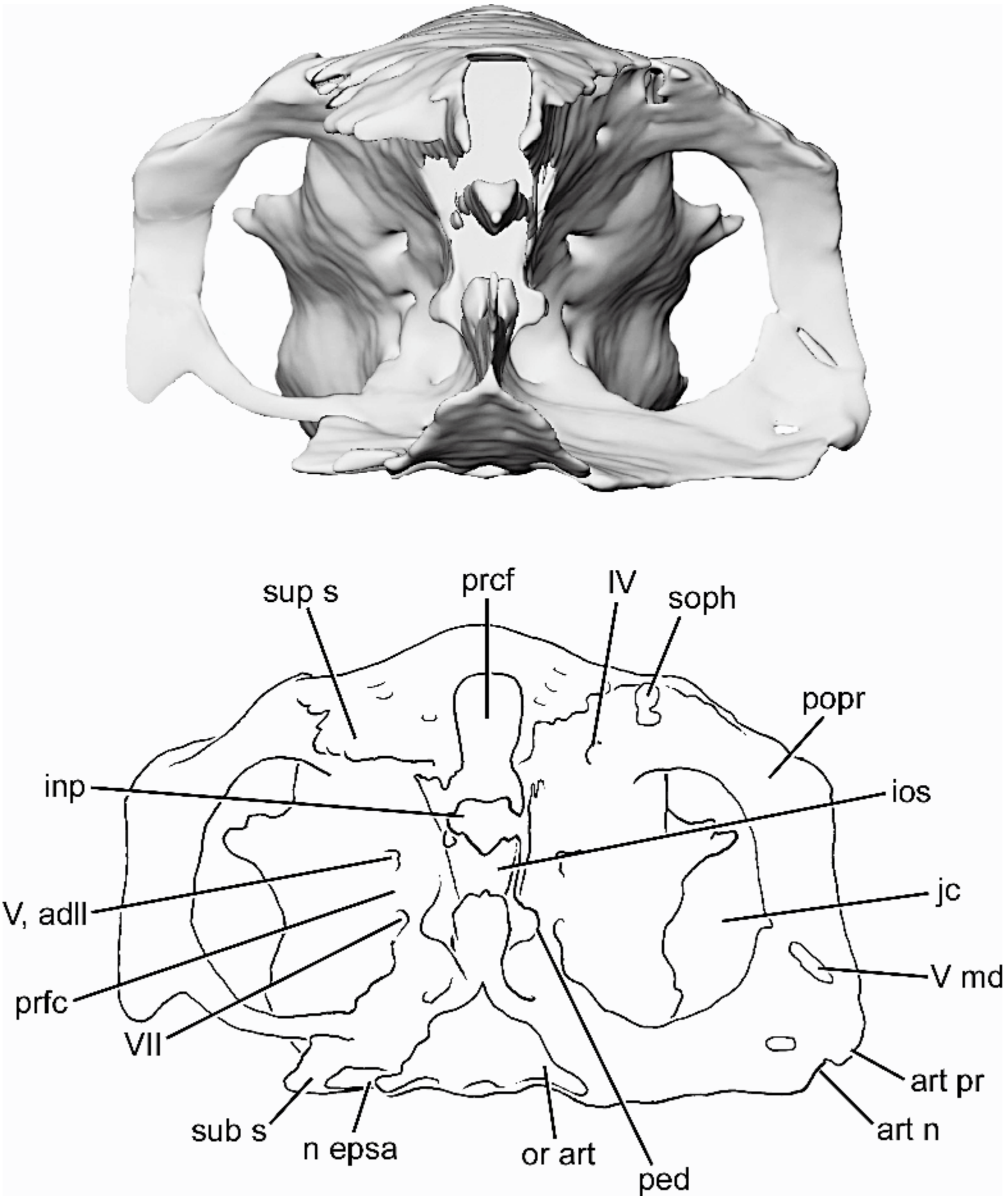

Fig. 10. FMNH PF 13242 ("*Cobelodus*"). Anterior view of contour-based surface rendering generated from CT-scan slices.

glossopharyngeal canal and the metotic part of the fissure is closed, as in *Cladodoides* (Maisey, 2004a, 2005). There is no clearly defined hyomandibular fossa.

In dorsal view (fig. 7), the cranial roof is relatively featureless, apart from a small median opening that corresponds to the posterior dorsal fontanelle in *Cladodoides* and to the endolymphatic (parietal) fossa in modern elasmobranchs (Maisey, 2004a, 2004b, 2005). The orbitotemporal region is strongly tapered anteriorly and a narrow, elongated precerebral fontanelle is present, although it is much smaller than in most modern sharks or in extinct ones such as *Hybodus* and *Orthacanthus*. Comparison

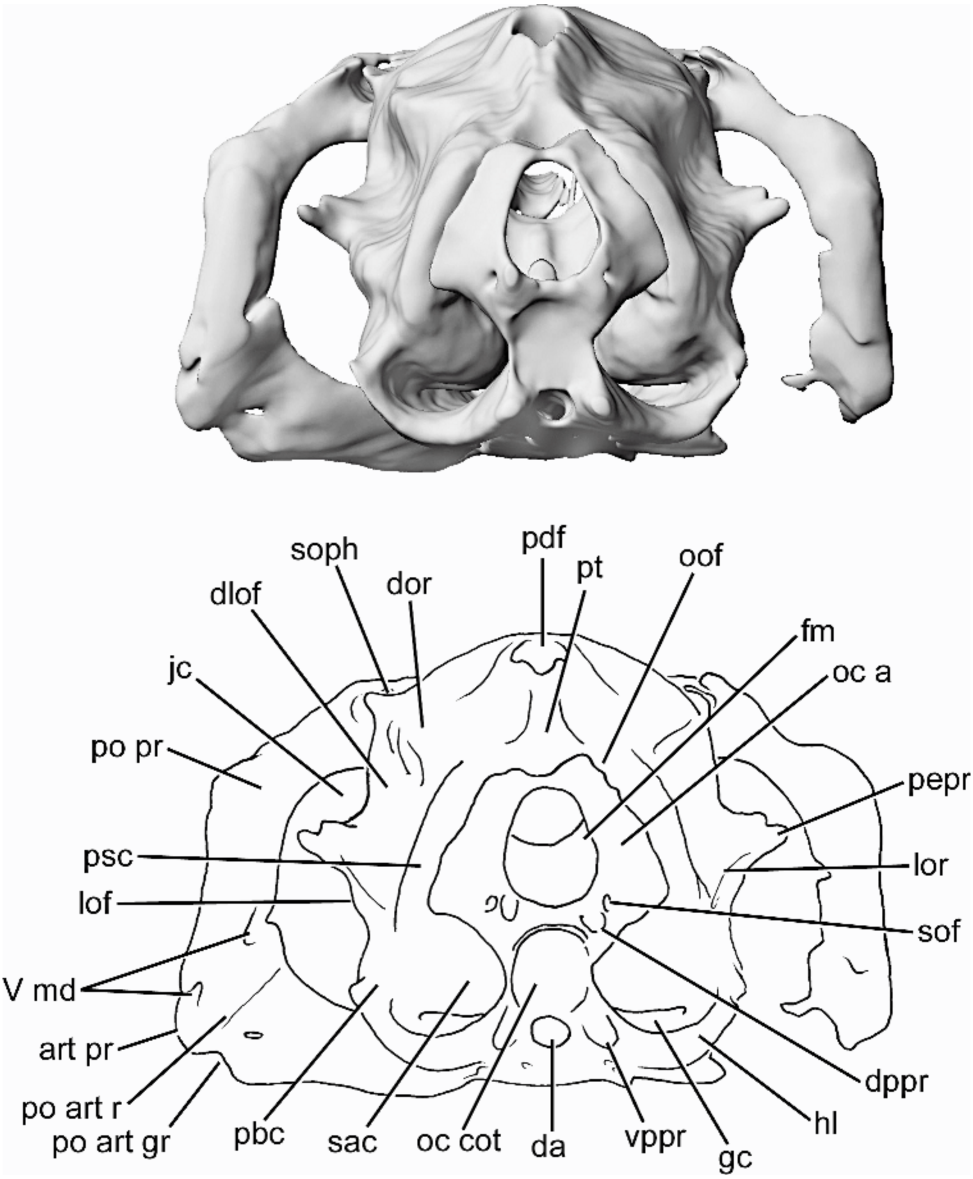

Fig. 11. FMNH PF 13242 ("*Cobelodus*"). Posterior view of contour-based surface rendering generated from CT-scan slices.

with X-ray plates of flattened symmoriiform braincases suggests that the ethmoid region (including the olfactory capsules) were originally extensive and that may have extended the length of the braincase by as much as 30%. The orbital region broadens posteriorly and is widest between the postorbital processes, which form complete but narrow arcades surrounding a large space that presumably housed the lateral head vein and other structures (i.e., it functioned as a jugular canal). The arcade projects posterolaterally rather than laterally from the braincase and is confluent with the supraorbital shelf dorsally, suggesting that it formed as in modern elasmobranchs (where the embryonic lateral commissure fuses secondarily with the primary postorbital process arising at the posterior end of the supraorbital cartilage; Holmgren, 1940).

In the otic region, the positions of the semicircular canals are marked by low ridges. The ridges of the anterior and posterior canals converge dorsally just behind the dorsal fontanelle rather than at the fontanelle itself. On the lateral wall of the otic capsule, approximately midway along the ridge for the external (horizontal) semicircular canal, a small process (the periotic process; see below) extends laterally and slightly posteriorly. The otic region is separated from the occipital arch by a persistent otico-occipital fissure as in many other Paleozoic sharks (e.g., *Orthacanthus*, *Tamiobatis*, *Cladodoides*, *Akmonistion*), but the posterior tectum between the fissure and the posterior dorsal fontanelle is much deeper anteroposteriorly than in these other taxa. Thus, the posterior dorsal fontanelle is completely isolated from the otico-occipital fissure both by the posterior tectum and by the dorsal part of the labyrinth (crus commune).

The ventral view (fig. 8) reveals a constriction in the basicranium immediately behind the postorbital process, forming a distinct waist. The ventral arm of the postorbital arcade is directed laterally rather than posterolaterally and meets the side wall of the braincase somewhat posterior to the dorsal arm. The interorbital cartilage is narrow and comparatively short, forming an ovoid area with large, paired lateral recesses, which probably housed the efferent pseudobranchial arteries. A large central basicranial fenestra is also present, but no grooves or canals for internal carotid arteries are discernible on the ventral surface. Furthermore, the fenestra has no connection with the overlying hypophyseal chamber. Farther posteriorly, the basicranium below the otic capsules forms a broad hypotic lamina (presumably derived from the embryonic parachordal cartilage, as in modern elasmobranchs). The posterior region of the basicranium is pierced by paired aortic canals that merge to form a single median canal farther posteriorly. Paired occipital condyles are present on either side of the aortic canal.

In medial view (sagittal section, fig. 9), the tropibasic arrangement is clearly evident from the depth of the interorbital septum below the cranial cavity. The ventral surface of the braincase is gently curved, with a convex anterior part between the orbits, a gently concave area below and slightly behind the level of the dorsum sellae, and another slightly convex region posteriorly, below the otic capsules. The dorsum sellae represents an important developmental landmark; in modern elasmobranchs, it marks the position of the embryonic polar cartilage between the prechordal trabeculae and parachordals (De Beer, 1931, 1937; Holmgren, 1940; El-Toubi, 1949). On that basis, the convex anterior part of the basicranium in "*Cobelodus*" can be regarded as having formed from the embryonic trabecular-polar cartilage and the convex posterior part from the parachordals, while the concave area between them may represent the region of embryonic cranial flexure. The basicranial fenestra is located more or less in the center of the anterior convex area and forms a small pocket within the thickness of the basicranial cartilage. Although the fenestra does not communicate with the hypophyseal chamber farther dorsally, there are paired openings in its roof leading to the floor of the orbit on either side of the interorbital septum. Thus, there is no contiguous bucco-hypophyseal chamber as in many other gnathostomes, but rather two separate chambers: a buccal fenestra ventrally and the hypophyseal chamber (continuous with the cranial cavity) farther dorsally. Consequently, there is no possibility of a direct internal carotid supply to the brain via the basicranial fenestra and hypophyseal chamber (discussed further below).

The dorsum sellae forms a prominent internal partition that curves above the expansive internal hypophyseal chamber and separates it from the otic region. In the digital reconstruction, a small canal seems to pass transversely through the dorsum sellae from orbit to orbit. However, inspection of CT scan slices shows that this is merely an artefact resulting from digital smoothing of the computer-generated isosurface. In life, a thin cartilaginous floor probably divided this "canal" into left and right pits. Corresponding pits are present in *Cladodoides* and probably housed the external rectus muscle; in *Cladodoides*, however, cartilage forming this part of the basicranium is much wider and the pits do not coalesce at the midline (Maisey, 2005: figs. 17B, 18A). The dorsum sellae is typically much smaller in modern elasmobranchs, hybodonts, and *Orthacanthus*, and it is absent in adult batoids, but it is large in *Cladodoides* (Maisey, 2004a, 2005).

The general morphology of the vestibular region in ''*Cobelodus*'' is similar to that in *Cladodoides*, although it differs in its proportions (especially in length). The median aortic canal is visible in the posterior part of the basicranium below the occipital cotylus. Where the canal seems to terminate anteriorly, it actually branches into left and right lateral aortae, and therefore moves out of the sagittal plane. The occipital arch in ''*Cobelodus*'' is short anteroposteriorly, but the occipital pila (containing at least four spino-occipital foramina) extends farther anteriorly between the otic capsules than the exposed dorsal part of the arch. The internal surface of the posterior dorsal fontanelle forms a short ventral extension above and anterior to the crus commune, which lies below and behind the fontanelle.

In anterior view (fig. 10), absence of the ethmoidal and olfactory region helps reveal the massive size of the orbits, as well as the narrowness of the interorbital septum related to the tropibasic arrangement, the narrowness of the precerebral fontanelle and the ethmoid region, and the enormous size of the jugular canal. The floor of the precerebral fontanelle is elevated and separated from the basicranium by the deep internasal/interorbital septum.

In posterior view, the extent of the postorbital arcade and jugular canal is again evident (fig. 11). An articular surface for the palatoquadrate can be observed on the ventrolateral part of the postorbital arcade, in the same general location as in *Orthacanthus* and *Cladodoides* (Schaeffer, 1981; Maisey, 2004a, 2005). The dorsal and lateral otic ridges are both very evident in this view, as is the shallow dorsolateral otic fossa and the periotic process. The posterior dorsal fontanelle is surrounded by a curious raised lip, forming a short ''chimney'', which elevates the opening above the general level of the cranial roof. Behind the otic capsule, the occipital arch completely surrounds the foramen magnum. The arch is separated from the otic region by the otico-occipital fissure, which extends ventrally to include the glossopharyngeal canal (represented by an expansion within the fissure below the otic capsules).

ETHMOID REGION: Very little of the ethmoidal region is preserved. The entire cartilaginous roof of the braincase is extremely thin anteriorly, and some local areas are incomplete or broken (probably a result of postmortem damage). Despite this, the remains of a narrow, slotlike precerebral fontanelle are discernible.

The sagittal view of the braincase shows the precerebral fontanelle opening into a narrow precerebral fossa. This is continuous with the cranial cavity posteriorly, as in elasmobranchs generally, with no evident boundary between the cerebral and precerebral regions (fig. 9). The side walls of the fontanelle are continuous and are not pierced by basal communicating canals. The chondrified roof of the braincase behind the fontanelle is also continuous (although it is extremely thin), and there is no evidence of a separate pineal opening, suggesting that the epiphysis probably extended anteriorly to the chondrified region and may have opened into the ''precerebral'' fossa, as in *Notorynchus* and certain other modern elasmobranchs (Maisey, 2004b). In that case, the dura mater surrounding the brain in ''*Cobelodus*'' probably extended into the posterior part of the fossa, but this cannot be established with confidence because topographic features delimiting the former extent of the dura are lacking.

The internasal plate is extremely narrow from side to side, suggesting that olfactory capsules lay close to the midline. The floor of the braincase behind the internasal septum is very short and was membranous or unchondrified beneath the precerebral fontanelle. There is only a narrow transverse platform here, possibly a remnant of the internasal plate anterior to the hypophyseal chamber. There is a gap in the side wall of the braincase between the internasal plate and the hypophyseal chamber farther posteriorly. The posterior border of this space is marked by a vertical cartilaginous projection adjacent to the optic foramen, corresponding topographically to the presphenoid ledge (*Praesphenoïdvorsprung* of Gegenbaur, 1872) in modern elasmobranchs. The internasal plate is broad in some modern elasmobranchs but narrow in others. The distance between the olfactory capsules is consequently quite variable. This also seems to be the case in symmoriiforms. The internasal plate in "*Cobelodus*", *Stethacanthulus*, and *Falcatus* is extremely narrow from side to side, suggesting that olfactory capsules lay close to the midline. However, it is much broader in *Cobelodus aculeatus*, where the olfactory capsules are spaced widely apart (Zangerl and Case, 1976: figs. 2, 3, 7). As shown below, the internasal plate is also comparatively broad in *Stethacanthus altonensis*, *S.* cf. *S. productus*, and *Akmonistion zangerli* (Lund, 1974: fig. 3; 1985b: fig. 1; Coates and Sequeira, 1998: 68: fig. 5; 2001a: fig. 2). A broad internasal plate is present in *Orthacanthus*, *Tamiobatis vetustus*, *Gutturensis nielsoni*, and *Doliodus* (Schaeffer, 1981; Sequeira and Coates, 2000; Miller et al., 2003; Maisey, 2005). A narrow internasal plate is comparatively unusual and is a potential synapomorphy of "*Cobelodus*", *Stethacanthulus meccaensis*, and *Falcatus falcatus* within symmoriiformes.

The telencephalic chamber in "*Cobelodus*" is extremely short and narrow above the internasal plate (see description of endocast below). Its side walls are thin areas and parts were probably membranous and unchondrified. The anterior course of the terminal nerve, profundal nerve, and anterior cerebral vein are unknown. There is no evidence of a lateral hypophyseal ridge along the inner wall of the telencephalic region like that found in *Cladodoides* and some modern elasmobranchs.

No parts of the postnasal wall, ectethmoid chambers, ethmoid and/or ectethmoid processes, orbitonasal canals, olfactory capsules or olfactory tracts are preserved.

ORBIT AND INTERORBITAL SEPTUM: The orbits in "*Cobelodus*" are remarkably large and comprise half the length of the preserved part of the braincase. The orbits are almost circular and only their upper parts are separated by the cranial cavity. Very large, round orbits are also present in other symmoriiforms (e.g., "*Cobelodus*", *Cobelodus aculeatus*, *Stethacanthulus meccaensis*, *Falcatus falcatus*, *Damocles serratus*, *Stethacanthus altonensis*; Lund, 1974, 1985a, 1985b, 1986; Zangerl and Case, 1976; Williams, 1985). Large eye size is sometimes indicated by a ring of what is probably sclerotic cartilage (e.g., *C. aculeatus*, *Stethacanthulus meccaensis*), or by a ring of numerous small bony plates (e.g., *Falcatus*, *Damocles*, Pennsylvanian "stethacanthids" from Arkansas). It is clear from such structures that the eye was extremely large and almost filled the orbit in the majority of symmoriiforms. No comparable ring of sclerotic cartilage or plates has been identified in *Akmonistion* (Coates and Sequeira, 2001a).

As in other gnathostomes, the entire trabecular region in "*Cobelodus*" is prechordal in position. In "*Cobelodus*", a narrow but extremely deep interorbital septum separates the orbits below the cranial cavity and connects the basicranium to the overlying cranial wall. Comparison with modern elasmobranchs suggests that the upper part of the septum in "*Cobelodus*" formed from the embryonic orbital cartilage, which became fused with the trabeculae ventrally. However, unlike in most modern elasmobranchs, the trabeculae in the floor of the orbit of "*Cobelodus*" must have been very narrow, forming a trabecula communis as in modern tropibasic osteichthyans (the trabecular region is also extremely narrow in some modern dalatiiforms; e.g., *Miroscyllium shekoi*, *Trigonognathus kabeyi*; Shirai and Nakaya, 1990; Shirai and Okamura, 1992).

In "*Cobelodus*", the region presumed to have formed in the preoptic and metoptic pilae (respectively anterior and posterior to the optic foramen) were not completely chondrified. Instead, there is a large, irregular interorbital fenestra extending posteriorly as far as the lateral projection forming the base of the optic pedicel. A chondrified triangular dorsal projection partially separates the optic foramen from an unchondrified space farther posteriorly, possibly representing part of the trabecula communis below the metoptic pila. The optic pedicel is presumably attached to the base of the antotic pila between the embryonic metoptic and prootic foramina, as in *Squalus* (El-Toubi, 1949). From the positions of the efferent pseudobranchial foramen, optic pedicel attachment, and the interorbital canal, the polar cartilage presumably formed a significant part of the interorbital septum posteriorly.

SUPRAORBITAL SHELF: A supraorbital shelf is present anteriorly, but the CT scan reveals that what seems to be the shelf on the specimen (fig. 5) consists mostly of matrix, and the shelf extends anteriorly only as far as the middle of the orbit (figs. 6, 7), possibly an indication that the eyeball was extremely large. The lateral margin of the supraorbital shelf is irregular and contains foramina and notches for ascending branches of the superficial ophthalmic ramus. Since these rami pass between the embryonic orbital and supraorbital cartilage in modern sharks, the presence of open notches suggests that the supraorbital cartilage was very poorly developed in "*Cobelodus*" and probably did not reach the postnasal wall. Distinct foramina for the superficial ophthalmic rami are present only in the posterior part of the orbit, where the supraorbital cartilage merges with the dorsal part of the postorbital arcade as in elasmobranchs generally.

SUBORBITAL SHELF: The "*Cobelodus*" braincase superficially appears to have a continuous suborbital shelf, extending below the orbit from the ethmoidal region to the postorbital process (fig. 5). However, CT scanning reveals that much of this area consists only of matrix and that the actual shelf is very narrow, with separate anterior and posterior regions divided by a deep notch close to the basicranial fenestra (figs. 6, 8, 10). The anterior region tapers anteriorly and includes an anterior articular surface for the palatoquadrate. The posterior region is continuous with the ventral arm of the postorbital arcade and is interrupted only by a canal that probably contained the orbital artery and the anterior ramule of the palatine ramus (fig. 10). A groove passes medially from the notch separating the anterior and posterior regions of the suborbital shelf and extends to the foramen of the efferent pseudobranchial artery, suggesting that the vessel passed across the dorsal surface of the shelf toward the interorbital septum. In modern elasmobranchs, the efferent pseudobranchial artery usually enters the braincase directly from the orbit, and only rarely passes through the suborbital shelf (e.g., *Scyliorhinus*; Holmgren, 1940). However, the artery also probably passed through the shelf in *Cladodoides* and *Orthacanthus* (Maisey, 2005), suggesting that this was a common pattern in Paleozoic sharks.

The suborbital shelf is also narrow in other symmoriiforms (e.g., *Cobelodus aculeatus*, *Stethacanthulus meccaensis*, *Damocles serratus*, *Falcatus falcatus*, *Akmonistion zangerli*; Zangerl and Case, 1976; Williams, 1985; Lund, 1985a, 1986; Coates and Sequeira, 1998, 2001a), although its extent is unknown in *Denaea fournieri*, *Symmorium reniforme*, and Bear Gulch specimens referred to *Stethacanthus* (Fournier and Pruvost, 1922; Williams, 1985; Lund, 1974, 1985b). In *Akmonistion zangerli*, the basicranium is constricted slightly behind the internasal plate in the expected position of the palatobasal articulation (= "posterior ethmoid process" of Coates and Sequeira, 1998), and in *Falcatus falcatus* there are openings in the floor of the orbit adjacent to the palatobasal articulation that may have contained the efferent pseudobranchial and ophthalmic arteries (Lund, 1985a: fig. 10).

In "*Cobelodus*", the articular surface for the palatoquadrate is small and lacks the vertical ridges found in some other Paleozoic sharks (e.g., *Cladodoides*, *Orthacanthus*; Gross, 1937; Schaeffer, 1981; Maisey, 2005). The orientation of these ridges suggests that vertical translation of the palatoquadrate was possible, but that other ranges of motion were probably very limited (protrusion would also have been restricted by the postorbital articulation). Despite the absence of ridges on the facet in "*Cobelodus*", limited vertical translation of the palatoquadrate may have been possible, but the postorbital articulation probably precluded jaw protrusion as in *Notorynchus*, in which palatoquadrate movement along the orbital articulation is limited to translation down the long axis of the articular surface and is constrained by its contact with the cranium, while ventral translation is controlled by the extent to which surrounding ligaments can be extended (Wolfram, 1984).

OPTIC NERVE, OPTIC PEDICEL, OCULOMOTOR NERVE, AND PITUITARY VEIN: Above the notch for the efferent pseudobranchial artery, the interorbital septum is widened and contains short passages for the efferent pseudobranchial and ophthalmic arteries. These passages extend dorsally toward the optic foramen and the pedicel attachment area. However, in "*Cobelodus*" there is no direct course for the internal carotids into the cranial cavity as in other elasmobranchs. The optic (retinal) artery and optic nerve presumably emerged from the braincase centrally in the orbit via the large optic foramen. This is located immediately anterior to a distinct horizontal ridge in the outer calcified layer of the orbit wall that probably forms the pedicel attachment area. This ridge is uncalcified anteriorly (presumably where the pedicel was attached in life), unlike the underlying internal surface of the orbit wall, which is completely calcified. The pedicel ridge is positioned lateral to the hypophyseal chamber, as in *Cladodoides* and unlike in modern sharks, whose pedicel attachment is typically located above the level of the chamber (fig. 12; see also Maisey, 2004a, 2005).

The oculomotor foramen is located just above the pedicel ridge almost directly below the trochlear foramen, and leads into the cranial cavity adjacent to the dorsal margin of the dorsum sellae as in *Cladodoides* and modern sharks. In modern elasmobranchs, the oculomotor nerve typically divides within the orbit into a dorsal ramus, which passes above the optic pedicel to supply the superior and internal rectus muscles, and a ventral ramus that passes behind and below the pedicel to supply the inferior rectus and inferior oblique. The pituitary vein foramen in "*Cobelodus*" is located just below the pedicel ridge, again as in *Cladodoides* and modern elasmobranchs (Maisey, 2005).

TROCHLEAR NERVE: In modern gnathostomes (though not in placoderms; Young, 1986), the trochlear nerve originates in the anterior part of the orbit to supply the superior oblique eye muscle. The trochlear foramen in "*Cobelodus*" is located high in the posterior part of the orbit, directly above the oculomotor foramen and the pedicel ridge. Its general configuration is therefore similar to that in modern elasmobranchs, *Cladodoides*, and *Orthacanthus* (Maisey, 1983, 2005; cf. Schaeffer, 1981).

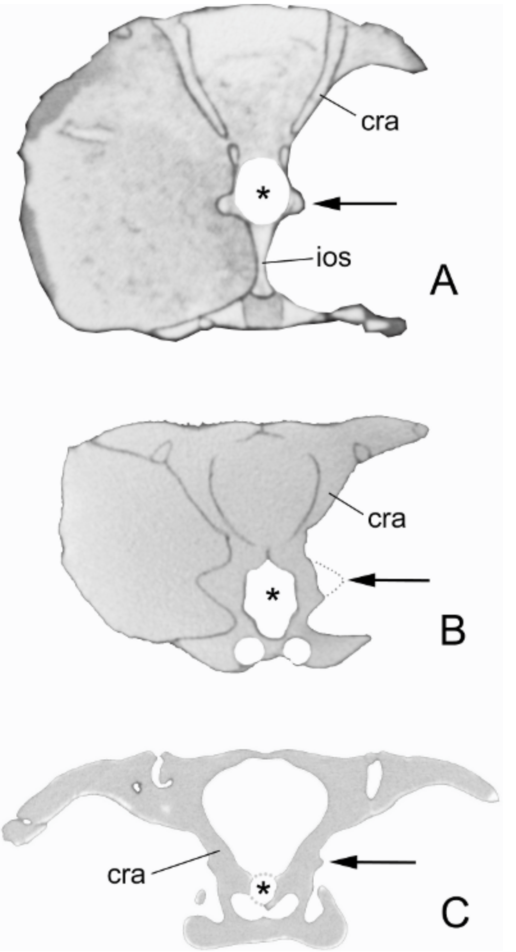

Fig. 12. Transverse CT scan slices through the orbit in the vicinity of the optic pedicel (arrowed). Star indicates bucco-hypophyseal fossa. **A**, "*Cobelodus*" FMNH PF 13242; **B**, *Cladodoides*; **C**, *Notorynchus*.

EXTERNAL RECTUS MUSCLE: Below the posterior part of the pedicel ridge is a shallow recess containing the foramen of the pituitary vein anteriorly, and a small, deep pit farther posteriorly (figs. 6, 13). Similar paired pits in *Cladodoides* probably housed the origin of the external rectus muscle, although they are widely separated by the cranial walls (Maisey, 2005: fig. 17). Nevertheless, these pits probably correspond to part of the trigemino-facialis recess in modern elasmobranchs and osteichthyans, but in *Cladodoides* and "*Cobelodus*" they do not contain the trigeminal or facial foramina.

TRIGEMINAL, PROFUNDAL, AND ANTERODORSAL LATERAL LINE NERVES: In lateral view, the trigeminal foramen can be seen in the posterior part of the orbit, just anterior to the postorbital arcade and above the pedicel ridge (fig. 6). The middle cerebral vein may also have left the braincase via the trigeminal foramen, as in modern elasmobranchs. Since the arcade is swept back posterolaterally and the jugular canal is expanded, however, the trigeminal foramen in "*Cobelodus*" is actually located *behind* the arcade, as in certain other Paleozoic sharks (e.g., *Cladodoides*, "*Tamiobatis* sp." AMNH 2140). In *Cladodoides*, the trigeminal foramen is located behind the orbit and is separated both from the pituitary foramen and the pit for the external rectus muscle by the postorbital process (Gross, 1937; Maisey, 2005). The arrangement of these nerve foramina in "*Cobelodus*" and *Cladodoides* is therefore similar, despite the obviously different proportions of their postorbital regions.

In many modern elasmobranchs the profundal, trigeminal, and anterodorsal lateral line nerves often leave the braincase together. A separate profundal foramen is absent in "*Cobelodus*", but there is a notch in the anterior margin of the trigeminal foramen, suggesting that the profundal and trigeminal nerves separated as they entered the orbit (figs. 6, 9, 13). A separate profundal foramen has been identified in *Cladodoides* (Maisey, 2005; = abducent foramen of Gross, 1937).

The trigeminal nerve in "*Cobelodus*" was probably accompanied by the anterodorsal lateral line nerve as it left the braincase, since there is no evidence of a separate foramen for the latter nerve, although there is an opening for its superficial ophthalmic ramus directly above the trigeminal foramen, leading to a short anteroposteriorly directed canal through the dorsal part of the postorbital process. A shared exit for these nerves has also been suggested in *Cladodoides*, and a very similar arrangement is also possible in "*Tamiobatis* sp." (except that its superficial ophthalmic ramus probably passed just beneath the roof of the arcade instead of through it; Maisey, 2005). It cannot be determined whether the superficial ophthalmic ramus of the trigeminal nerve was separate as in *Squalus* (Norris and Hughes, 1920), or intimately associated with the superficial ophthalmic ramus of the anterodorsal lateral line nerve as in *Chlamydoselachus* (Allis, 1923).

The course of the maxillary ramus of the trigeminal nerve is speculative, but it presumably turned anteriorly and ventrolaterally to pass into the orbit (perhaps as part of a bucco-maxillary complex, as in modern elasmobranchs). Alternatively, it may have continued farther laterally to reach a canal in the lateral part of the postorbital arcade (fig. 13), after which it probably separated from the rest of the bucco-maxillary complex and extended laterally below and in front of the postorbital articulation (i.e., in a comparable position to modern hexanchiforms; Luther, 1908). From there it probably extended posteriorly across the lateral surface of the jaw adductor musculature toward the jaw joint. A similar arrangement of the trigeminal and anterodorsal lateral line nerves has been suggested in *Cladodoides* (Maisey, 2005: 34). A bucco-maxillary complex is commonly found in modern elasmobranchs, but none of its constituent nerves pass through either the postorbital arcade (where present) or its embryonic precursors; instead, the nerves emerge in the trigemino-pituitary fossa of the orbit and pass in front of the postorbital process (although ramules arising from the buccal ramus of the anterodorsal lateral line nerve sometimes penetrate the postorbital process, as in *Chlamydoselachus*; Allis, 1923). There is no evidence that buccal ramules entered the postorbital arcade in "*Cobelodus*".

To summarize, in "*Cobelodus*" the trigeminal trunk (which perhaps formed a nerve complex with the profundal and anterodorsal lateral line nerves) probably emerged from the braincase via a single foramen and then branched to form separate dorsal (superficial ophthalmic) and ventral (bucco-maxillary) complexes. The mandibular branch of the trigeminal nerve presumably then separated from the bucco-maxillary complex and traversed the jugular canal, passing through the postorbital arcade laterally. The remainder of the complex probably turned anteriorly within the jugular canal and entered the orbit, passing beneath the rectus muscula-

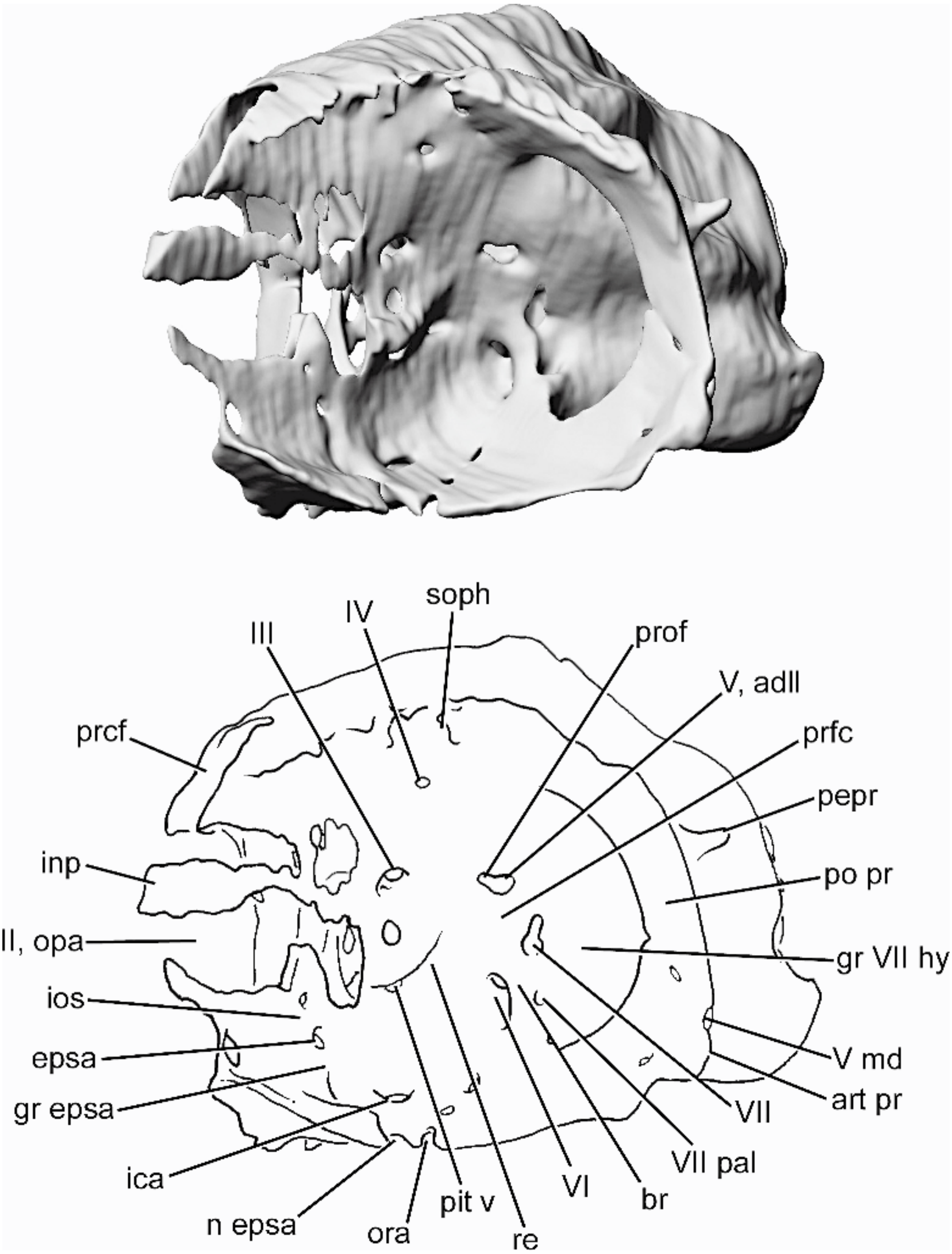

Fig. 13. FMNH PF 13242 ("*Cobelodus*"). Oblique anterolateral view of contour-based surface rendering generated from CT-scan slices to show arrangement of foramina within the orbit.

ture. The superficial ophthalmic complex passed through a short canal in the dorsal part of the postorbital arcade and emerged below the roof of the orbit in the usual gnathostome fashion. The profundal nerve in "*Cobelodus*" probably separated from the trigeminal trunk soon after entering the orbit, whereas in *Cladodoides* these nerves separated inside the braincase and emerged independently.

FACIAL AND ABDUCENT NERVES: In "*Cobelodus*", the foramen for the main (hyomandibular) trunk of the facial nerve is located at the base of the ventral arm of the postorbital arcade, below and behind the trigeminal foramen (fig. 13). Inside the cranial cavity, this foramen lies behind the dorsum sellae and just medial to the base of the utricular recess (see description of the cranial cavity, below). Below the facial-abducent foramen is a shallow but distinct concavity that probably contained the geniculate ganglion, indicating the point at which the main facial trunk divided into anterior (palatine) and posterior (mandibular-hyoidean) rami after leaving the braincase. A canal for the palatine ramus passes dorsoventrally through the floor of the postorbital arcade and divides ventrally within this cartilage, forming two divergent passages for the anterior and posterior ramules of the palatine ramus. Both passages open into the groove for the orbital artery, which traverses the basicranium close to the base of the postorbital arcade. The mandibular-hyoidean ramus of the facial nerve presumably passed medial and ventral to the lateral head vein (as in gnathostomes generally) and subsequently divided into separate mandibular and hyoidean rami, but it is unclear whether the posterior ramus passed lateral to the hyomandibula as in modern chondrichthyans, or medial to it as in modern osteichthyans (see Goodrich, 1930: fig. 446).

The abducent and facial foramina in "*Cobelodus*" are separated only by a narrow, oblique bar of cartilage (fig. 13) and lie much closer together than in *Cladodoides* (Maisey, 2005: figs. 7, 17). It is possible that the abducent nerve was accompanied by the mandibular ramus of the facial nerve, as in modern elasmobranchs. In both "*Cobelodus*" and *Cladodoides*, the abducent foramen is located just behind the pedicel attachment area and the presumed origin of the external (posterior) rectus muscle of the eye (supplied by the abducent nerve), low down on the outer wall of the utricular recess.

The bar of cartilage separating the abducent and facial foramina in "*Cobelodus*" probably formed in membranous tissue within the embryonic prootic fissure, as in modern elasmobranchs (e.g., *Squalus*, *Scyliorhinus*; Holmgren, 1940: 114, 154). The abducent nerve passes through the base of the embryonic antotic pila in some amniotes (e.g., *Lacerta*; Goodrich, 1930: figs. 263, 271), but such an arrangement is unknown in fishes and is considered implausible in "*Cobelodus*". Comparison with modern elasmobranchs also suggests that the facial foramen in *Cladodoides* and "*Cobelodus*" represents parts of the embryonic prootic fissure that became separated from the trigeminal foramen by the prefacial commissure. However, in "*Cobelodus*" this region is located close to the pedicel attachment area, and the area between the oculomotor foramen and utricular recess is comparatively smaller than in *Cladodoides*. Consequently, in "*Cobelodus*" the dorsum sellae rises much more steeply in front of the utricular recess than in *Cladodoides*, and the prefacial commissure (separating the recess from the rest of the endocranial cavity) is comparatively narrow.

The palatine ramus of the facial nerve in *Squalus* initially arises extracranially from the hyomandibular trunk, then passes ventrally through the embryonic lateral commissure (which later chondrifies, so this part of the nerve becomes intracranial; Holmgren, 1941). The palatine ramus divides into anterior and posterior ramules only below the lateral commissure and lateral head vein (Norris and Hughes, 1920; Holmgren, 1941). In many other modern elasmobranchs, the lateral commissure is unchondrified or only weakly chondrified. In *Squalus*, the anterior ramule of the palatine ramus passes between the braincase and palatoquadrate anteriorly, to supply the dorsal oral epithelium. The posterior ramule extends around the mesial ventral border of the palatoquadrate toward the spiracle, then turns and passes along the dorsolateral surface of Meckel's cartilage (Norris and Hughes, 1920). The courses of the anterior and posterior ramules in "*Cobelodus*" and *Cladodoides* below the neurocranium were presumably similar, the only notable difference from *Squalus* being the division of the anterior and posterior ramules within the lateral commissure rather than below it.

In embryonic chimaeroids, the palatine and mandibular-hyoidean rami of the facial nerve pass downward through a space between the trabecular-polar cartilage and the otic process of the palatoquadrate (the cranioquadrate passage of De Beer and Moy-Thomas, 1935). In adult chimaeroids, this space is reduced to three foramina in the floor of the orbital region, containing (from front to back) the efferent pseudobranchial artery, the palatine ramus and orbital artery, and the mandibular-hyoidean ramus and lateral head vein (see also Schauinsland, 1903; Goodrich, 1930; De Beer, 1937; Holmgren, 1942). The mandibular-hyoidean ramus divides into mandibular and hyoidean ramules only as it passes lateral to the (nonsuspensory) epihyal (De Beer and Moy-Thomas, 1935: fig. 1). Although the visceral arches lie essentially behind the neurocranium in elasmobranchs but beneath it in chimaeroids, the fundamental relationship of the facial nerve to the hyoid arch is the same in both groups.

POSTORBITAL ARCADE: A complete postorbital arcade is present in "*Cobelodus*", suggesting that the embryonic lateral commissure was completely chondrified during ontogeny (a widespread condition in Paleozoic chondrichthyans). The topographic relationship of the postorbital arcade to the cranial roof suggests that the embryonic lateral commissure was attached dorsally to the posterior end of the supraorbital cartilage (which forms the primary postorbital process in modern elasmobranchs; Holmgren, 1940).

In certain respects, the postorbital arcade in "*Cobelodus*" is unusual in comparison with other elasmobranchs. The ventral attachment of the arcade in "*Cobelodus*" apparently extended to the ventrolateral border of the polar cartilage, instead of meeting the ventrolateral wall of the otic capsule as in modern elasmobranchs (Holmgren, 1940). The postorbital arcade in "*Cobelodus*" is extremely large, but is also very slender, forming a wide hoop surrounding an unusually wide and deep jugular canal behind the orbit. Dorsally, the arcade is attached to the braincase at the posterior end of the supraorbital shelf, where it is penetrated anteroposteriorly by the superficial ophthalmic canal. Ventrally, the base of the arcade broadens where it meets the basicranium lateral to the groove for the orbital artery. The arcade projects posterolaterally from the braincase and is swept back slightly, with the result that the trigeminal and facial foramina can be seen within the arcade in lateral view although they actually lie behind it (fig. 6). A slender "*Cobelodus*"-like postorbital arcade is also present in many other symmoriiforms (e.g., *Cobelodus aculeatus*, *Stethacanthulus meccaensis*, *Symmorium reniforme*, *Falcatus falcatus*, and *Damocles serratus*; see below), but the arcade is apparently more robust in *Akmonistion zangerli* (Coates and Sequeira, 1998).

In "*Cobelodus*", there is an articular surface for the palatoquadrate on the posterior surface of the ventrolateral part of the arcade. The articular surface consists of two parts, an upper transverse ridge containing the canal for the bucco-maxillary nerve complex, and a lower transverse groove. The ridge and groove are both angled downward ventrolaterally (fig. 11), in such a way that an axis drawn through the width of each articular facet would meet its antimere some distance above the cranium. This orientation of the principal postorbital facets effectively precludes the possibility of any anteroposterior shifting of the jaws and no translation is possible, since motion in the plane of one articular surface would be inhibited by the alignment of the other. However, limited palatoquadrate rotation at the postorbital articulation may have been possible, providing a restricted arc of rotation along the orbital articulation farther anteriorly.

At the lateral end of the articular surface there is a short, rounded process above a shallow, rounded notch in the margin of the postorbital arcade (figs. 10, 11, 13). The lateral process corresponds topographically with a "short cartilaginous prong originating from the ventrolateral surface of the arcade" in *Cobelodus aculeatus* (Zangerl and Case, 1976: 117). Consequently, the "prong" probably represents the lateral part of the postorbital articulation as in "*Cobelodus*", rather than "a third, hitherto unknown attachment point of the palatoquadrate to the neurocranium" as they suggested.

The lateral part of the postorbital arcade in "*Cobelodus*" is comparatively straight and extends almost vertically above the postorbital articulation. The posteromedial surface of this region is slightly raised, forming a faint, narrow vertical platform. This area presumably faced the anterolateral margin of the palatoquadrate otic process and may even have contacted it, possibly forming a supplemental attachment surface above the principal postorbital articulation. Postorbital movement in "*Cobelodus*" may therefore have been restricted by ligamentous connections dorsal to the principal postorbital articulation and extending from the otic process to the vertical platform of the postorbital arcade. An "articular" surface has also been reported high on the lateral surface of the palatoquadrate otic process in other symmoriiforms (e.g., *Cobelodus aculeatus*, *Symmorium reniforme*, *Stethacanthulus meccaensis*, *Akmonistion zangerli*; Zangerl and Case, 1976; Williams, 1985; Coates and Sequeira, 2001a). This surface seems to correspond to the narrow vertical platform on the postorbital arcade in "*Cobelodus*", but not with its primary articular surface farther ventrally. The supposedly lateral articular surface on the palatoquadrate in symmoriiforms may therefore represent a secondary attachment site rather than the principal postorbital articulation. According to Coates and Sequeira (2001a), the articular fossa is directed laterally in *Cladoselache*, but this has not been verified.

ARTERIAL SUPPLY TO THE HEAD: The aortic canal in "*Cobelodus*" is unpaired where it enters the basicranium posteriorly between the paired ventral occipital condyles (figs. 6, 9, 11, 14). The canal is visible in the sagittal view of the braincase (fig. 9), but it disappears from view where the aorta divides below the otic capsules. Paired aortic canals emerge beneath the basicranium and continue anteriorly as grooves except where they pass briefly through short canals at the narrowest part of the basicranium (fig. 8). The paired grooves diverge anterolaterally and each extends to the margin of the suborbital shelf. Canals for the anterior and posterior ramules of the palatine ramus open in the roof of each groove as it reaches the postorbital process. These parts of the grooves/canals are clearly homologous to those for the orbital artery in *Cladodoides* and *Tamiobatis vetustus*. However, there are no grooves or other features in the basicranium to indicate the positions of the internal carotid and efferent hyoidean arteries, and reconstructing the entire basicranial arterial circuit is therefore somewhat speculative.

A median aortic canal is also present in *Cobelodus aculeatus*, in a Virgilian symmoriiform from Texas, and in Pennsylvanian symmoriiforms from Arkansas (see below), as well as in *Akmonistion zangerli* (Coates and Sequeira, 1998) and in *Cladoselache* (see below). Previous reconstructions of *Cobelodus aculeatus* showing paired aortic canals are erroneous (e.g., Zangerl and Case, 1976: 117; Schaeffer, 1981: fig. 13). Most modern elasmobranchs have paired aortae, but a median aorta extends beneath the basicranium in the squaloid *Aculeola nigra*, almost reaching the bucco-hypophyseal fenestra before dividing into short lateral aortae that meet the internal carotid and efferent hyoidean arteries as in other elasmobranchs (personal obs.).

There are no basicranial grooves for internal carotids in "*Cobelodus*", nor is there any communication between the basicranium and hypophyseal chamber (figs. 8, 9, 12A). Even if internal carotid arteries were present, they could not have entered the basicranium via the chamber as in modern elasmobranchs, where these arteries typically enter the hypophyseal chamber via the bucco-hypophyseal fenestra or via a separate opening behind it (when a precarotid commissure is present; Holmgren, 1940).

It is conceivable that internal carotid arteries were absent in "*Cobelodus*", in which case the brain presumably received its blood supply entirely via the efferent pseudobranchial arteries. Absence of internal carotids is certainly unusual, but in modern chimaeroids (where there is no hyoid pseudobranch) the embryonic internal carotids become atrophied and do not enter the braincase (De Beer and Moy-Thomas, 1935); instead, the brain receives a supply of blood from the uninterrupted efferent "pseudobranchial" artery (= mandibular efferent of Jollie, 1962). However, the presence of a spiracular notch in the palatoquadrates of some symmoriiform sharks (Lund, 1985b) suggests that

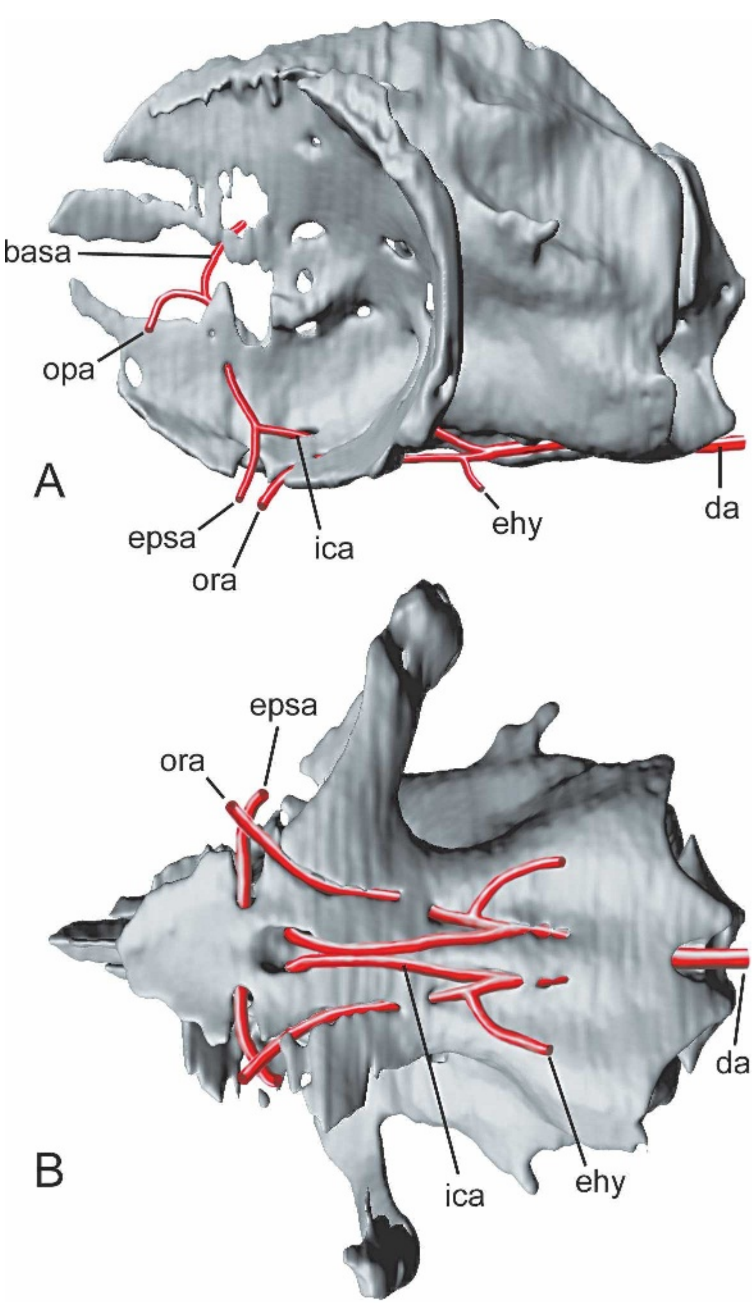

Fig. 14. Reconstruction of the basicranial arterial circuit in "*Cobelodus*" assuming that internal carotid arteries were present. **A**, lateral view; **B**, ventral view. Exposed portions of arteries shown in red. Note the unusual position of the connection between the internal carotid and efferent pseudobranchial arteries within the orbit.

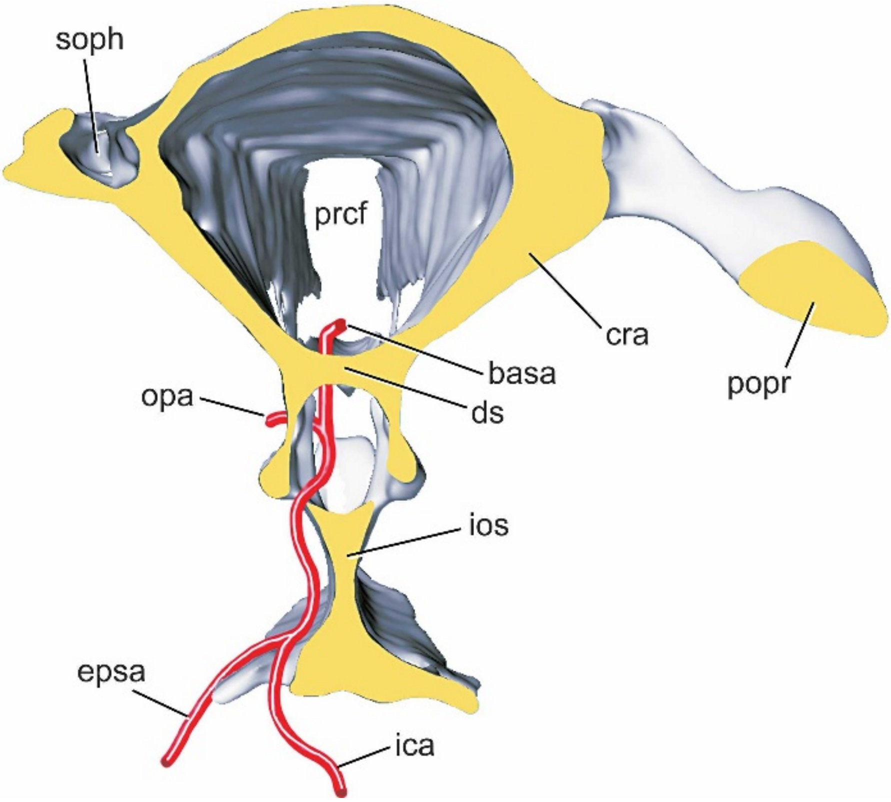

Fig. 15. View of anterior part of the orbit in "*Cobelodus*" showing the proposed arrangement of the efferent pseudobranchial artery.

a hyoid pseudobranch was present, in which case the symmoriiform efferent artery was probably interrupted, as in modern elasmobranchs.

The basicranial fenestra in "*Cobelodus*" is also unusual in having paired openings in its roof on either side of the interorbital septum and medial to the notch for the efferent pseudobranchial artery in the suborbital shelf (ica: figs. 6, 8). Since this fenestra has no connection with the overlying hypophyseal chamber, it clearly did not provide the internal carotids with direct access to the cranial cavity, but may instead have allowed the internal carotids to connect with their respective efferent pseudobranchial arteries within the orbit before the combined vessel entered the cranial cavity via the efferent pseudobranchial foramen. Internally, the combined vessel may then have branched as usual into optic, ophthalmic, cerebral, and basilar arteries (figs. 14, 15).

Such a connection between the internal carotid and efferent pseudobranchial would still have been dorsal to the embryonic trabecular cartilage (as in modern elasmobranchs), but would have lain outside rather than inside the cranial cavity, i.e., lateral to the embryonic trabecula communis forming the interorbital septum (fig. 16D). This remarkable arrangement has no modern gnathostome paradigm. In modern elasmobranchs (fig. 16B), the efferent pseudobranchial enters the cranium before meeting the internal carotid. The efferent pseudobranchial in osteichthyans primitively meets the internal carotid below the trabeculae, irrespective of whether the braincase is morphologically platybasic (fig. 16A) or tropibasic (fig. 16C). Thus, the basicranial circuit hypothesized in "*Cobelodus*" implies a unique ontogenetic pattern in which the embryonic trabecula communis represents an extension of the trabecular plate *medial* to the internal

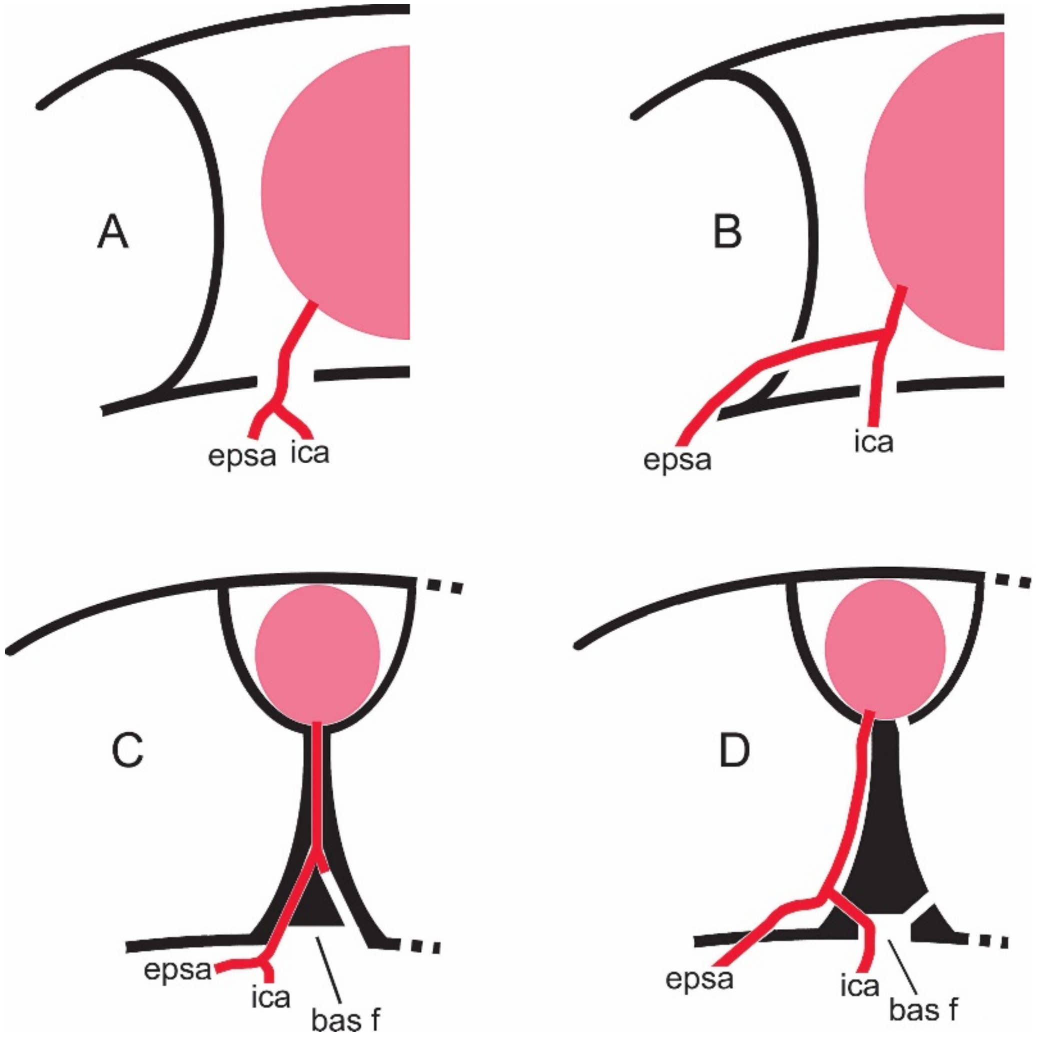

Fig. 16. Diagrams summarizing variation in the relationships of the internal carotid and efferent pseudobranchial arteries to the basicranium in: **A**, platybasic osteichthyan (arteries meet ventral to trabeculae); **B**, platybasic shark (arteries meet dorsal to trabeculae); **C**, tropibasic osteichthyan (brain receives arterial blood via basisphenoid pillar); **D**, "*Cobelodus*" (brain receives arterial blood via orbit).

carotid/efferent pseudobranchial arteries. By contrast, the internal carotid in tropibasic osteichthyans enters the cranial cavity *within* the trabecula communis (typically passing through the basisphenoid pillar; fig. 16C), a completely different arrangement from that hypothesized in "*Cobelodus*".

Grooves for internal carotid arteries are also absent in *Cobelodus aculeatus* and perhaps in *Stethacanthulus meccaensis* (see below), but are present in *Akmonistion zangerli* (Coates and Sequeira, 1998). It is uncertain whether the internal carotids in *A. zangerli* entered the cranial cavity directly or passed into the orbit as hypothesized in "*Cobelodus*" (figs. 14, 15).

Another unusual feature of the arterial supply to the head in "*Cobelodus*" is evident only in CT scan slices through the otico-occipital region below the posterior ampulla, where the canal for the dorsal aorta gives off a single pair of small canals dorsally between the first and second spino-occipital nerve foramina (described below). These canals

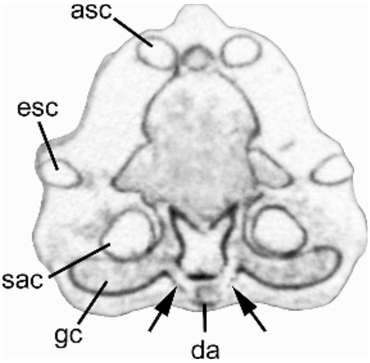

Fig. 17. Transverse CT scan slice no. 167, through the otico-occipital region of the "*Cobelodus*" braincase FMNH PF 13242. Note paired canals arising dorsally from the dorsal aortic canal.

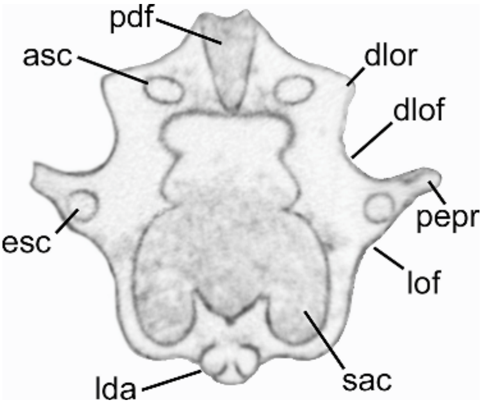

Fig. 18. Transverse CT scan slice no. 144, through the otic region of FMNH PF 13242 to show periotic process overlying the external semicircular canal. This section also shows the transition from median to paired aortic canals.

pass directly through the hypotic lamina and enter the glossopharyngeal canal (their position is marked by arrows in fig. 17). They probably contained encephalic occipital arteries that passed vertically through the anteriormost part of the otico-occipital fissure, between the occipital cartilage and the inner wall of the posterior ampulla, possibly meeting the basilar artery within the cranial cavity. The canals are positioned anteroposteriorly between the first and second spino-occipital nerve canals, suggesting that the occipital artery in "*Cobelodus*" was probably associated with the second permanent myomere as in osteichthyans, *Acanthodes*, and the placoderm *Brindabellaspis* (discussed in Gardiner, 1984a: 208). Corresponding paired canals are also present in *Tamiobatis* and *Cladodoides*. Similar canals for encephalic occipital arteries have been identified in osteostracans, just medial to the vagobrachial canal and apparently anterior to all the spino-occipital canals (e.g., *Norselaspis*, *Tremataspis*; Janvier, 1981, 1985).

OTIC REGION: The otic region of "*Cobelodus*" is extensive, comprising about half the overall preserved length of the braincase (figs. 6–9). Its dorsal surface is gently arched above the cranial cavity. Paired dorsal otic ridges extend posteriorly from the postorbital arcade and converge on either side of the posterior dorsal fontanelle toward the occipital arch, but die away before meeting the otico-occipital fissure (figs. 7, 11). Dorsal otic ridges are strongly developed in other extinct sharks (e.g., *Orthacanthus*, *Tamiobatis*; Schaeffer, 1981), where they overhang a concave area (dorsolateral otic fossa) that merges posteriorly with the dorsal surface of the lateral otic process, whose lower margin is defined by the lateral otic ridge. In "*Cobelodus*", the dorsolateral otic fossa forms the steeply sloping upper lateral part of the capsular wall above the well-defined lateral otic ridge. Below this ridge is another concave area, corresponding topographically with the lateral otic fossa in other Paleozoic sharks. "*Cobelodus*" thus shares the presence of dorsal and lateral otic ridges, dorsolateral fossa, and lateral otic fossa with platybasic Paleozoic sharks such as *Orthacanthus* and *Tamiobatis*.

"*Cobelodus*" nevertheless differs from many Paleozoic sharks in lacking a posterolaterally directed lateral otic process (sensu Schaeffer, 1981, enclosing the loop of the posterior semicircular canal immediately in front of the otico-occipital fissure, and forming the posterior part of the hyomandibular articulation). Instead, there is a delicate calcified process (here termed the periotic process), located on the lateral capsular wall, about halfway along the lateral otic ridge (figs. 6–8, 11) and overlying the external semicircular canal (fig. 18). It is uncertain whether the periotic process is homologous to the lateral otic process in other sharks. No case of conjunction between them is known to falsify that possibility, but they differ in their topographic relations to the otic capsule. A periotic process may also be present in *Stethacanthus altonensis* (Lund, 1974: fig. 3) and in *Falcatus falcatus* (Lund, 1985a: fig. 9C), and seems to occur only within symmoriiforms. The only symmoriiform shark in which a lateral otic process has been identified is *Akmonistion zangerli* (Coates and Sequeira, 1998), which lacks a periotic process.

There is no clearly defined hyomandibular fossa in "*Cobelodus*", despite the fact that the lateral wall of the otic capsule is well preserved. This is of interest because it has been claimed that symmoriiform sharks were aphetohyoidean (i.e., with an "unmodified" nonsuspensory hyoid arch; Zangerl and Williams, 1975; Zangerl and Case, 1976; Zangerl, 1981; see discussion). Absence of a pronounced facet suggests that the epihyal in "*Cobelodus*" was less strongly braced against the neurocranium than in modern elasmobranchs and may only have been held in place by ligaments (possibly attached to the periotic process and/or to the posterolateral part of the capsular wall).

The internal arrangement of the vestibular chambers and semicircular canals will be described along with the cranial endocast (below).

OCCIPITAL REGION: There is no occipital half-centrum in "*Cobelodus*" and the occipital cotylus simply forms a shallow fovea as in many other Paleozoic sharks (figs. 11, 19). The CT scan suggests that a notochordal canal was probably absent. There is also no evidence in the scan of a subnotochordal septum or paired subnotochordal chambers like those described in *Cladodoides* or "*Tamiobatis* sp." (Maisey, 2005). Above and below the occipital fovea there are small, paired dorsal and ventral paroccipital processes that presumably contributed to the craniovertebral joint. Each dorsal paroccipital process lies just behind the last spino-occipital nerve foramen (fig. 6). The ventral processes flank a median canal for the dorsal aorta and are evident in ventral view (figs. 5B, 4). Below the fovea is the median opening for the dorsal aorta. The occipital arch is separated from the otic region by a persistent otico-occipital fissure dorsally and laterally, but is fused to cartilage derived from the embryonic parachordals ventrolaterally (figs. 5A, 6, 7, 9, 11). Formation of the posterior basicapsular commissure appears to have involved secondary overgrowth of the fissure by cartilage, because individual CT scan slices reveal a secondary cartilaginous plug within the metotic fissure, connecting the floor of the saccular chamber to the hypotic lamina, suggesting that the metotic fissure was initially filled by membranous tissue continuous with the perichondrium (figs. 20, 21). There is no ventral otic fissure.

A comparison of the occipital region in "*Cobelodus*" and *Cladodoides* reveals several important differences (fig. 19). First, the occipital cotylus in "*Cobelodus*" is located directly between the glossopharyngeal canals, whereas in *Cladodoides* it is located farther ventrally. Consequently, the occipital arch and foramen magnum are situated above the level of the glossopharyngeal canals in "*Cobelodus*" but between them in *Cladodoides* (this arrangement can also be observed in transverse sections through the otico-occipital region; e.g., figs. 20, 22). Second, the hypotic lamina in "*Cobelodus*" curves below the canal and extends from the occipital region to the posterior basicapsular commissure. The glossopharyngeal canal is therefore oval in posterior view, except where the saccular chamber bulges into its roof dorsally and dorsolaterally (fig. 11). By contrast, in *Cladodoides wildungensis*, *Tamiobatis vetustus*, and *Orthacanthus*, the glossopharyngeal canal is much wider than deep and the hypotic lamina meets the occipital region laterally instead of ventrolaterally. Third, the occipital cotylus in "*Cobelodus*" is about the same width as the foramen magnum, whereas in *Cladodoides* it is more than three times wider. Consequently, the lateral part of the occipital arch overhangs the glossopharyngeal canal in "*Cobelodus*" to a greater extent than in *Cladodoides*. Fourth, the cotylus in "*Cobelodus*" is flanked dorsolaterally and ventrolaterally by paroccipital processes, but these are generally absent in Paleozoic sharks with an elongated occipital region (e.g., *Cladodoides*, *Orthacanthus*, *Tamiobatis*). Finally, the aortic canal in "*Cobelodus*" is medial rather than paired.

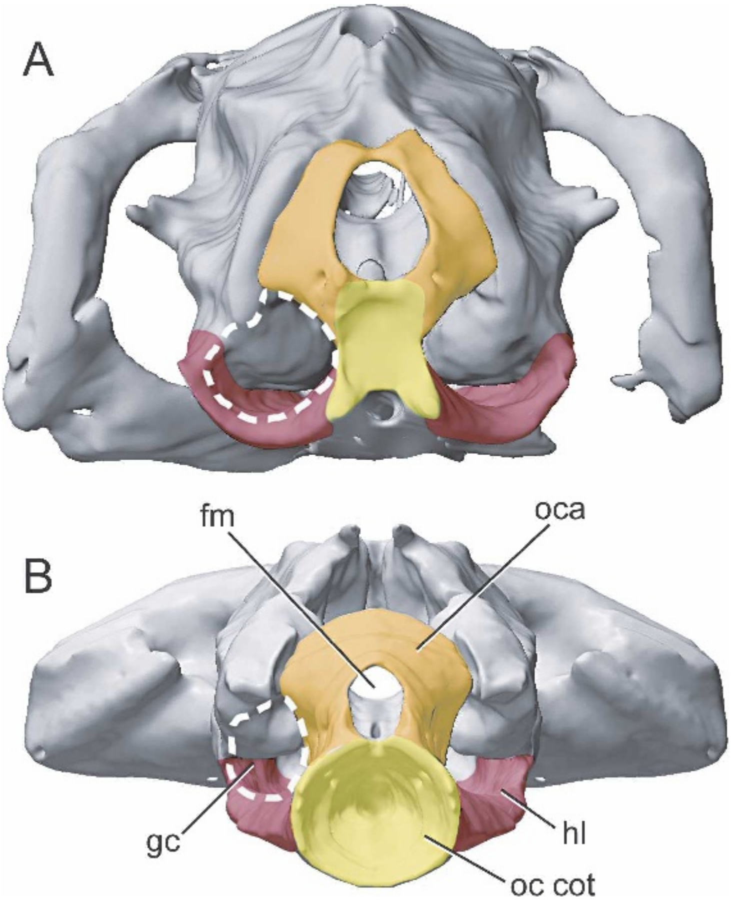

Fig. 19. Posterior views of the occipital region in **A**, "*Cobelodus*"; **B**, *Cladodoides*. Occipital cotylus in yellow, occipital arch in orange, hypotic lamina in red, glossopharyngeal canal represented by dashed white line. Not to scale.

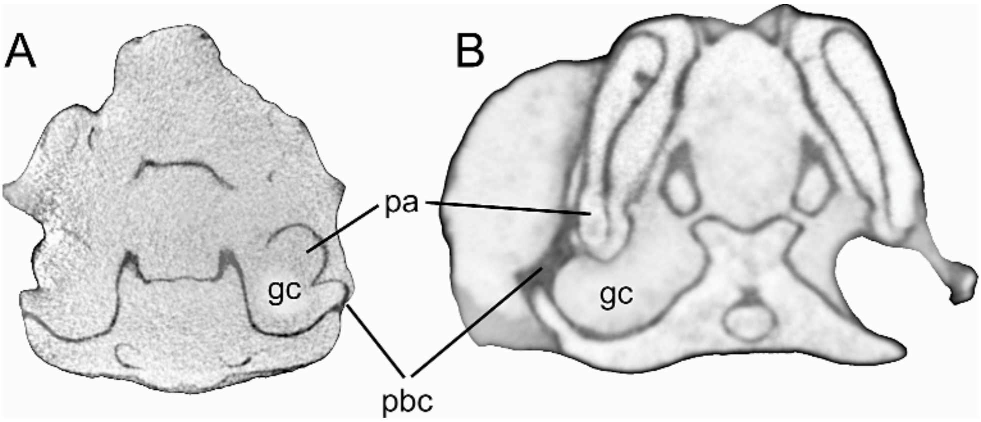

Fig. 20. Transverse CT scan slices through the posterior basal commissure. **A**, *Cladodoides wildungensis* slice 240; **B**, "*Cobelodus*" FMNH PF 13242, slice 181.

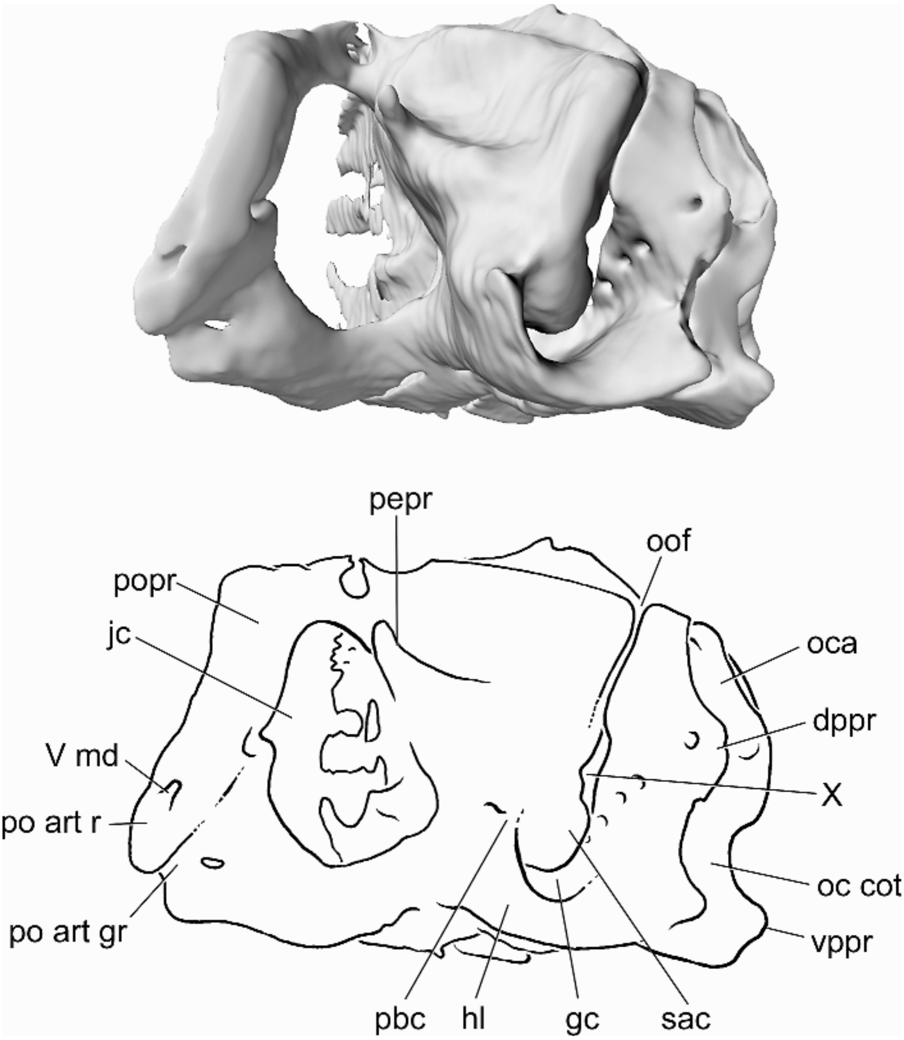

Fig. 21. FMNH PF 13242 ("*Cobelodus*"). Oblique posterolateral view of contour-based surface rendering generated from CT-scan slices.

The unusual arrangement of the otico-occipital region in "*Cobelodus*" suggests that extensive developmental remodeling has occurred, leading to a narrowing of the occipital region and elevation of the occipital arch above the level of the glossopharyngeal canals. Similar deepening and narrowing characterizes the prechordal part of the basicranium, especially within the orbit, where the interorbital septum separates the cranial cavity from the basicranium. Thus, similar ontogenetic changes were probably responsible for tropibasia in the prechordal region and for the peculiar morphology of the otico-occipital region in "*Cobelodus*".

The occipital arch in "*Cobelodus*" is much shorter anteroposteriorly than in *Orthacanthus*, *Tamiobatis*, *Cladodoides*, and *Cladodus* (Maisey, 2004a, 2005). A relatively short occipital region is also present in other symmoriiforms (e.g., *Stethacanthus altonensis*, *Damocles serratus*, *Falcatus falcatus*, *Cobelodus aculeatus*, *Stethacanthulus meccaensis*, *Symmorium reniforme*, *Akmonistion zangerli*, *Gutturensis nielsoni*; Lund, 1974, 1985a, 1985b, 1986; Zangerl and Case, 1976;

Williams, 1985; Coates and Sequeira, 1998; Sequeira and Coates, 2000). Dorsal and ventral paroccipital processes like those in "*Cobelodus*" are also present in *Cobelodus aculeatus*, *Stethacanthulus meccaensis*, and *Akmonistion zangerli* (Zangerl and Case, 1976: fig. 5; Williams, 1985: figs. 3, 6; Zidek, 1992: fig. 4; Coates and Sequeira, 1998: fig. 4).

OTICO-OCCIPITAL FISSURE: Schaeffer's (1981: fig. 26) suggestion that a persistent otico-occipital fissure is a synapomorphy of *Orthacanthus* and *Tamiobatis* has been refuted by discovery of the fissure in several other Paleozoic sharks (e.g., *Cladodoides wildungensis*, *Cladodus elegans*, *Akmonistion zangerli*, *Gutturensis nielsoni*; Coates and Sequeira, 1998; Sequeira and Coates, 2000; Maisey, 2004a, 2005), as well as in the primitive chondrichthyan *Pucapampella* (Janvier and Suárez-Riglos, 1986; Maisey, 2001a; Maisey and Anderson, 2001). In "*Cobelodus*", the upper part of the otico-occipital fissure is narrowest where it passes between the posterior semicircular canal and the occipital arch. The fissure expands just medial to the posterior ampulla, in the expected position of the vagal nerve (fig. 21). A corresponding expansion of the fissure is present in *Cladodoides wildungensis* (Maisey, 2005: fig. 28). Farther ventrally, the fissure broadens considerably and opens into a wide glossopharyngeal canal that extends laterally beneath the floor of the saccular chamber.

In *Cladodoides wildungensis* and "*Cobelodus*", most of the ventrolateral (metotic) part of the fissure is closed, and there is no ventral otic notch like that described by Schaeffer (1981) in *Orthacanthus.* Closure of the posterior basicapsular commissure in "*Cobelodus*" and *Cladodoides* apparently involved secondary chondrification of membranous tissue within the metotic fissure (fig. 20). The much longer ventral otic notch in *Orthacanthus* may also have been filled with membranous tissue that simply failed to chondrify in the adult (i.e., there is no posterior basicapsular commissure). In *Pucapampella*, the metotic part of the fissure extends along the entire lateral margin of the parachordal plate and meets the ventral otic fissure (a posterior basicapsular commissure is again absent).

SPINO-OCCIPITAL NERVES: The occipital arch in "*Cobelodus*" is comparatively short, with only two spino-occipital foramina being visible externally (fig. 6). However, CT scanning reveals five canals within the occipital block (fig. 22), showing how easily the total number of spino-occipital nerves in fossil sharks may be underestimated simply from external appearance. The precise number of spino-occipital nerve canals is unknown in the majority of symmoriiforms, as in most cases only the externally visible foramina have been recognized. Only a single pair has been identified in *Akmonistion zangerli* (Coates and Sequeira, 1998: fig. 4), one unpaired foramen was found in *Gutturensis nielsoni* (Sequeira and Coates, 2000: 160), and two (probably paired) foramina have been illustrated in *Cobelodus aculeatus* (Zangerl and Case, 1976: fig. 9a). Presumably, the deeper-lying spino-occipital canals have simply not been detected in these forms.

In *Cladodoides wildungensis*, five spino-occipital canals are present (Maisey, 2005), although only the last three are visible externally (fig. 23). There are four (possibly five) paired spino-occipital canals in "*Tamiobatis* sp." (AMNH 2140) and in *Cladodus elegans* (Maisey, 2005; Ginter and Maisey, 2007). Three or four paired canals are seen in CT scan sections of *Pucapampella*, in which the occipital arch is comparatively short (Janvier and Suárez-Riglos, 1986; Maisey, 2001a; Maisey and Anderson, 2001). In the well-preserved serially sectioned xenacanth braincases investigated by Schaeffer (1981), however, only three spino-occipital canals were identified, despite the considerable length of its occipital region. Three have also been identified in CT scans of the hybodonts *Tribodus limai* and *Egertonodus basanus*, but up to six canals may be present in *Hybodus reticulatus* (Maisey, 1987).

The number of nerves incorporated into the occipital region in elasmobranchs is evidently not a simple correlation with length; a relatively high number may be present in "short" forms (e.g., "*Cobelodus*"), and a lower number is sometimes present in "long" forms (e.g., *Orthacanthus*). Three or more canals may represent a cladistically primitive condition for chondrichthyans, and a lower number (one or two) is probably derived, but the number is far less

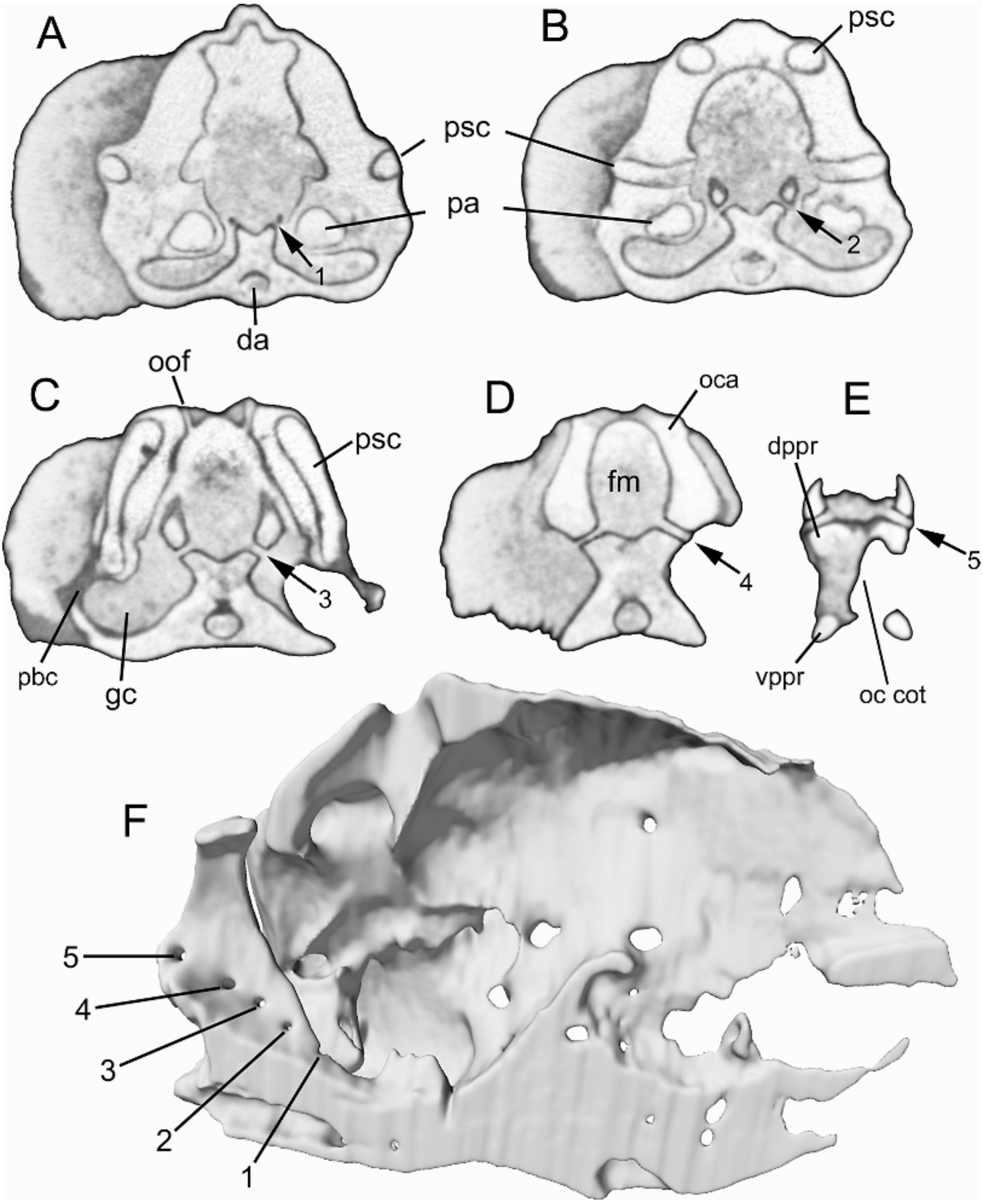

Fig. 22. Spino-occipital nerve canals in "*Cobelodus*". A–E, CT scan slices through successive canals. **A**, canal 1 (incompletely formed; CT scan slice 163); **B**, canal 2 (slice 172); **C**, canal 3 (slice 181); **D**, canal 4 (slice 190); **E**, canal 5 (slice 201); **F**, medial view of digital reconstruction, showing location of spino-occipital canals.

variable than the proportions of the occipital region. A "long" occipital region with at least three spino-occipital foramina occurs in some placoderms (Goujet, 2001), although as many as seven may be present (e.g., *Buchanosteus*; Young, 1979: fig. 11). Three may represent the primitive condition for gnathostomes (Bemis and Forey, 2001).

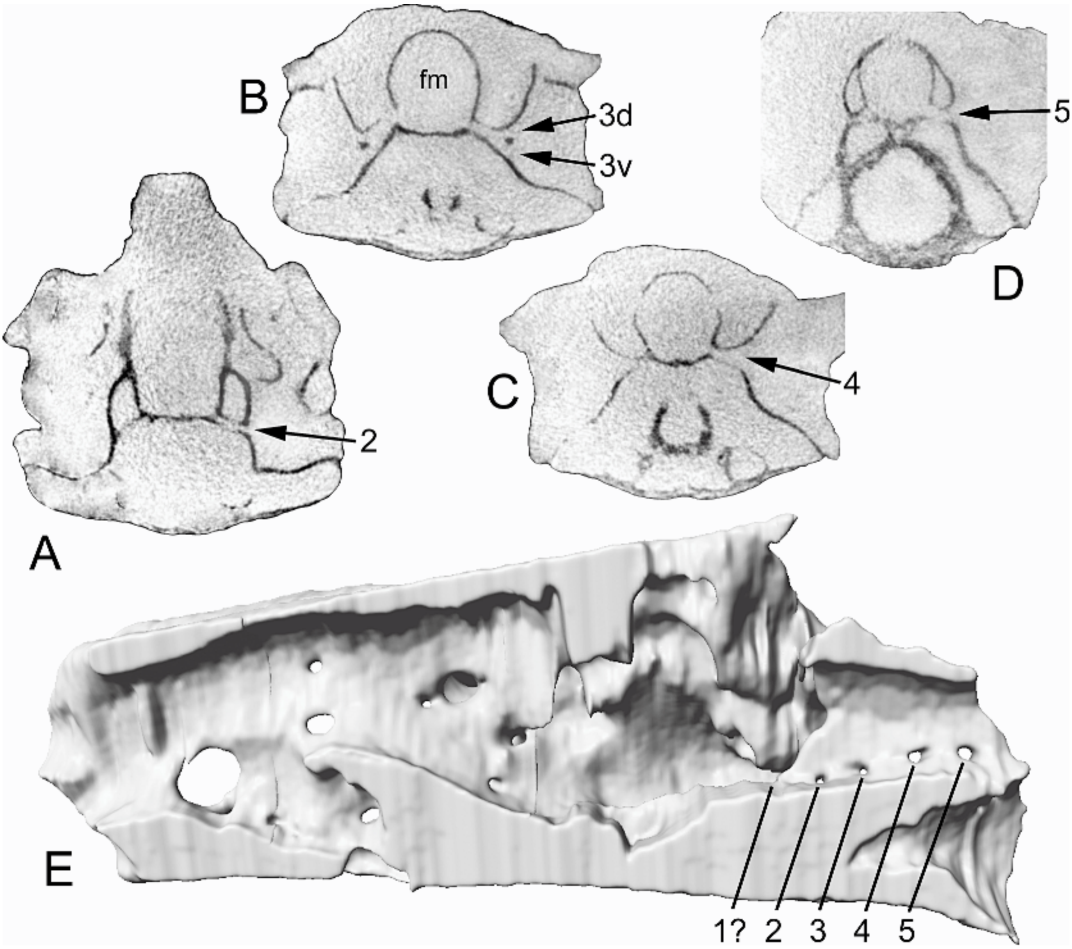

Fig. 23. Spino-occipital nerve canals in *Cladodoides wildungensis* for comparison with previous figure. A–D, CT scan slices through successive canals. Canal 1 is represented only by a slight embayment in the reconstruction and is poorly resolved in sectional views. **A**, canal 2 (does not widen or divide; CT scan slice 246); **B**, canal 3 (divides into dorsal and ventral branches; slice 260); **C**, canal 4 (widens externally but does not divide; slice 272); **D**, canal 5 (does not widen or divide; slice 287); **E**, medial view of digital reconstruction, showing location of spino-occipital canals.

Schaeffer (1981: 59) argued that the number of spino-occipital canals in the occipital arch may not accurately reflect the total number of nerves because some of them "leave the braincase through the vagal canal or behind the condyles". However, even the anteriormost occipital nerves in *Squalus acanthias* pass through the side wall of the occipital cartilage prior to entering the vagal canal (Norris and Hughes, 1920: 373f.), and it is unclear why a nerve located "behind the condyles" would be regarded as anything other than a normal spinal nerve. In modern elasmobranchs with a short occipital arch (e.g., *Squalus*), only two or three paired occipital nerves are typically present and even fewer are visible externally (Fürbringer, 1897; Norris and Hughes, 1920). In modern sharks with a relatively long occipital region (e.g., *Chlamydoselachus*, *Notorynchus*; Gegenbaur, 1872; Allis, 1923), three paired nerves are often present although the number is not constant; for example, three or four have been reported in *Notorynchus* (Fürbringer, 1897; Daniel, 1934).

Fürbringer (1897) identified three occipital nerves, x, y, and z (with x anteriormost), in

Squalus acanthias. All three arise from the ventral motor column (unlike the visceral motor roots of the vagus) and supply the interbasal muscles (see also Norris and Hughes, 1920). Fürbringer (1897) found four occipital nerves in *Notorynchus* (w, x, y, and z), but according to his findings only w and x are purely motor (i.e., completely ventral in origin), whereas y and z have a small sensory dorsal root (see Daniel, 1934: fig. 204). Although Fürbringer (1897) and Norris and Hughes (1920) found slightly differing patterns in *Squalus*, they agree that all three occipital nerves supply the first and perhaps the second and third interbranchial muscle. By contrast, the first three spinal nerves in *S. acanthias* include both motor and sensory components, and the motor root of each nerve divides into a dorsal and ventral ramus after leaving the vertebral column. According to Norris and Hughes (1920), the ventral ramus of the first spinal nerve joins occipital nerves y and z to supply the first interbasal muscle. The ventral ramus of the second spinal nerve fuses with the trunk formed by the occipital and first spinal nerves, forming the cervical plexus (which is eventually also joined by the third spinal nerve). The dorsal ramus of each motor root passes around its respective spinal ganglion, apparently without receiving any sensory elements. Thus, the occipital nerves in *Squalus* differ from the spinal nerves farther posteriorly in lacking any sensory component, in not forming dorsal and ventral rami, and in lacking the equivalent of a spinal ganglion. Only the two anteriormost occipital nerves in *Notorynchus* agree in all respects with those in *Squalus*, however, since the last two have a dorsal ramus with a sensory component (although they still lack ganglia, the only remaining difference from "true" spinal nerves farther posteriorly).

The canals in "*Cobelodus*" show no evidence of branching (fig. 22), but in *Cladodoides* (fig. 23C), canal 3 includes dorsal and ventral branches and canal 4 is significantly wider at its outer end; canals 1, 2, and 5 are unbranched and narrow for their entire length. The branching of canal 3 within the cartilage is certainly unusual for an occipital nerve, but does not clarify whether a sensory dorsal ramus was present as in nerves y and z of *Notorynchus*, as it is possible that the motor root in canal 3 simply branched earlier than usual, before leaving the cartilage.

The otic capsule and occipital arch are both comparatively longer in *Cladodoides* than in "*Cobelodus*" (fig. 58). The presumed anteroposterior extent of the synotic tectum is also greater in *Cladodoides*, but by contrast its posterior tectum was comparatively small. This difference may be related to the different size and shape of the posterior dorsal fontanelle in these forms.

CRANIAL ENDOCAST: The cranial and labyrinth cavities in "*Cobelodus*" have been reconstructed digitally using two different methods: first, by creating a sagittal view of the contour-based surface rendering (figs. 9, 22); and second, by making a separate rendering of the cranial endocast as a solid object (figs. 24–30). The medial capsular wall is unmineralized and the labyrinth chamber is therefore confluent with the cranial endocast, as in *Cladodoides wildungensis* (Maisey, 2005: figs. 23–26). The semicircular canals were omitted from one side of the reconstruction in order to show features of the labyrinth that would otherwise be obscured. Comparison with the endocast in other elasmobranchs is still seriously impaired by the fact that very few taxa have been investigated. Furthermore, there is often little correlation between internal and external morphological features of the braincase in those forms that have been investigated (Maisey, 2004b, 2005).

The telencephalic region in "*Cobelodus*" is very narrow (figs. 27, 28A) and the floor of the precerebral cavity is short, sloping posteriorly downward toward the origination of the optic foramen (which is only partially preserved), immediately anterior to the efferent pseudobranchial foramen (figs. 24, 25). The floor of the braincase was probably membranous and weakly chondrified anteriorly, as in *Cladodoides*. In many modern elasmobranchs, this entire region is well chondrified and is often quite thick (e.g., *Notorynchus*; Maisey, 2004b: fig. 11). It is also heavily chondrified in *Tamiobatis vetustus* (NMNH 1717), "*Tamiobatis* sp." (AMNH 2140), the xenacanth *Orthacanthus*, and hybodonts such as *Tribodus* (Schaeffer, 1981; Maisey, 2004a).

In "*Cobelodus*", a small precerebral fontanelle is present, forming a narrow vertical slot

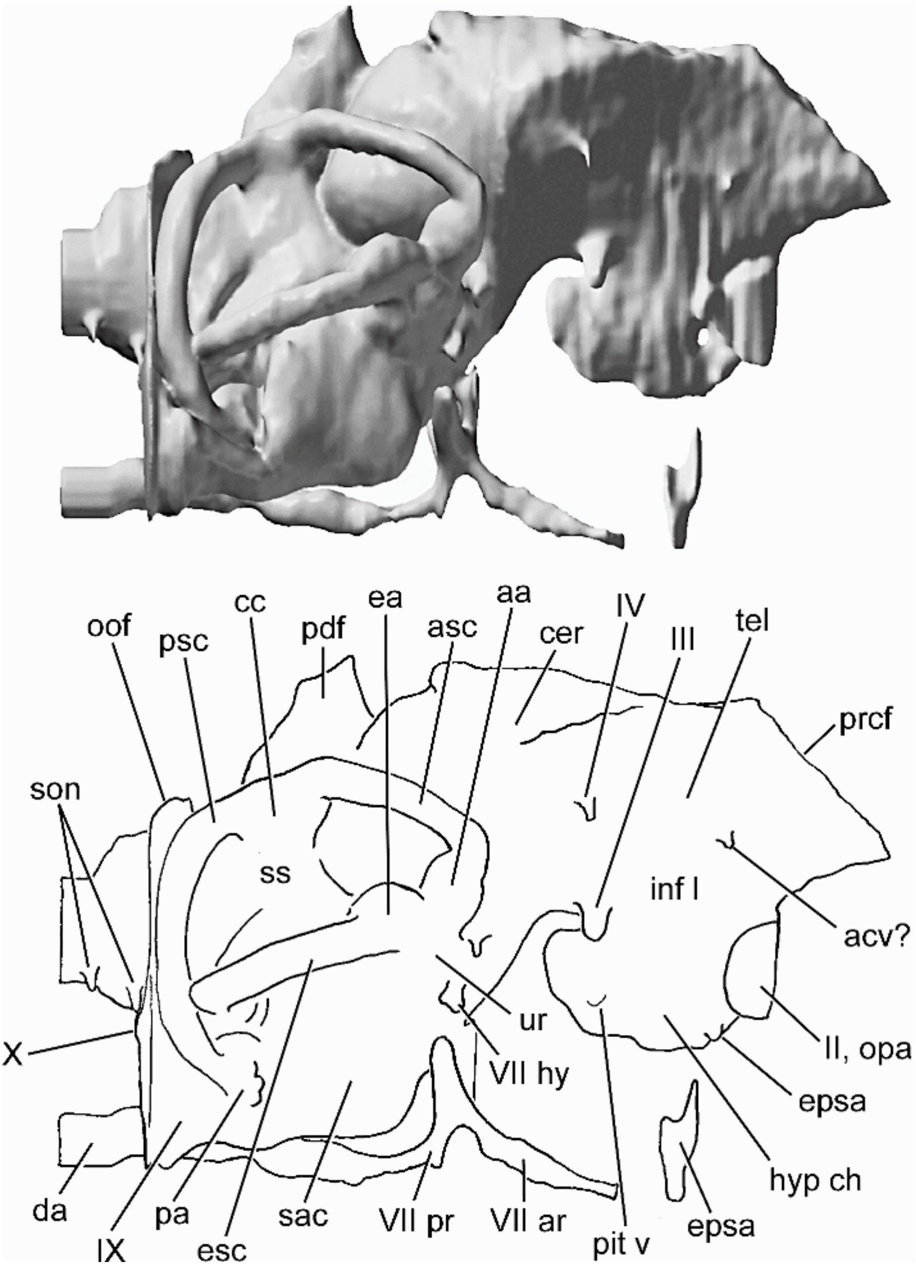

Fig. 24. FMNH PF 13242 ("*Cobelodus*"). Contour-based surface reconstruction of cranial endocast generated from CT-scan slices. Right side, with semicircular canals and ampullae.

anteriorly. The fontanelle is poorly known in other symmoriiforms although one is present in *Cobelodus aculeatus*, *Stethacanthulus meccaensis*, and *Falcatus falcatus* (Zangerl and Case, 1976: fig. 2; Williams, 1985:92; Lund, 1985a). A wide precerebral fontanelle is present in many platybasic Paleozoic sharks including *Cladodoides*, *Orthacanthus*, and *Tamiobatis* (Gross, 1937; Schaeffer, 1981; Maisey 2004a, 2004b, 2005), as well as in Mesozoic hybodonts and modern elasmobranchs.

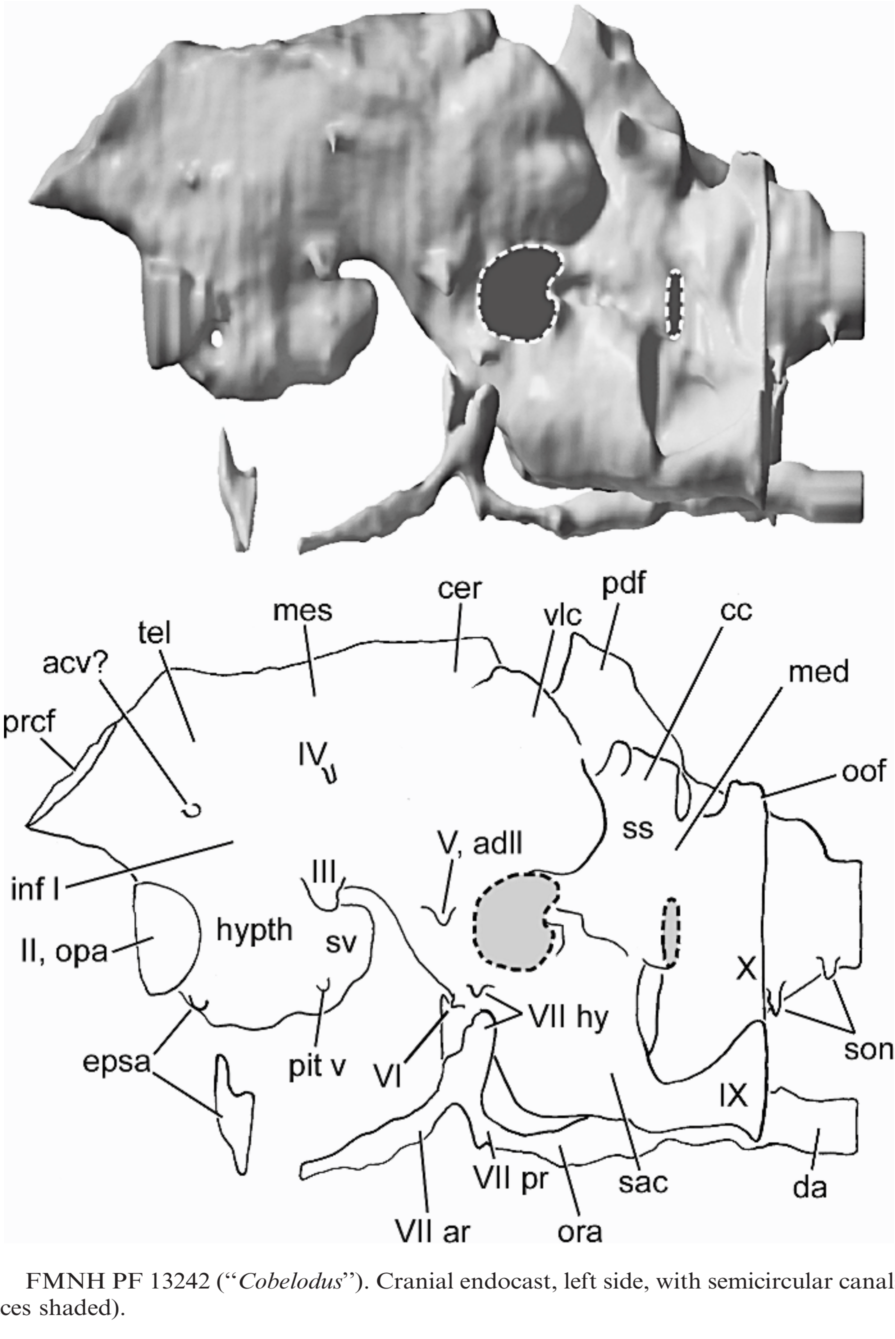

Fig. 25. FMNH PF 13242 ("*Cobelodus*"). Cranial endocast, left side, with semicircular canals removed (cut surfaces shaded).

There is no evidence of a pineal opening in "*Cobelodus*". A small median opening is present in the roof of the neurocranium in *Cladodoides*, but is too far posterior to have contained the epiphysis (Maisey, 2005: 40). A pineal opening is absent in "*Cobelodus*", *Akmonistion*, *Orthacanthus*, *Tamiobatis vetustus*, *Egertonodus*, *Tribodus*, and *Tristychius* (Dick, 1978; Schaeffer, 1981; Maisey, 1983, 2004a), but one is known in a few modern sharks (e.g., *Scymnorhinus*, *Etmopterus*; Holmgren, 1941). Although the "fronto-parietal" fontanelle in batoids lies behind the precerebral fontanelle, it represents a per-

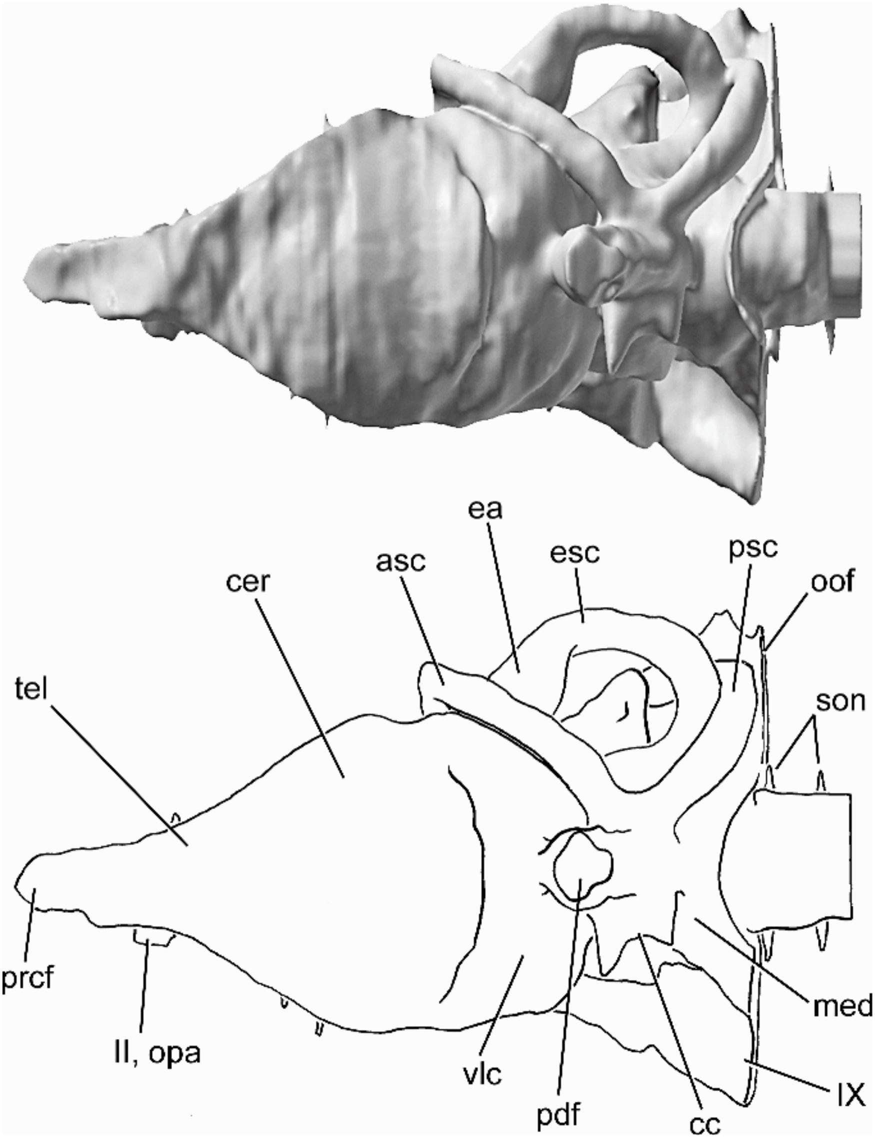

Fig. 26. FMNH PF 13242 (“*Cobelodus*”). Cranial endocast, dorsal view.

sistent unchondrified space in the braincase roof that lies between the embryonic epiphyseal bridge and synotic tectum in all elasmobranchs, and is not homologous to the epiphyseal foramen (e.g., *Etmopterus*; Holmgren, 1940: fig. 97).

The telencephalic chamber in “*Cobelodus*” is presumably short, although its precise extent is difficult to delineate because it merges posteriorly with the mesencephalic chamber and there is no constriction between them as found in some modern sharks. A presphenoid ledge is present along the inner wall of the telencephalic chamber near the anterior margin of the hypophyseal chamber (fig. 9). *Cladodoides* may also have had a weak presphenoid ledge below the optic foramen (Maisey, 2005: fig. 7). In *Orthacanthus*, the presphenoid ledge may be represented by a low ridge in the floor of the cranial cavity anterior to the hypophyseal chamber (Schaeffer, 1981: fig. 14), but in the

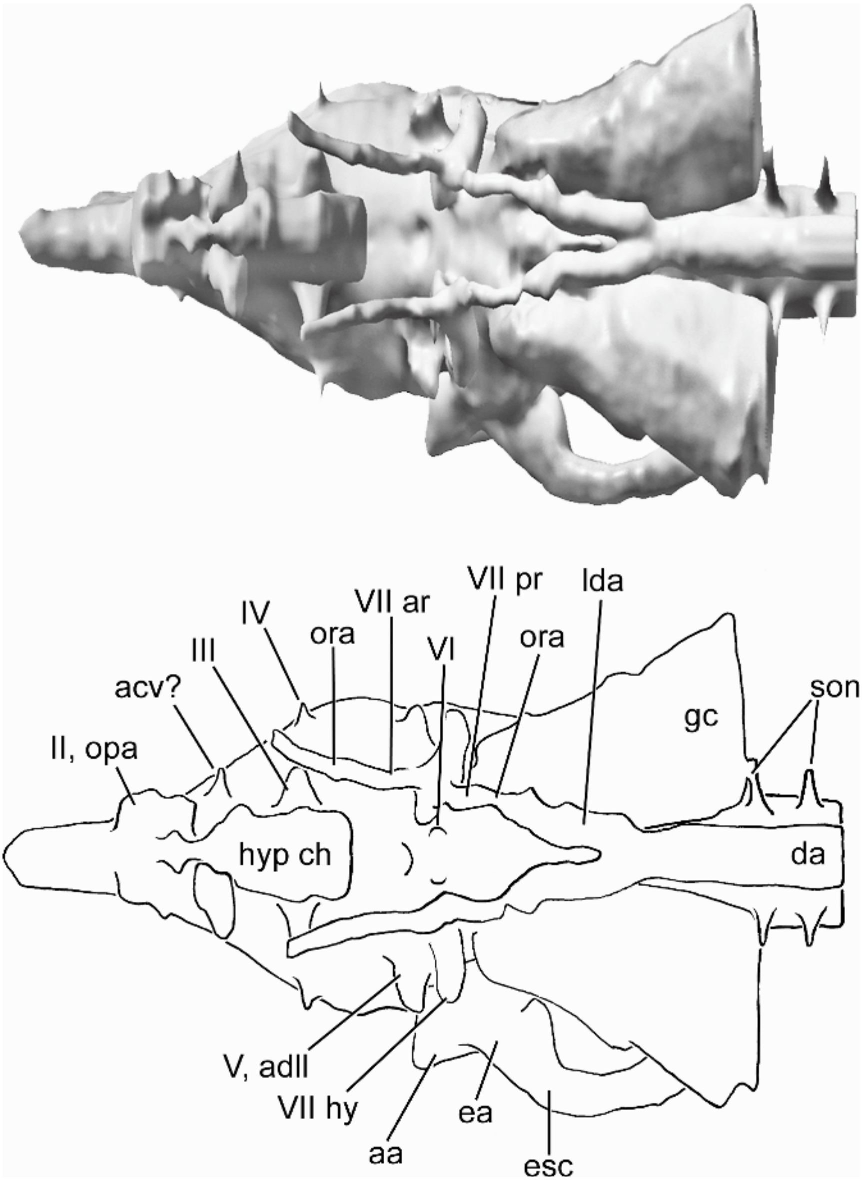

Fig. 27. FMNH PF 13242 ("*Cobelodus*"). Cranial endocast, ventral view (also shows aortic canals).

hybodont *Tribodus* this region is virtually flat and the ledge is probably absent (Maisey, 2004a: fig. 5a). A presphenoid ledge is present in some modern sharks (e.g., *Heptranchias*, *Squalus*, *Dalatias*, *Deania*, *Mustelus*; Maisey, 2004b: 42), but is absent in others. No phylogenetically consistent signal can be discerned regarding the presence/absence of the presphenoid ledge.

The configuration of nerve openings in the mesencephalic part of the endocast is similar in "*Cobelodus*" and *Cladodoides*, despite obvious differences in the associated parts of the braincase. The trochlear nerve entered the cartilage directly above the oculomotor nerve (figs. 24, 25), as in *Orthacanthus* (Maisey, 1983: fig. 13A), not anterior to it as in modern elasmobranchs and hybodonts

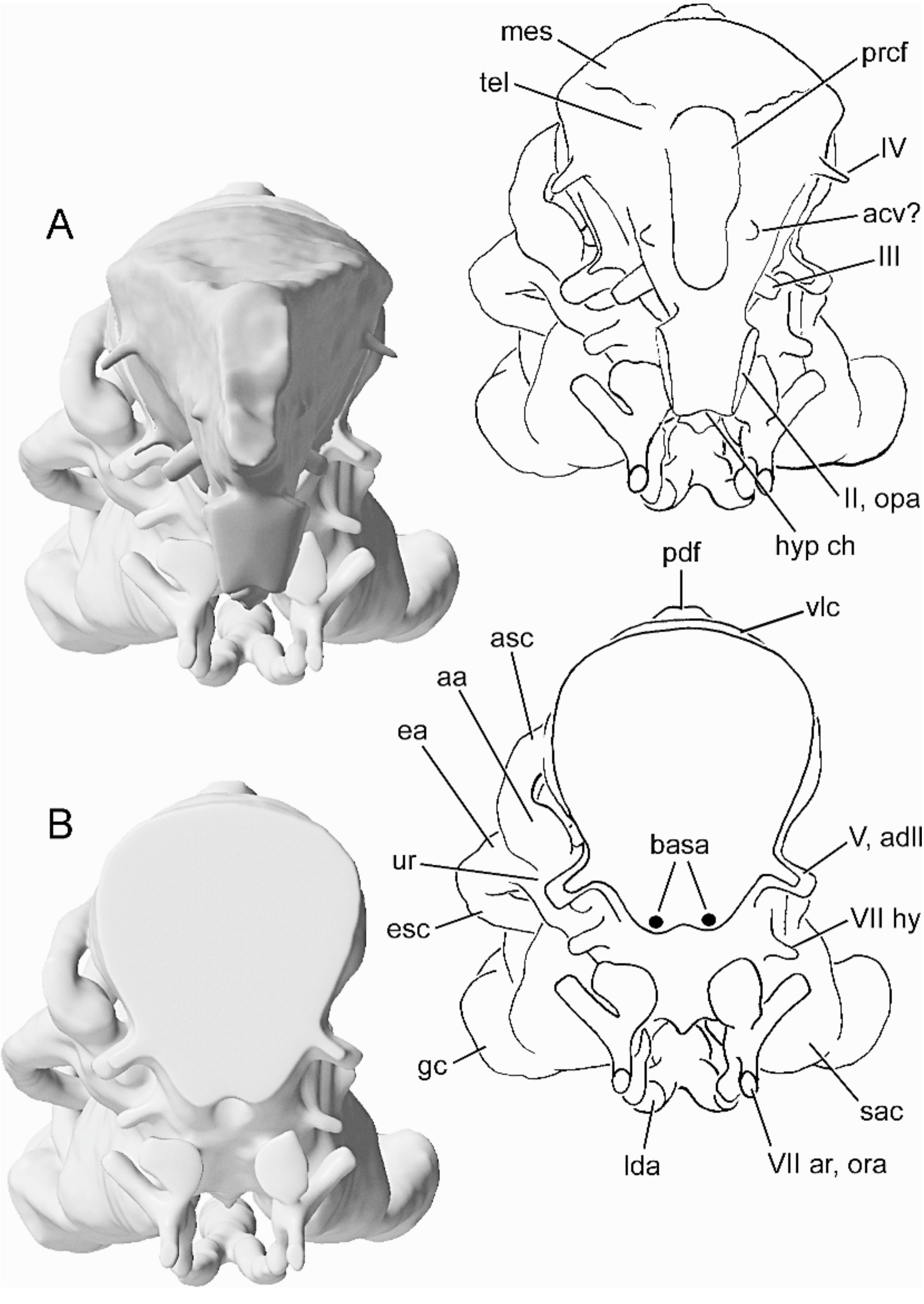

Fig. 28. FMNH PF 13242 ("*Cobelodus*"). Cranial endocast, anterior views. **A**, entire endocast; **B**, endocast with anterior half removed.

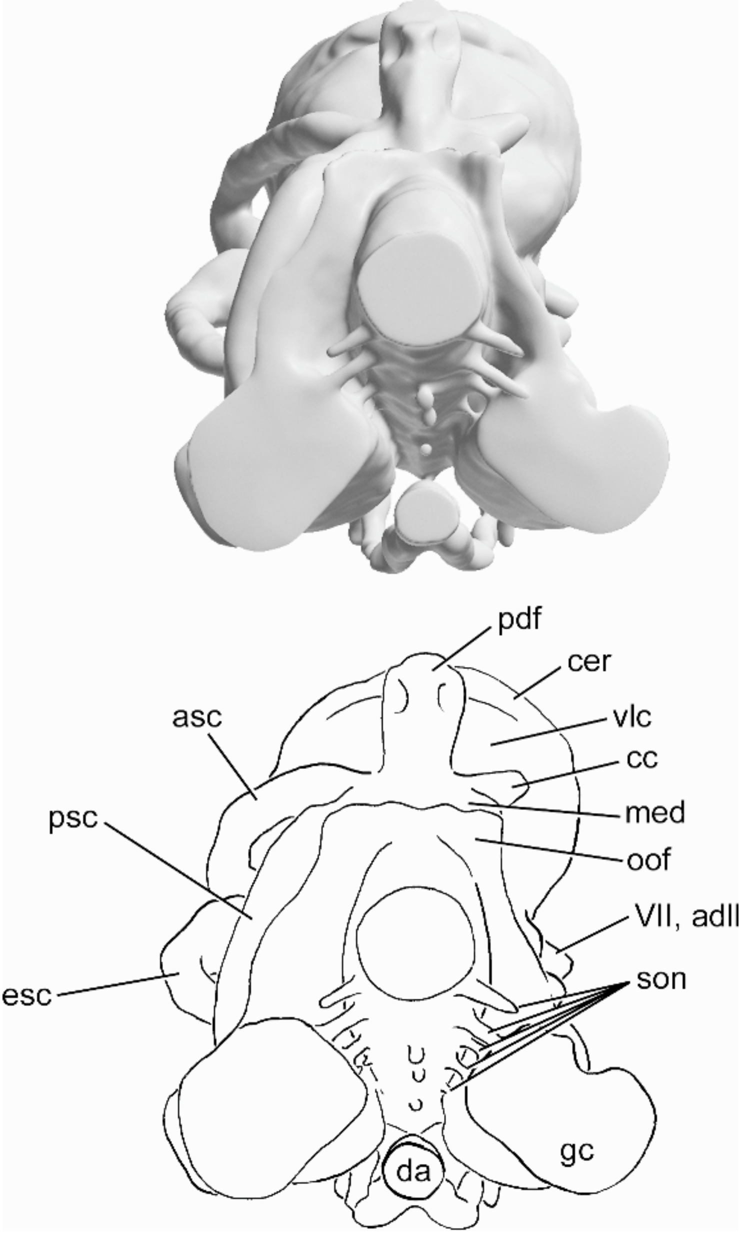

Fig. 29. FMNH PF 13242 (''*Cobelodus*''). Cranial endocast, posterior view.

(in the latter, the trochlear foramen is located even farther anteriorly; Coates and Sequeira, 1998). The trigeminal and facial nerves entered the cartilage respectively above and below the utricular recess, just above and behind the dorsum sellae (see also fig. 9).

In dorsal view, the ''*Cobelodus*'' endocast broadens sharply in the cerebellar region, but there is a distinct constriction between the posterior ends of the cerebellar chamber and the vestibulolateral (auricular chambers) located farther posteriorly (vlc, fig. 26). By contrast, in *Notorynchus* and *Cladodoides* endocasts, the cerebellar and vestibulolateral chambers are indistinct (Maisey, 2004b: fig. 7; 2005: fig. 24). Optic lobes are not evident

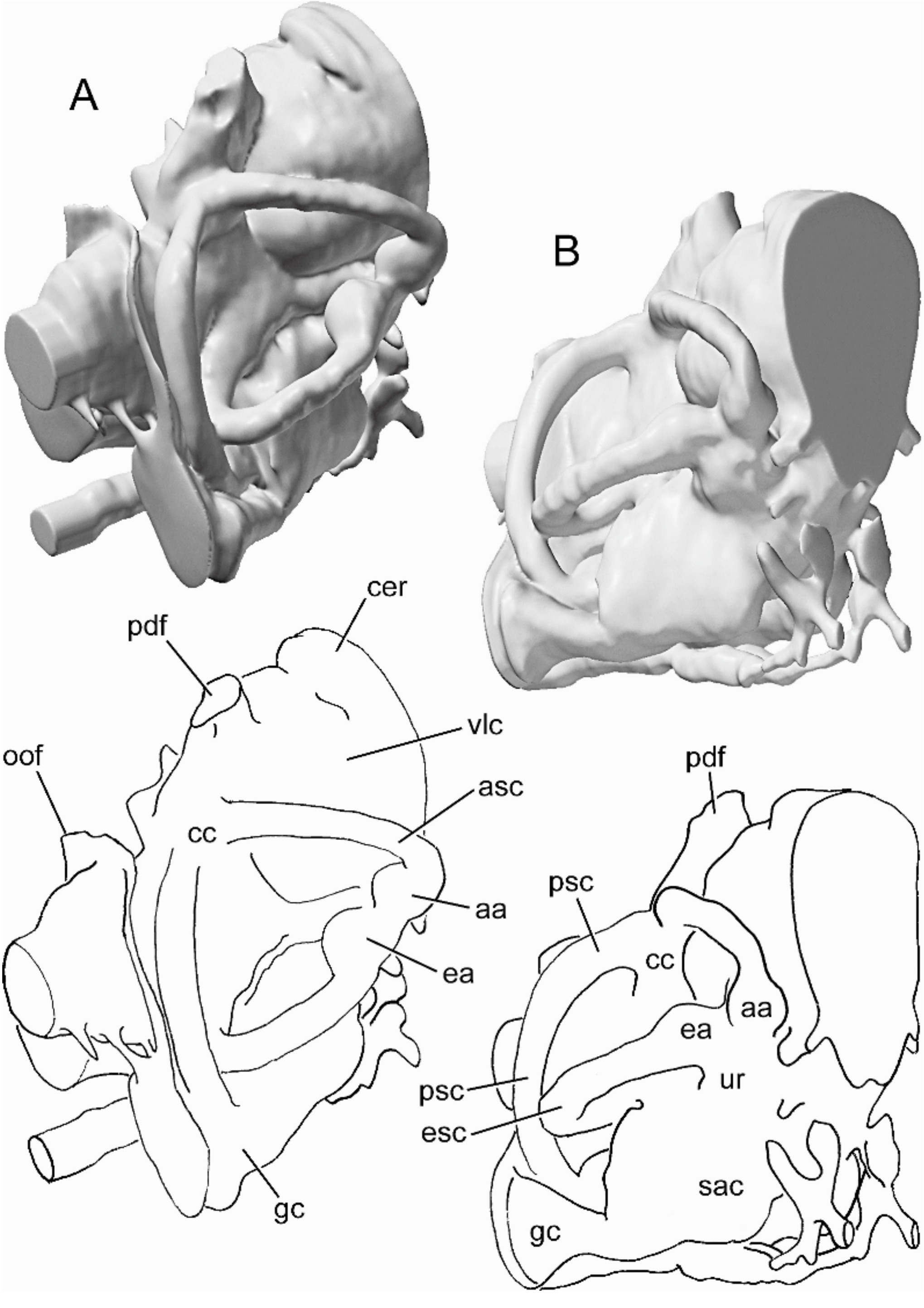

Fig. 30. FMNH PF 13242 ("*Cobelodus*"). Endocast of otico-occipital and labyrinth regions, oblique orthographic views. **A**, postero-dorsolateral view; **B**, anterolateral view.

in the "*Cobelodus*" endocast, and the mesencephalic and metencephalic regions simply merge. The crus commune (connecting the anterior and posterior semicircular canals) is confluent with the dorsolateral part of the anterior medullary region. Medial to the crus, the endocast is raised into a distinct "chimney" representing the posterior dorsal fontanelle. The anterior semicircular canals converge on the crus and each is located within a recess along the posterior margin of the vestibulolateral chamber. The medullary region can be viewed when the semicircular canals are removed, and it extends behind the otic capsules. Canals for the spino-occipital nerves are represented in the endocast by a series of short bridges between the medullary chamber and glossopharyngeal canal anteriorly, and by distinct ventrolateral projections farther posteriorly.

DIENCEPHALON AND HYPOPHYSEAL CHAMBER: The diencephalic region (including the hypophyseal chamber) in "*Cobelodus*" is as extensive as in *Cladodoides* (Maisey, 2005: fig. 23), and much larger than in modern elasmobranchs (fig. 31). However, the hypophyseal chamber is much narrower from side to side than in most platybasic sharks (probably related to the development of the interorbital septum; fig. 27), and as noted earlier it lacks any communication with the roof of the mouth. Most of the hypophyseal chamber in "*Cobelodus*" was probably filled by the hypothalamus, except for small regions for the saccus vasculosus (posteriorly) and the pituitary gland (ventrally).

Immediately behind the hypophyseal chamber, the floor of the cranial cavity is formed by the sloping upper surface of the dorsum sellae. This surface forms a low median ridge, which is represented in the endocast by a distinct concavity visible in ventral view (fig. 27) and in anterior view after the ethmoidal region is digitally removed (fig. 28B). In modern elasmobranchs, the basilar artery is paired as it loops around either side of the hypothalamus, but the branches merge into a single median vessel that traverses the dorsum sellae behind the hypophyseal chamber. Since the basilar artery presumably followed a similar path in "*Cobelodus*", the median ridge may therefore represent the point at which the paired arteries merged (suggested in figure 28B; ba).

The hypothalamus (forming the walls and floor of the third ventricle of the brain) is a prominent feature of the diencephalon in modern elasmobranchs, in which it is located below the posterior commissure of the brain at the base of the optic lobe and beneath the level of the cerebellum (e.g., *Notorynchus*; fig. 31C). In *Orthacanthus* (Schaeffer, 1981: fig. 14) and hybodonts (e.g., *Tribodus*; Maisey, 2004a: fig. 5), the cerebellar and hypophyseal chambers lie one above the other, suggesting that the hypothalamus lay below the cerebellum as in modern elasmobranchs. In "*Cobelodus*" and *Cladodoides*, however, the hypophyseal chamber is located completely anterior to the level of the chamber housing the cerebellum (fig. 31A, B). In modern elasmobranchs, the polar cartilage forms the side walls of the hypophyseal chamber and meets the acrochordal or parachordal posteriorly (Holmgren, 1940; El-Toubi, 1949). Hypertrophy of the polar cartilage in "*Cobelodus*" and *Cladodoides* probably led to the anterior displacement of the hypophyseal chamber and adjacent parts of the cranial wall, as well as to enlargement of the dorsum sellae. By contrast, *Orthacanthus* does not have a deep dorsum sellae and there is no evidence of an enlarged polar cartilage, despite the general similarity of its neurocranium to those of *Cladodoides* and *Tamiobatis* (Schaeffer, 1981).

If the architecture of the cranial endocast in "*Cobelodus*" reflects the morphology of the brain, however, this explanation alone is insufficient, since the hypothalamus is also anterior to the level of the cerebellum in lampreys and osteichthyans (where the polar cartilage is absent or small). The cranial endocasts of "*Cobelodus*" and *Cladodoides* suggest that the ventral part of the brain was organized somewhat differently from modern elasmobranchs, so that the tegmentum was elongated above the dorsum sellae and the hypothalamus was displaced anteriorly. The mesencephalon is generally straighter in modern lampreys and osteichthyans than in modern elasmobranchs, where it is folded into a tight "S" around the posterior commissure of the brain. A comparatively straight mesencephalon is also inferred from the shape of

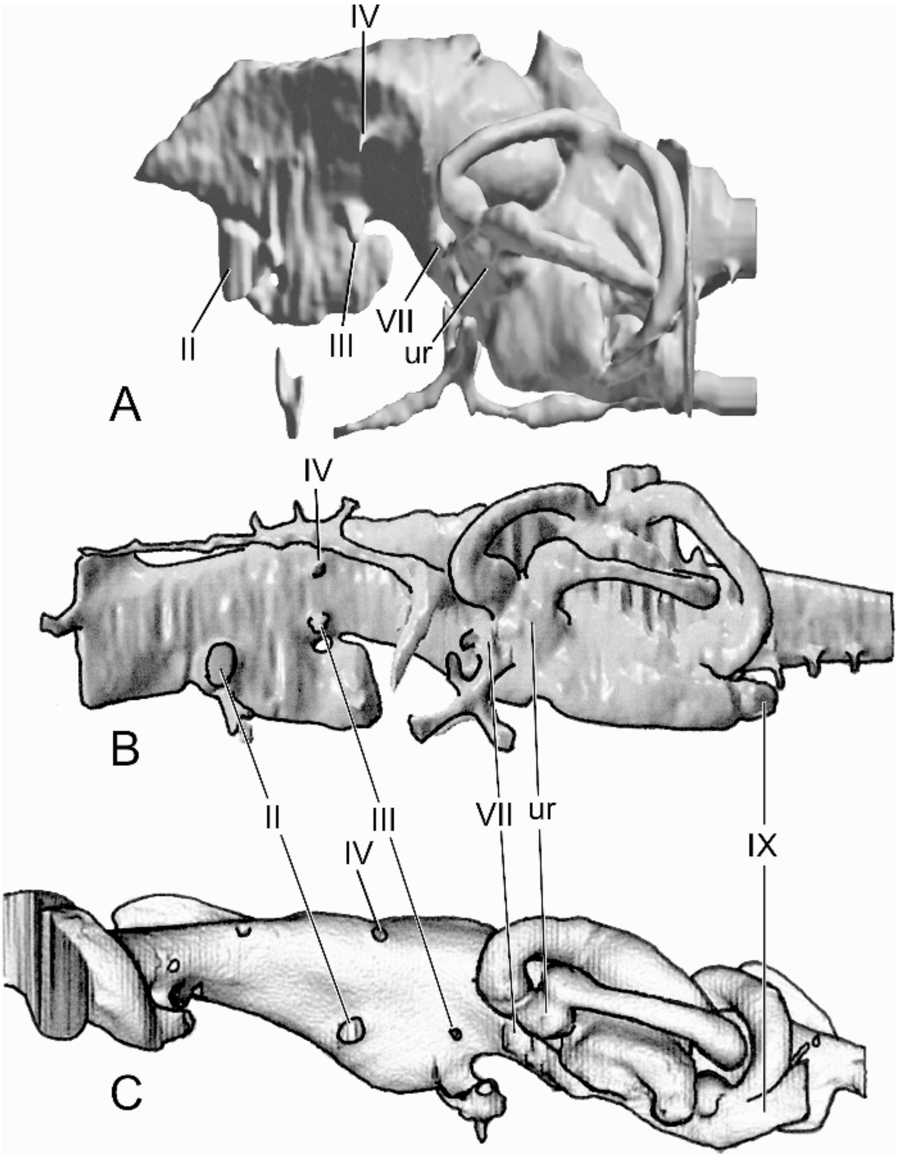

Fig. 31. Left lateral view of cranial endocast in: **A**, "*Cobelodus*"(extinct tropibasic shark braincase); **B**, *Cladodoides* (extinct platybasic shark braincase); **C**, *Notorynchus* (modern platybasic shark braincase). Views are aligned at the level of the utricular recess. Note the relatively anterior position of the hypophyseal chamber and nearby nerve foramina relative to the otic capsule and the trochlear foramen in "*Cobelodus*" and *Cladodoides*, implying elongation of the tegmentum and anterior displacement of the hypothalamus in the brain. This may have been correlated developmentally to hypertrophy of the polar cartilage, since it occurs in both tropibasic and platybasic forms. Not to scale.

the endocast in *Cladodoides* and "*Cobelodus*" (fig. 31). Presence of a tight "S" in the mesencephalon around the posterior commissure is a potentially apomorphic character of modern elasmobranchs that may be shared with hybodonts and xenacanths.

The bucco-hypophyseal chamber is very deep in Dalatiiformes with an exaggerated basal angle (e.g., *Trigonognathus*), but unlike in "*Cobelodus*" the chamber has retained its primitive connection with the roof of the mouth. The walls of the chamber contain foramina for the efferent pseudobranchial and internal carotid arteries, which presumably unite before supplying the brain as in other modern elasmobranchs.

LABYRINTH ENDOCAST: Certain features of the labyrinth region are best viewed in oblique views (fig. 30). The labyrinth displays the general gnathostome arrangement, including anterior, posterior, and external (horizontal) semicircular canals and their ampullae, and a large vestibular chamber ventrally. As in *Cladodoides*, the medial part of the vestibular region is not separated from the cranial cavity in the endocast, suggesting that there was no cartilaginous medial capsular wall (unlike in modern elasmobranchs and in placoderms). The external (horizontal) semicircular canal lay within the capsular wall just beneath the lateral otic ridge and was overlain by the periotic process as described earlier. The external and anterior ampullae only just meet each other and probably had separate openings into the utricular recess. The latter is represented by a low bulge on the lateral part of the endocast, but is less distinct than in *Cladodoides*. A wide connection between the cranial cavity and labyrinth presumably housed the octaval nerve, but there is no evidence of a narrow octaval nerve canal like that found in *Cladodoides*, (Maisey, 2005: fig. 18E). The recess for the octaval canal reported in *Cobelodus aculeatus* by Zangerl and Case (1976: figs. 8, 9) opens into the utricular recess, and therefore corresponds to the wide opening for this nerve in "*Cobelodus*".

The posterior semicircular canal in "*Cobelodus*" passes close to the anterior face of the otico-occipital fissure (seen as a continuous wall in the endocast). Its ampulla is confluent with the vestibular chamber, and there is no evidence of a preampullary extension of the canal. The vestibular chamber is not clearly divided into utricular and saccular chambers (apart from the utricular recess). As in *Cladodoides*, the anterior and posterior ampullae in "*Cobelodus*" lie approximately the same distance from the midline (in modern elasmobranchs and hybodonts, the posterior ampulla is closer to the midline; Maisey, 2005). The external semicircular canal in "*Cobelodus*" turns inside the loop of the posterior canal before it merges with the endocast (as in gnathostomes generally), but the two canals approach each other more closely than in *Cladodoides* (Maisey, 2005: fig. 23). The orientation of the labyrinth in these taxa is also different (relative to the anteroposterior axis of the braincase). This is best illustrated by comparing the angular relationship of the plane containing the external semicircular canal to a longitudinal axis drawn through the occipital region (fig. 32). In "*Cobelodus*", this plane is tilted upward anteriorly and intersects the axis approximately at the level of the external ampulla, but in *Cladodoides*, the plane intersects the corresponding axis only behind the occipital region. Furthermore, in "*Cobelodus*", the external semicircular canal lies mostly below the level of the axis whereas in *Cladodoides* it lies mostly above the axis. However, the posterior ampulla lies below the axis in both forms, while the anterior and external ampullae lie approximately lateral to it. Since this axis corresponds to the principal axis of the vertebral column (and therefore the principal axis of thrust), its consistent orientation with respect to the ampullae suggests an important biomechanical relationship between them.

These illustrations also show that the floor of the vestibular chamber and the glossopharyngeal canal in "*Cobelodus*" extends much farther ventrally than the hypophyseal chamber (the posterior view of the endocast also shows the vestibular chamber extending below the level of the medullary region; fig. 29). Elevation of the hypophyseal chamber relative to other structures is undoubtedly related to reorientation of the entire cranial cavity associated with the formation of a deep interorbital septum. The vestibular chamber and glossopharyngeal canal also extend below the level of the medullary chamber in *Cladodoides*, but not to the same extent as in "*Cobelodus*". By contrast, in *Notorynchus* and *Squalus*, the plane of the external semicircular canal is almost parallel to the braincase long axis, the hypophyseal chamber extends farthest ventrally, and the vestibular region extends only slightly below the

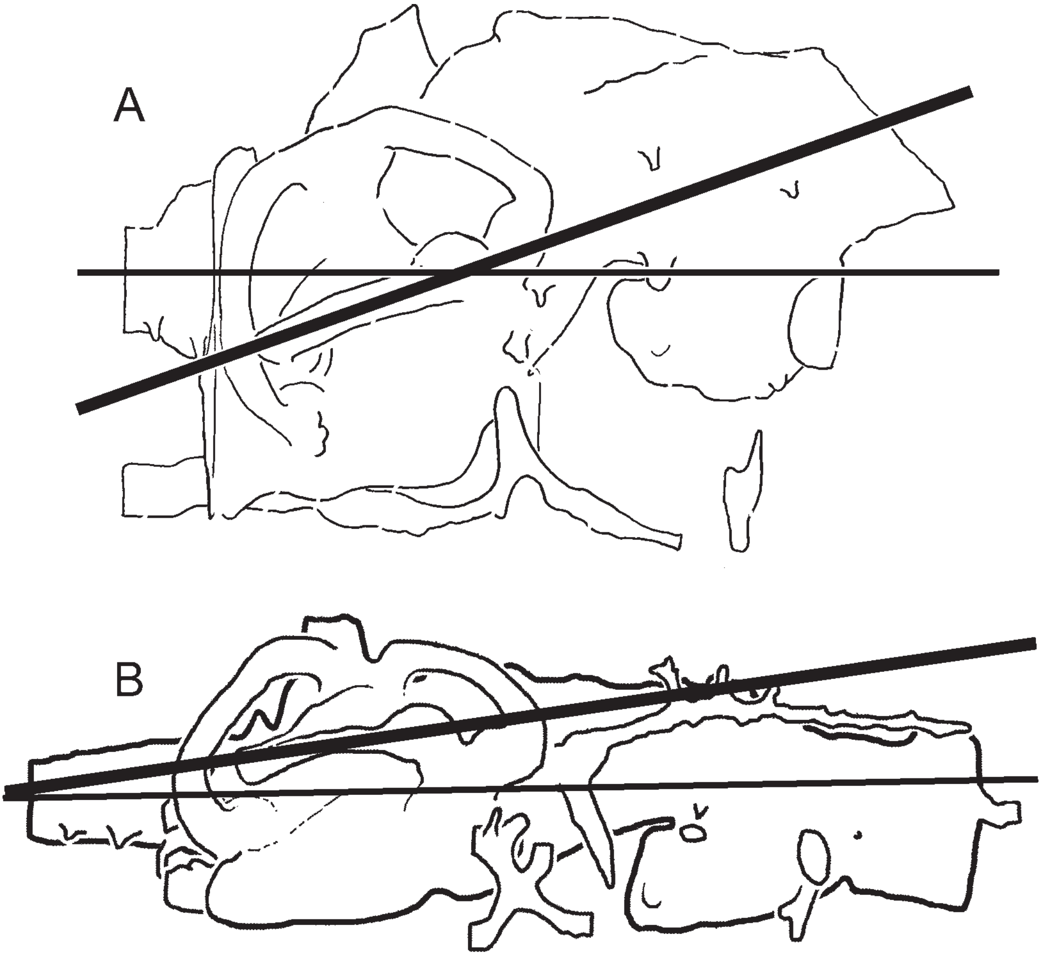

Fig. 32. Lateral view of the endocast in "*Cobelodus*" (**A**) and *Cladodoides* (**B**), showing different angular relationships of the plane containing the external semicircular canal (heavy line) to the endocast long axis (thinner line). Not to scale.

floor of the medullary region. The semicircular canals in both "*Cobelodus*" and *Cladodoides* are slender, which may be correlated with a high turning speed as in *Squalus* (Young, 1981).

Despite these unusual features, the vestibular apparatus in "*Cobelodus*" and *Cladodoides* conforms to the conserved crown-group gnathostome pattern seen in modern chimaeroids and osteichthyans (Maisey, 2005: 86). In particular, there is no evidence of the specializations toward low-frequency phonoreception found in modern elasmobranchs (for details, see Maisey, 2001b).

OTHER SYMMORIIFORM REMAINS FROM ARKANSAS

MATERIAL EXAMINED: OUZC 5300–5305, articulated symmoriiform heads, all with braincase, visceral skeleton, and pectoral girdle, somewhat compressed laterally and obliquely, Fayetteville Formation (lower shale member), Chesterian, Upper Pennsylvanian, outcrops in the bed of Trace Creek, Leslie 7½ ft Quadrangle, Arkansas.

GENERAL REMARKS: These articulated symmoriiform specimens from the Fayetteville Shale of Arkansas (Desmoisnian, late

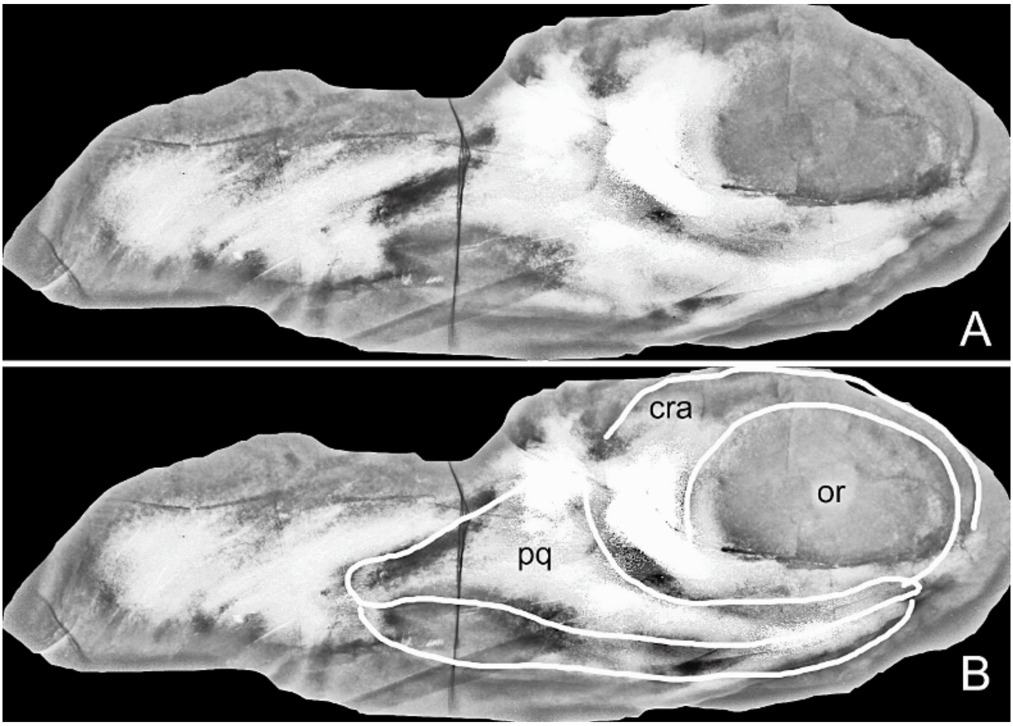

Fig. 33. **A**, X-ray of the head in a Pennsylvanian symmoriiform (possibly the same taxon represented by the "*Cobelodus*" braincase), from the Fayetteville Shale of Arkansas, OUZC 5300. **B**, same with orbit, palatoquadrate, and Meckel's cartilage outlined in white. Anterior to right.

Pennsylvanian) possess teeth that are very similar to those of *Stethacanthus* and *Akmonistion*, and the median cusp is as slender as in *Stethacanthus* described from the Sunbury Shale (Williams, 1985). The head of some specimens is covered by "*Lambdodus*" denticles like those described in *Stethacanthus altonensis* and *Akmonistion zangerli* (e.g., Williams, 1985: pl. 15, fig. 2; Coates and Sequeira, 2001a: fig. 13). However, none of the Fayetteville Shale specimens is associated with a dorsal spine, and so far no isolated "stethacanthid" spines have been reported from these deposits. The Fayetteville Shale material (much of which is still unprepared) will be left in open nomenclature until a more detailed investigation can be completed.

DESCRIPTION: In several of the Fayetteville Shale specimens, the braincase and visceral skeleton is preserved intact and all the major elements are still articulated. Although the specimens are all obliquely compressed and slightly flattened, they have suffered much less compaction than coeval fossils from the Pennsylvanian black shales of Indiana. The Arkansas material is still being investigated at the time of writing and only a few observations are presented here.

X-rays of these specimens show an extremely large orbit and a palatoquadrate with a very deep otic process and a comparatively slender tooth-bearing palatine ramus (e.g., OUZC 5300, 5301; figs. 33, 34). Furthermore, CT-scanning provides strong evidence that the braincase in these sharks is tropibasic, revealing the presence of a slender interorbital septum between the cranial cavity and suborbital shelf (e.g., OUZC 5300; fig. 35). As far as can be determined, the cranial morphology of the Fayetteville material resembles that in "*Cobelodus*" (it is even possible that the "*Cobelodus*" braincase and the Fayetteville Shale "*Stethacanthus*" specimens represent the same species, since they all come from the same stratigraphic unit and general collecting area). These articulated

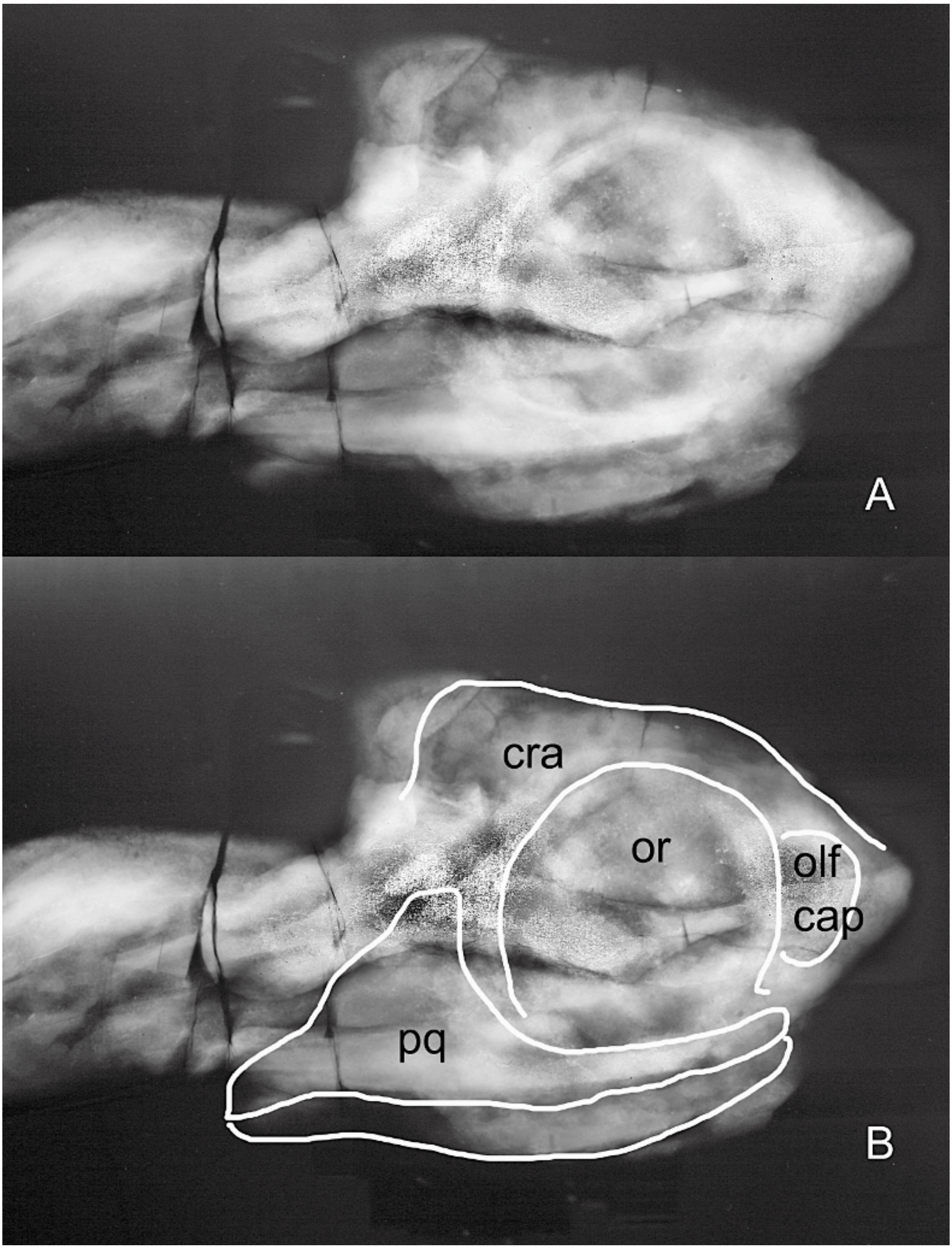

Fig. 34. **A**, X-ray of the head in a Pennsylvanian symmoriiform from the Fayetteville Shale of Arkansas, OUZC 5301. **B**, Same with orbit, palatoquadrate, and Meckel's cartilage outlined in white. Anterior to right. Large opaque structure running across the orbit is the palatoquadrate of the opposite side.

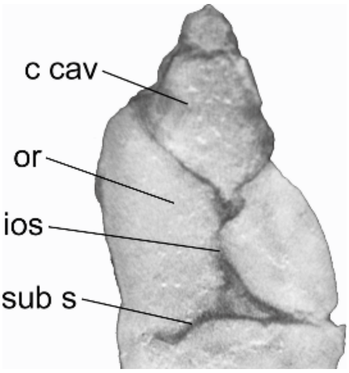

Fig. 35. Transverse CT-scan slice 395 through the midorbital region of the head in a Pennsylvanian symmoriiform from the Fayetteville Shale of Arkansas, OUZC 5300. Note the presence of a thin but continuous interorbital septum between the cranial cavity and the suborbital shelf.

remains from Arkansas are therefore important, because they provide the first conclusive evidence of a tropibasic braincase in a shark with *Stethacanthus*-like teeth.

VIRGILIAN SYMMORIIFORM BRAINCASE

MATERIAL EXAMINED: OUZC 5204, an isolated and incomplete but three-dimensional symmoriiform braincase including parts of the cranial endocast and chondrocranium, Graham Formation, Finis Shale Member (Upper Mississippian, Virgilian), New Jacksboro Lake Spillway, Texas. Collected by Dr. Royal Mapes (Ohio State University). This locality has also produced numerous well-preserved specimens of actinopterygian braincases similar to those described by Watson (1925) and Poplin (1974) from the Carboniferous of Kansas.

DESCRIPTION: The specimen consists mostly of the cranial endocast to which pieces of the chondrocranial walls are still attached (fig. 36). Unfortunately, no associated teeth or other dermal elements are available to aid in its identification. Its salient morphological features are nevertheless remarkably similar to those of "*Cobelodus*", suggesting that it also came from a symmoriiform shark.

Similarities with "*Cobelodus*" include: the medullary region is aligned below the level of the mesencephalic and telencephalic regions farther anteriorly, and the floor of the diencephalic region slopes steeply upward anteriorly; the occipital fovea and the foramen magnum are approximately equal in width; dorsal and ventral paroccipital processes are present adjacent to the occipital fovea; a median aortic canal is present below the fovea; the posterior dorsal fontanelle is very small, triangular in dorsal view and widest anteriorly, and is widely separated from the otico-occipital fissure by a long posterior tectum; there is a crus commune behind the posterior dorsal fontanelle; the dorsal otic ridge is weak, and runs just above the upper part of the anterior semicicular canal; the glossopharyngeal canal is wide and rounded, with no lateral otic fissure; and the plane containing the external semicircular canal (which admittedly can be estimated only from the position of its broken extremities) intersects an axis through the medullary region at the approximate level of the utricular recess rather than behind the occiput as in *Cladodoides*.

Differences from "*Cobelodus*" include: the capsular wall is much thinner around the posterior semicircular canal, which is consequently recessed into the vestibular wall (in "*Cobelodus*", the endocast of the canal is widely separated from the vestibular chamber); the outer wall of the cranial vestibulolateral chamber is much thinner, and the anterior semicircular canal is recessed deeply into its surface (in "*Cobelodus*", the canal is separated by a space from the vestibulolateral chamber); the mesencephalic and telencephalic region does not taper anteriorly to the extent that it does in "*Cobelodus*"; the margins of the posterior dorsal fontanelle are not raised into a "chimney"; and only one pair of occipitospinal foramina can be observed on the outer surface of the occipital arch between the foramen magnum and the glossopharyngeal canal.

Some features cannot be compared in "*Cobelodus*" and OUXC 5204, including: the ethmoid region (not preserved in either specimen); the interorbital septum and suborbital region (not preserved in OUZC 5204); the dorsum sellae (although from the shape of the diencephalic chamber floor in OUZC 5204, the dorsum sellae was probably as deep as in "*Cobelodus*"); and features of the lateral capsular walls (e.g., lateral otic ridge, periotic process, lateral otic process; not preserved in OUZC 5204).

It is concluded that OUZC 5204 belongs to a tropibasic symmoriiform shark and therefore represents an incertae sedis member of the Order Symmoriiformes. It is morphologically similar to "*Cobelodus*" although it considerably older and possibly represents a different genus.

COBELODUS ACULEATUS (Cope, 1894)

Material Examined: Holotype FMNH UF576, partial skeleton with most of chondrocranium, jaws, pectoral girdle, and anterior part of vertebral column, plus X-rays (prepared by R. Zangerl); Court Creek, NE of Knoxville, Illinois; Mecca Quarry Shale, Liverpool cyclothem, Des Moines series, Westphalian Upper C, Pennsylvanian. Collected by F.R. Jelliffe, described by Cope (1894) and by Zangerl and Case (1976); FMNH PF3090, anterior portion of articulated skeleton in calcareous concretion, with partially exposed three-dimensional chondrocranium, silicone endocast of chondrocranium, plus X-rays; Hesler Quarry, Wabash Township, Parke County, Indiana (field number HQ 77); probably from the Velpen Limestone above the Mecca Quarry Shale, Westphalian (uncertain stratigraphic level), Pennsylvanian; FMNH PF7324, flattened chondrocranium associated with parts of vertebral column; FMNH PF7345, flattened chondrocranium and visceral arch elements; FMNH PF8011, gastric residue mass with chondrocranium and teeth, plus "Smoothon" peels and X-rays of all specimens; City Wide Rock and Excavation Co. (Hansen Quarry, Quarry 6), on route 370 between Papillion and Bellevue, Sarpy County, Nebraska; Wea Shale, Westerville formation, Kansas City group, Missourian, Westphalian D, Pennsylvanian; FMNH PF7347, excellent partially disarticulated skeleton (male individual according to Zangerl and Case, 1976), plus "Smoothon" peel and X-rays of chondrocranium; Logan Quarry, Parke County, Indiana (Zangerl and Richardson, 1963); Logan Quarry Shale, Lower Wiley cyclothem (Staunton formation), Des Moines Series, Westphalian Upper C, Pennsylvanian; FMNH PF7472, isolated chondrocranium plus "Smoothon" peel and X-ray; City Wide Rock and Excavation Co. (Iske quarry), River Road from Offutt Airbase, La Platte, Sarpy County, Nebraska; Wea Shale, Westerville formation, Kansas City group, Missourian, Westphalian D, Pennsylvanian. "Smoothon" peels were coated with black graphite and whitened with ammonium chloride to improve resolution.

General Remarks: The genus *Cobelodus* was erected by Zangerl (1973) to distinguish *Styptobasis aculeata* Cope, 1894 from the type species *S. knightiana* Cope, 1891 (for an account of the systematic history, see Zangerl and Case, 1976: 108). The genus was differentiated from other symmoriiforms chiefly on the basis of its distinctive dentition with numerous rows of minute teeth, and supposedly by unusual fanglike upper teeth with very small bases and simple pulp cavities. However, these "upper teeth" are not found associated with the palatoquadrates, and more likely represent dermal denticles from the head (M. Ginter, personal commun., 2006) *Cobelodus aculeatus* is the type species of the genus and is known principally from the Pennsylvanian (Westphalian and Stephanian) black shales of Illinois and Nebraska, although a partial skeleton from the Wild Cow Formation (Madera Group, late Missourian or early Virgilian) of New Mexico has been referred to the same species (Zidek, 1992; see below).

The braincase of *Cobelodus aculeatus* was described by Zangerl and Case (1976), based mainly on numerous compression fossils which were studied from X-rays and silicone peels, supplemented by data provided by a single three-dimensional endocast preserved in a concretion. Unfortunately, the cranial anatomy described in that work is so much at variance with the present findings in "*Cobelodus*" that a revision is clearly necessary (particularly since Zangerl firmly believed that these fossils were congeneric; various personal communications with the author). The material collected by him and now deposited in the Field Museum (including his extensive archive of X-ray plates) was therefore examined in order to compare the cranial morphology of *C. aculeatus* and

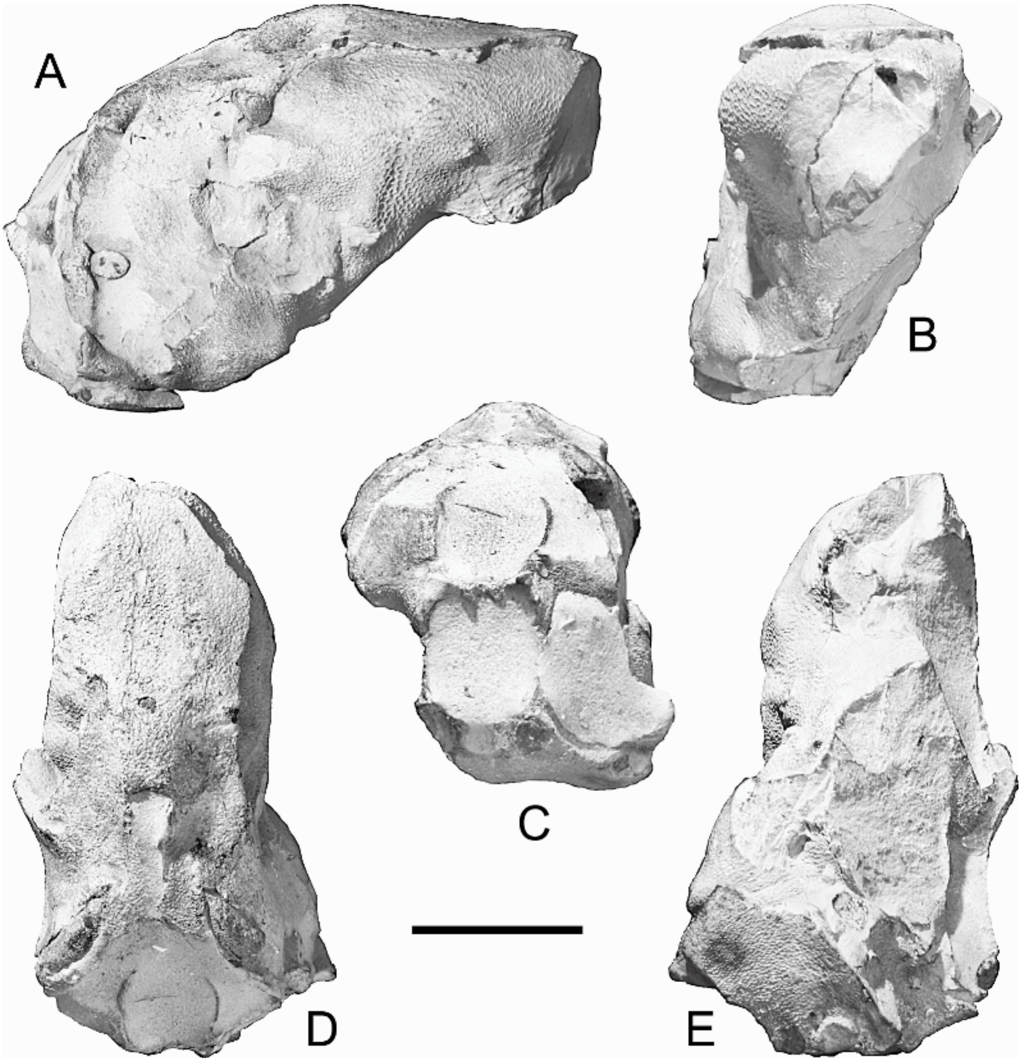

Fig. 36. Virgilian symmoriiform braincase from Texas, OUZC 5204. **A**, lateral view of right side; **B**, anterior view; **C**, posterior view; **D**, dorsal view; **E**, ventral view. Scale bar = 10 mm.

"*Cobelodus*". The material listed above represents only the most informative specimens forming the basis of the present description.

One of Zangerl's specimens (FMNH PF 3090) is uniquely preserved inside a concretion and includes parts of an uncrushed neurocranium, whose endocast has been partially excavated (Zangerl and Case, 1976: figs. 7–10). That specimen is more readily compared with the "*Cobelodus*" braincase than the almost flat compression fossils.

CONCRETION SPECIMEN: According to Zangerl and Case (1976: 120), the three-dimensional concretion specimen FMNH PF 3090 was discovered only after they had reconstructed the braincase of *Cobelodus aculeatus* from stereo X-rays of compression fossils. Although they attempted to incorporate new information provided by that specimen into their reconstruction, it is clear in hindsight that they made two crucial errors in their final version: first, they assumed that the braincase was morphologically platybasic (as in all elasmobranchs known at that time); and second, they concluded that the three-dimensional endocast had been split open along the

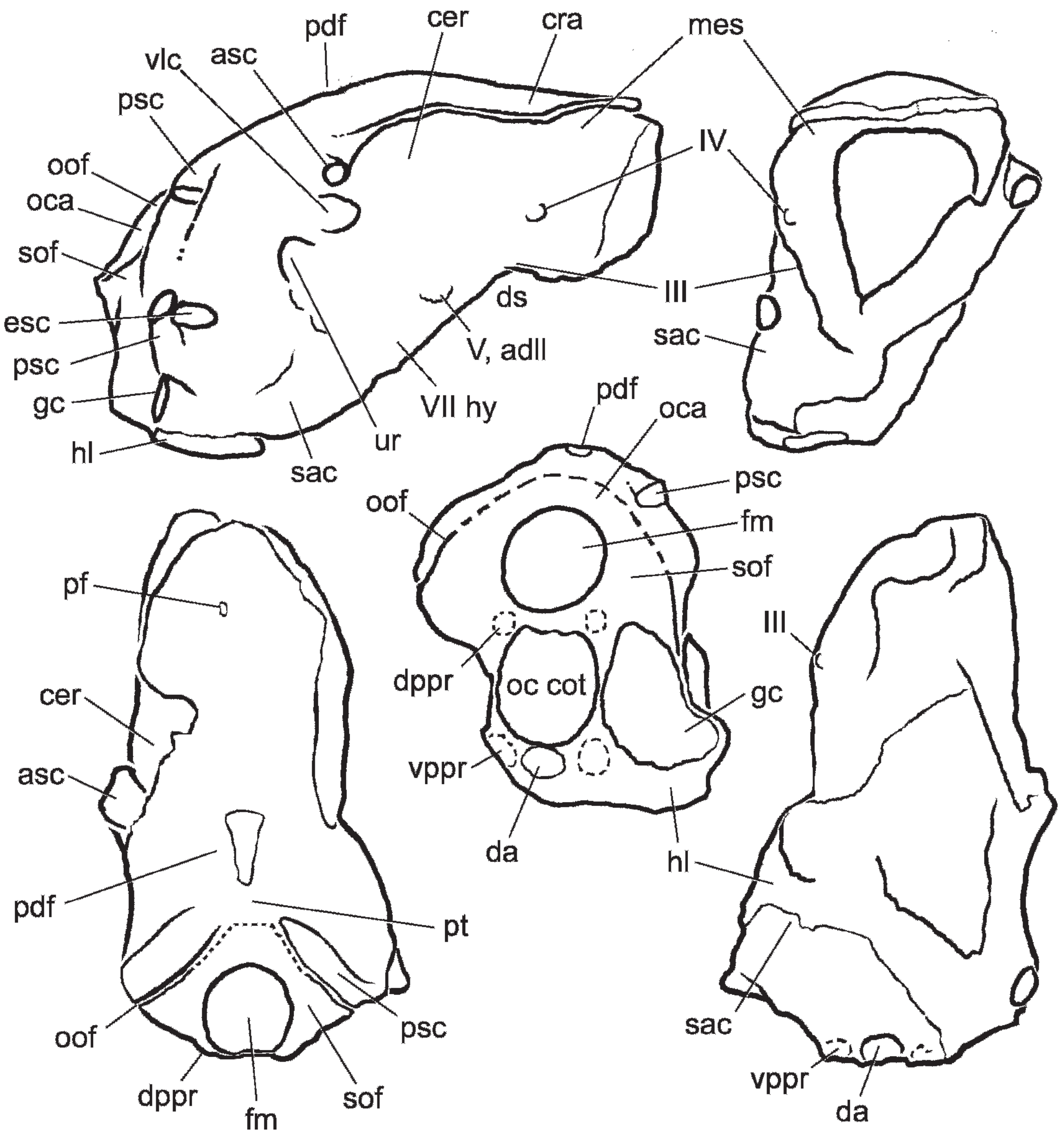

Fig. 36. Continued.

sagittal plane and did not show any left-right symmetrical features (Zangerl and Case, 1976: 125). In consequence, they effectively tried to fit a quart into a pint pot by reconstructing the endocast between the orbits and by doubling the number of structures, especially in the otic region (fig. 37). In addition, some features were misidentified in the original description, and several others were left without explanation. A new silicone endocast prepared from FMNH PF 3090 provided the basis for a comprehensive revision in which many previously unidentified structures and several bilaterally symmetrical features are recognized.

Once the cranial endocast is oriented correctly, its morphology is more readily established (fig. 38). In many respects, it is remarkably similar to the digitally generated endocast of "*Cobelodus*" and to the Virgilian

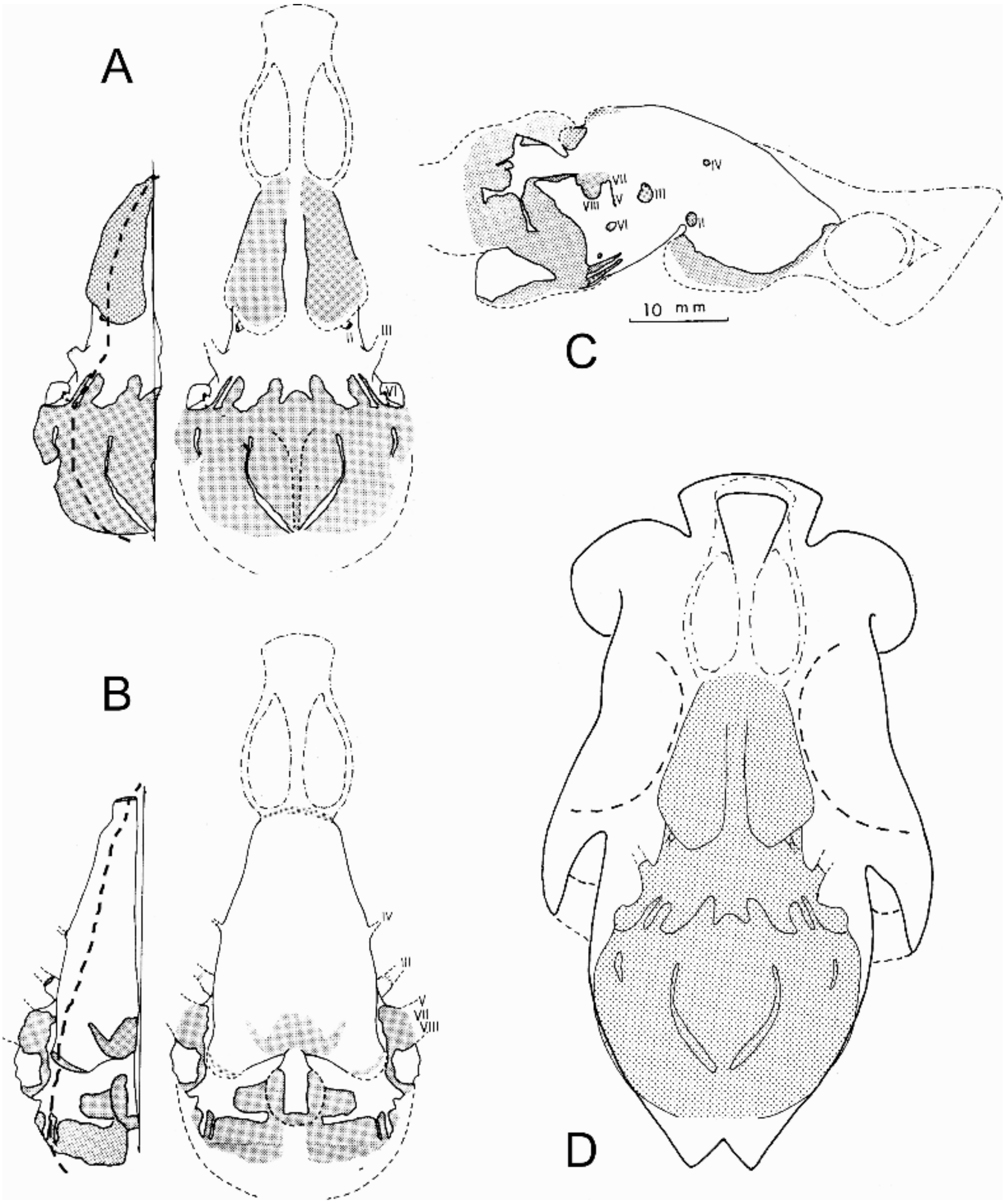

Fig. 37. Original reconstructions of the neurocranium in *Cobelodus aculeatus*, after Zangerl and Case (1976: figs. 7, 10). **A**, ventral reconstruction of endocast in FMNH PF 3090; **B**, dorsal reconstruction of endocast; **C**, lateral view of the endocast, with nerve canals identified; **D**, dorsal outline of the braincase with the endocast inexplicably shown in ventral view, and positioned completely between the orbits as in a platybasic braincase. Once the midline of the endocast is recognized (indicated here by heavy dashed lines added to the original reconstructions in A and B), the doubling-up of structures is immediately evident.

braincase OUZC 5204 described above (figs. 24–30, 36). Crucially, the specimen has *not* split through the sagittal plane as Zangerl and Case (1976) suggested; instead, the fracture surface is close to the midline only ventrally, but then passes obliquely through the left side of the braincase farther dorsally. Consequently, considerably more than half

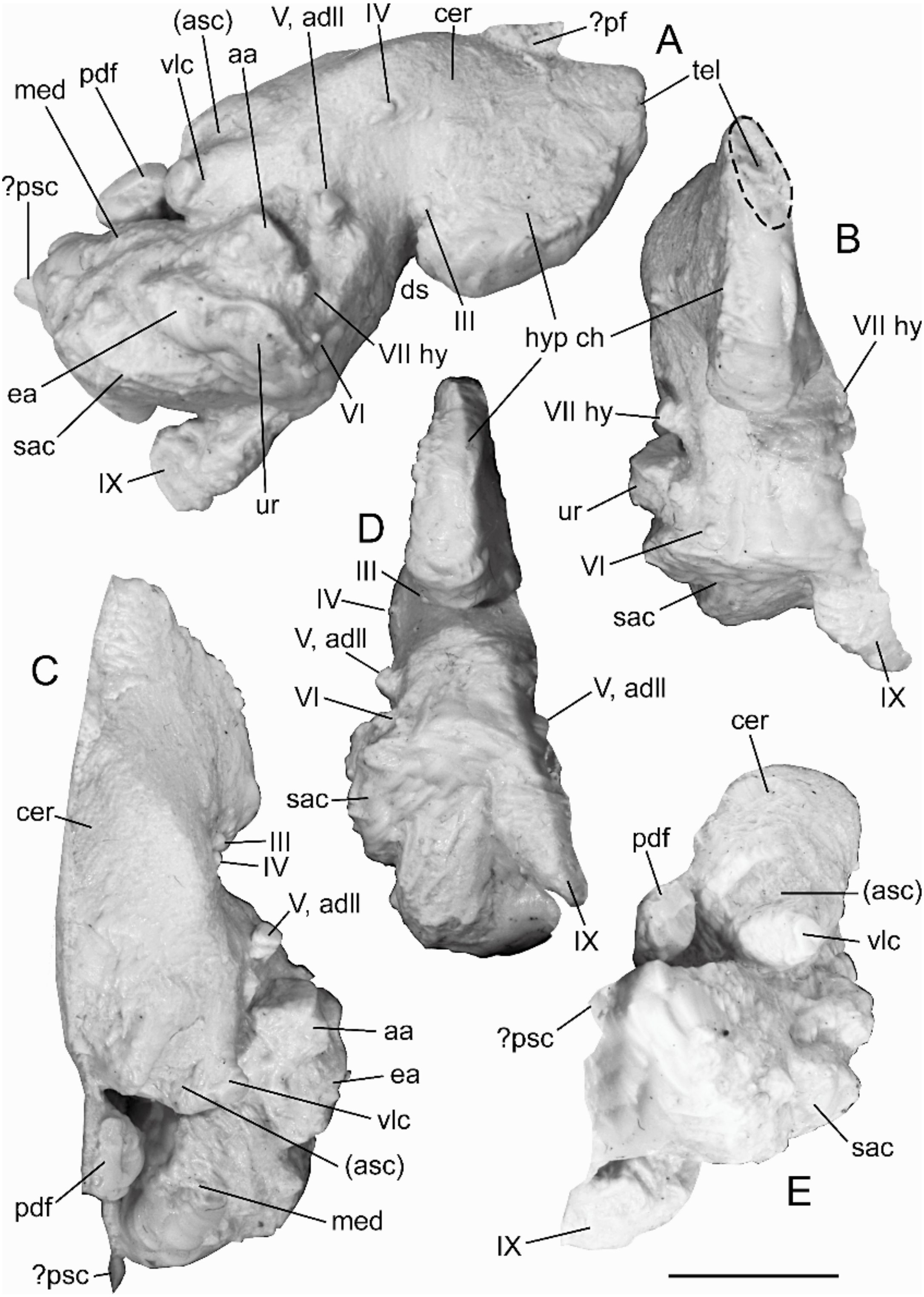

Fig. 38. A new silicone cranial endocast of *Cobelodus aculeatus* FMNH PF 3090. **A**, lateral view, right side; **B**, anterior view; **C**, dorsal view; **D**, ventral view; **E**, posterior view.

of the endocast is present (including the telencephalic, mesencephalic, and diencephalic chambers) and almost two-thirds of its dorsal surface is exposed. The right side is essentially complete, although some features have unfortunately been obliterated during earlier preparation and are seen only on the left side (e.g., the glossopharyngeal canal). Several bilaterally symmetrical structures are evident, including both sides of the large hypophyseal chamber (although its distal extremity is still filled with matrix and cannot be seen), the main exit of the facial nerve, the abducent foramen, and parts of both saccular chambers.

Many features in the endocast are readily identified by comparison with "*Cobelodus*" and OUZC 5204. One obvious landmark is the deep notch formed by the apex of the dorsum sellae (fig. 38A), adjacent to the oculomotor foramen (misidentified as the optic foramen by Zangerl and Case, 1976; in fact, that feature is not preserved). Only the proximal part of the hypophyseal chamber is preserved, so its depth is uncertain (although it must have been as long and narrow as in "*Cobelodus*"). Zangerl and Case (1976: 121) remarked that "the specimen does not exhibit a fossa hypophyseos". They attributed this to an artefact of preservation and did not understand the true nature of the specimen, but their observation is nevertheless important because the preserved part of the hypophyseal chamber certainly lacks any communication with the basicranium, as in "*Cobelodus*".

The roof of the hypophyseal chamber merges with the telencephalic region anterodorsally. This is very narrow from side to side (its broken cross section is indicated by a dashed line in fig. 38B). The olfactory tracts presumably diverged farther anteriorly, since there is no trace of them in the endocast but the olfactory capsules are spaced widely apart in X-rays of compression fossils (see below). The roof of the cerebellar chamber is fairly featureless, apart from a small mass of calcified cartilage along the dorsal midline that may represent the position of a pineal foramen. The position of the trochlear foramen (correctly identified by Zangerl and Case, 1976) is evident on the lateral wall of this region, more or less dorsal to the oculomotor foramen. The feature identified by them as the oculomotor foramen is identified here as the combined exit for the trigeminal and anterodorsal lateral line nerves. Farther ventrally, the foramen for the facial hyomandibular trunk lies just in front of the anterior ampulla. The abducent foramen (correctly identified by Zangerl and Case, 1976) is located even farther ventrally, near the base of the dorsum sellae.

Very little of the labyrinth endocast is preserved, apart from low mounds representing the anterior and external ampullae and the utricular recess. However, the position of the anterior semicircular canal is indicated by a deep diagonal groove in the roof of the vestibulolateral chamber. This shows that the canal was only thinly sheathed by cartilage, as in OUZC 5204 and unlike in "*Cobelodus*". The vestibulolateral chamber was not recognized as such by Zangerl and Case (1976: 121), although they correctly determined that it is a paired structure; they simply described it as "a very pronounced, posteriorly facing pit in the roof of the neurocranial cavity", but had "no idea as to its significance". The posterior end of this chamber seems unnatural and may have been slightly overexcavated during preparation.

The dorsal surface of the medullary region is poorly preserved and the area surrounding the fontanelle has been overexcavated during its original preparation. Consequently, some of its features are difficult to interpret. At the dorsal midline, medial to the vestibulolateral chamber there is a rounded projection, corresponding to the "chimney" for the posterior dorsal fontanelle in "*Cobelodus*" (pdf: fig. 38). It would have been flanked by the anterior semicircular canal after they passed over the roof of the vestibulolateral chamber (there is a shallow groove for the right canal in the roof of the vestibulolateral chamber). At the left posteriormost extremity of the endocast, there is a small protuberance that probably represents part of the (largely unexcavated) left posterior semicircular canal (?psc: fig. 38). Unfortunately, the posterior part of the medullary chamber has not been excavated and none of its features are evident. It cannot be determined from the endocast whether a persistent otico-occipital fissure was present, and passages for the

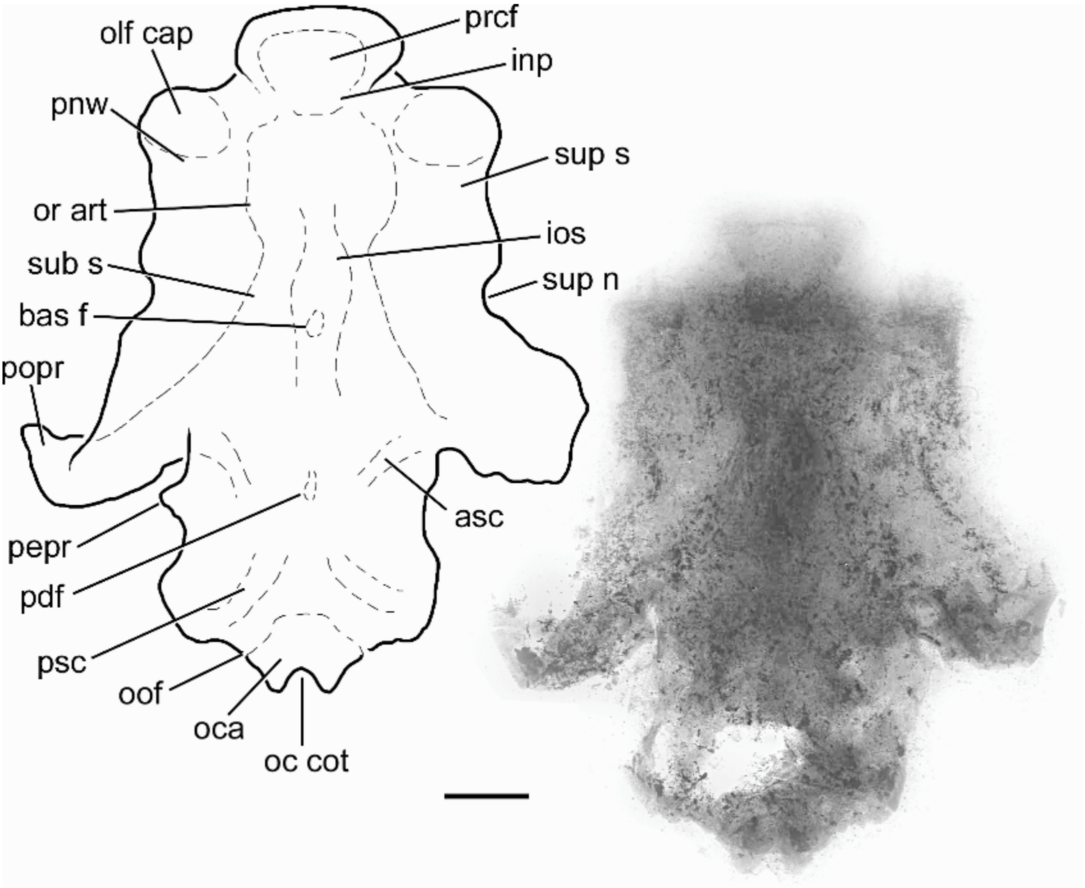

Fig. 39. *Cobelodus aculeatus* FMNH PF 7347. Enlarged image of braincase, positive print from an original X-ray by R. Zangerl. Scale bar = 10 mm.

vagal and occipital nerves cannot be seen. Most of the left glossopharyngeal canal has been excavated, but the right one is still filled with matrix. The specimen has split longitudinally through the occipital cotylus, which can be seen in sagittal section (Zangerl and Case, 1976: fig. 8A). Below the cotylus is a continuous unexcavated line of tesselate cartilage, which probably represents the basicranium. The space between this cartilage and the occipital cotylus probably contained an aortic canal, although this cannot be observed. Inspection of the counterpart suggests that parts of the basicranium and interorbital septum are preserved intact, but are still unprepared.

X-RAYS: Zangerl (1965) advocated the use of X-ray stereo images as a means of obtaining anatomical data in strongly compressed fossils, and much of his subsequent investigation of *Cobelodus aculeatus* was based on analysis of X-ray stereopairs (Zangerl and Case, 1976). Indeed, many of the best compression fossils of *C. aculeatus* are unprepared and can be investigated only from X-ray plates (including FMNH PF 7347, on which the original reconstruction was mainly based; fig. 39). Some specimens have been prepared mechanically to remove calcified cartilage leaving natural impressions, and silicone casts of these specimens are informative (see following section). The fossils have clearly suffered considerable diagenetic compression, which can be mimicked by reducing the y-axis dimension of the digital "*Cobelodus*" contour-based surface rendering by 90–95%, to create an orthographic "biscuit" that closely resembles the

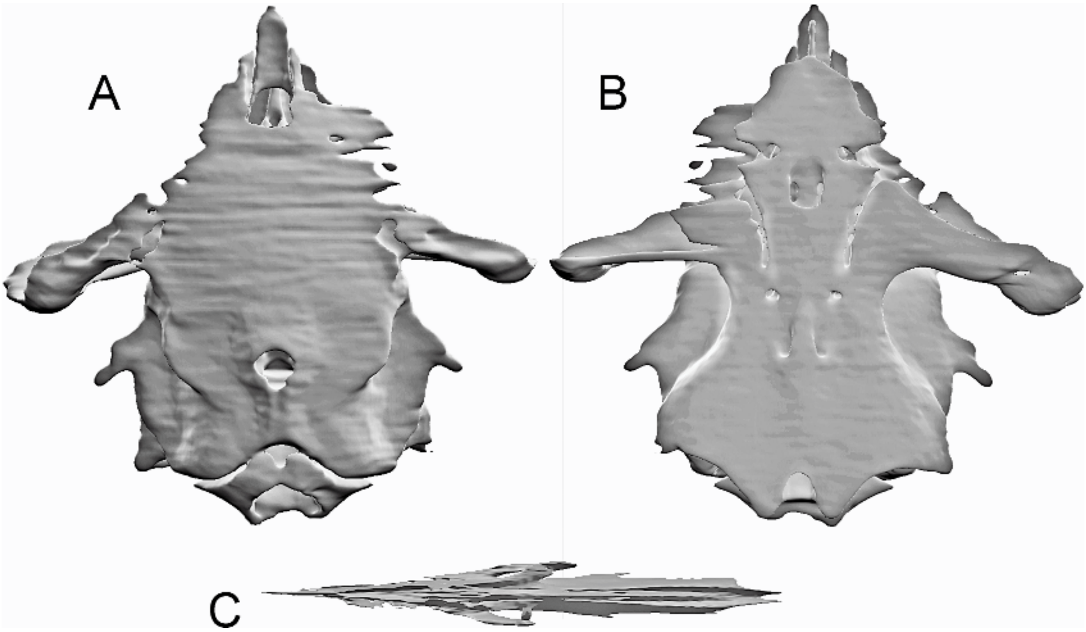

Fig. 40. "*Cobelodus* biscuit"; digitally flattened contour-based surface rendering (90% along the y axis, unaltered dimensions along x and z axes) for comparison with compression fossils. **A**, dorsal view; **B**, ventral view; **C**, slightly tilted lateral view.

compression fossils (fig. 40). Assuming that the braincase in *C. aculeatus* was originally as deep as in "*Cobelodus*", only 5–10% of the original depth is available for stereographic analysis of the X-rays. Despite this limitation, Zangerl and Case (1976) probably established the original depth of the neurocranium fairly accurately.

Stereo X-rays of the neurocranium in *Cobelodus aculeatus* have been reinterpreted here using the three-dimensional "*Cobelodus*" braincase as a guide. The braincase in *Cobelodus aculeatus* is wide and blunt anteriorly, with a short ethmoidal region that includes a subtriangular precerebral fontanelle (widest anteriorly), flanked by the olfactory capsules. Most of the ethmoidal region is lightly calcified and transparent to X-rays. More radio-opaque regions (which are strewn with minute pyrite crystals) include the margin of the precerebral fontanelle and parts of the olfactory capsule walls (especially laterally). Mesial and slightly posterior to the capsules are paired pyrite-lined channels. These are bilaterally symmetrical and appear to be real anatomical structures, possibly marking the course of the orbitonasal canal through the postnasal wall.

Immediately behind the ethmoidal region in *Cobelodus aculeatus* X-rays is an extensive radio-opaque central area extending back behind the orbits. This area consists of two distinct regions, but one is located directly above the other and they can be distinguished only in stereo images. The larger dorsal area extends from the postnasal wall, narrowing and then broadening again within the orbit and eventually merging with the upper part of the postorbital arcade. This is interpreted as the main cranial endocast, since it is apparently restricted to the upper part of the neurocranium as in "*Cobelodus*". The more ventral area runs posteriorly from the anterior part of the orbit and widens slightly toward the ventral part of the postorbital arcade, and probably represents the hypophyseal fenestra. This region is flanked by the suborbital shelf, which is narrower than in "*Cobelodus*" although its anteroposterior extent is about the same.

X-rays of *Cobelodus aculeatus* reveal a row of pyrite crystals along the margins of the supraorbital shelves, following a symmetrical course above both orbits. The row passes almost straight back from the ethmoid region, then makes a distinct midorbital inward flexure around a notch in the supraorbital shelf (possibly for the dorsal part of the eyeball) before continuing posterolaterally toward the lateral part of the postorbital arcade. A similar notch is present in the supraorbital shelf of *"Stethacanthulus" meccaensis* (Williams, 1985: plate 2, fig. 1; see below). There is no evidence of a pineal foramen in *C. aculeatus*.

As in "*Cobelodus*", the postorbital process in *Cobelodus aculeatus* is delicate, narrow, and directed posterolaterally. The lateral commissure was chondrified, forming a continuous postorbital arcade around a voluminous jugular canal and bearing an articular surface for the palatoquadrate otic process ventrolaterally.

In X-rays, some parts of the otic and occipital regions are much clearer than others (fig. 39). Faint traces of a median aortic canal are evident in the floor of the braincase beneath the occipital cotylus, and can be traced anteriorly between the otic capsules. Behind the postorbital arcade, this canal apparently branches into short, paired canals that open into elongated areas corresponding to the basicranial foramina observed in peels of other compression fossils (see below). However, it would be extremely difficult to interpret the aortic canal in these compression fossils without prior knowledge of the arrangement in "*Cobelodus*". The semicircular canals are difficult to follow in X-rays, as only those parts that are lined by pyrite crystals are seen clearly. Comparison with "*Cobelodus*" suggests that the central region of the medullary chamber has collapsed onto underlying structures, so that very little is discernible apart from a small triangular area in the expected position of the posterior dorsal fontanelle. A periotic process is faintly visible on the widest part of the otic capsule, but is partly obscured by the postorbital arcade, which has collapsed over it.

The occipital region is generally well preserved and has resisted compaction better than the otic capsules. Paired dorsal and ventral paroccipital processes are evident surrounding the occipital cotylus. The latter is as narrow from side to side as in "*Cobelodus*", not expanded laterally as in *Cladodoides*, *Tamiobatis*, and *Orthacanthus*. The occipital arch is short, and is separated at least posterolaterally by a narrow clear band just behind the posterior semicircular canal, probably representing a narrow otico-occipital fissure. A broad opening is present on each side of the occipital region, probably representing the glossopharyngeal canal. No canals for occipital nerves are discernible.

COMPRESSION SPECIMENS: The braincase in all the compression fossils of *Cobelodus aculeatus* examined was invariably crushed dorsoventrally. Its appearance in lateral view is therefore conjectural, although the original depth of the orbit can be estimated from associated elements (e.g., depth of the palatoquadrate otic process).

The "*Cobelodus* biscuit" (fig. 40) does not allow for differential diagenetic compaction and consequently lacks certain features that commonly show up in the compression fossils. Taphonomic artefacts formed by diagenetic compression are so common in compression fossils of *Cobelodus aculeatus* that some have been misinterpreted as anatomical features. For example, curved ridges extending posterolaterally from the posteriormost paired basicranial foramina were thought to mark the position of paired internal carotids (Schaeffer, 1981: fig. 13B). These ridges are interpreted here as the borders of paired collapse structures, where thinner parts of the basicranium associated with the glossopharyngeal canals, orbital arteries, and palatine rami became crushed against resistant internal structures such as the occipital cartilage and dorsum sellae, forming shallow craters on each side of the ventral midline (fig. 41). The same pattern of internal features is revealed when a clipping plane is introduced into the "*Cobelodus*" surface rendering to remove part of its ventral surface (fig. 42), as well as in orthographic three-slice mode views of the CT scan (fig. 43). Taphonomic artefacts may also have affected the interpretation of the braincase in *Ornithoprion* presented by Zangerl (1966).

Comparison of *Cobelodus aculeatus* compression fossils and the "*Cobelodus*" surface rendering suggests that the shape of the

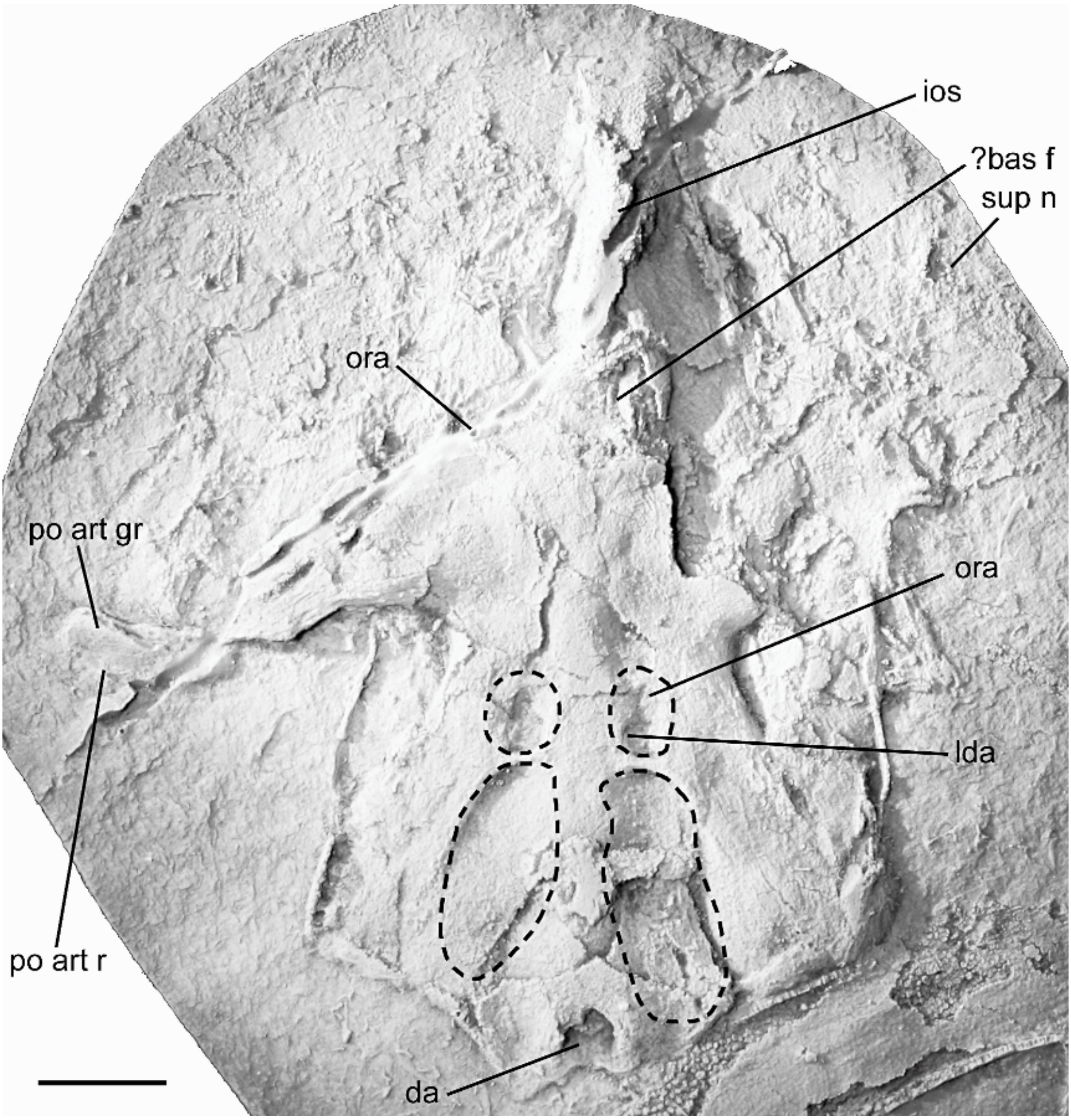

Fig. 41. *Cobelodus aculeatus* FMNH PF 7345. Silicone peel of braincase ventral surface, anterior to top. Dashed black outlines indicate paired collapse structures in the hypotic lamina. Smaller anterior and larger posterior craters are separated by curved ridges. Scale bar = 10 mm.

basicranium behind the postorbital arcade is very similar, and some of the compression specimens show a distinct "waist" where the arcade merges with the margins of basicranium (e.g., FMNH PF 8011; fig. 44). The area lateral to this "waist" probably represents a flattened lateral otic fossa in the outer capsular wall.

Most of the compression fossils examined are broken at the level of the postorbital arcade, so canals and foramina farther anteriorly are usually missing. A narrow suborbital shelf is discernible in the peel of FMNH PF 7345 (fig. 41) as well as in the X-ray of FMNH PF 7347 (fig. 39), although in both cases it is narrower than in "*Cobelodus*"

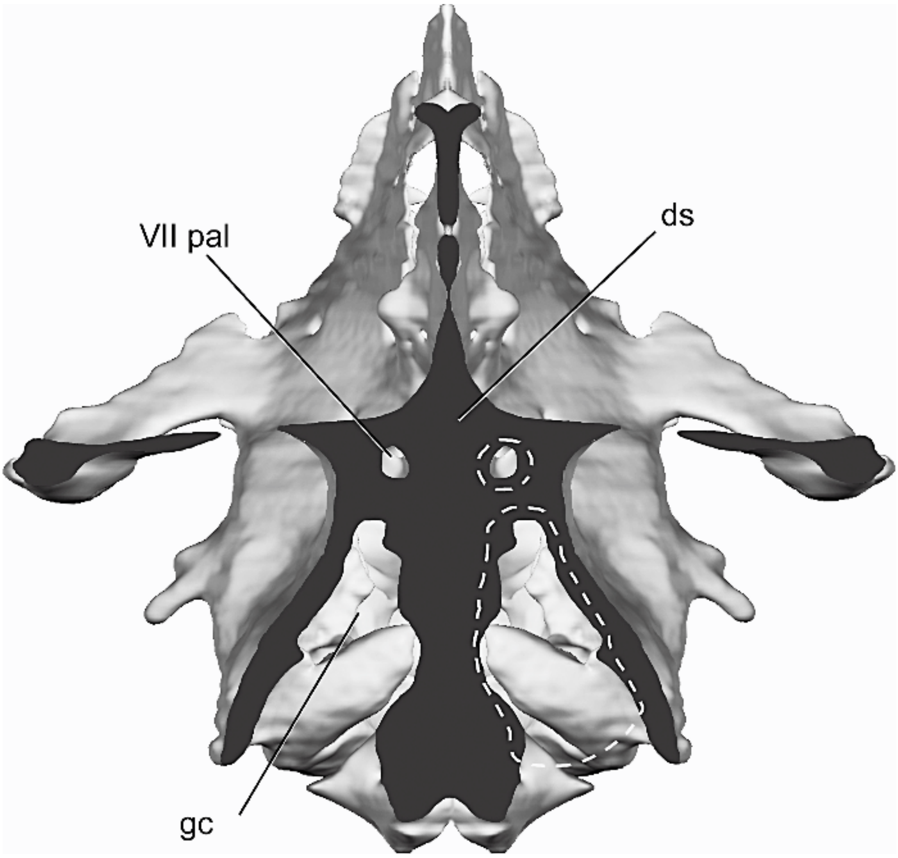

Fig. 42. "*Cobelodus*" contour-based surface rendering, ventral view with clipping plane introduced to remove parts of the basicranium, exposing the canal for the palatine ramus and the glossopharyngeal canal. Collapse of the basicranium below these structures (dashed white lines) creates paired ridges and depressions in compression fossils (see fig. 37).

(cf. fig. 8). In the peel of FMNH PF 7345 there is an uneven area of cartilage in the expected position of the basicranial fenestra, but no features could be identified with certainty. Although the presence of an interorbital septum cannot be confirmed from the compression specimens, their interorbital region is clearly too narrow to accommodate the endocast in the manner suggested by Zangerl and Case (1976: fig. 7). As in "*Cobelodus*", the ventral ramus of the postorbital arcade is short anteroposteriorly but projects a considerable distance posterolaterally (fig. 37D). At the distal end of this arcade is a transverse articular surface for the palatoquadrate, corresponding to the ridge and groove in "*Cobelodus*".

The paired foramina within the anterior paired collapse structures are considered to be real morphological features rather than taphonomic artefacts because they match foramina in the "*Cobelodus*" braincase. Zangerl and Case (1976: 117) described a single pair of foramina, more or less posteriorly directed with " very short canals behind them which converge and appear to meet a short distance behind the foramina." They suggested that the larger paired collapse structures represented passages for the internal carotids and concluded that the pair of foramina farther anteriorly housed the orbital arteries. That interpretation is clearly at odds with the arrangement of foramina and canals in "*Cobelodus*" and is probably erroneous

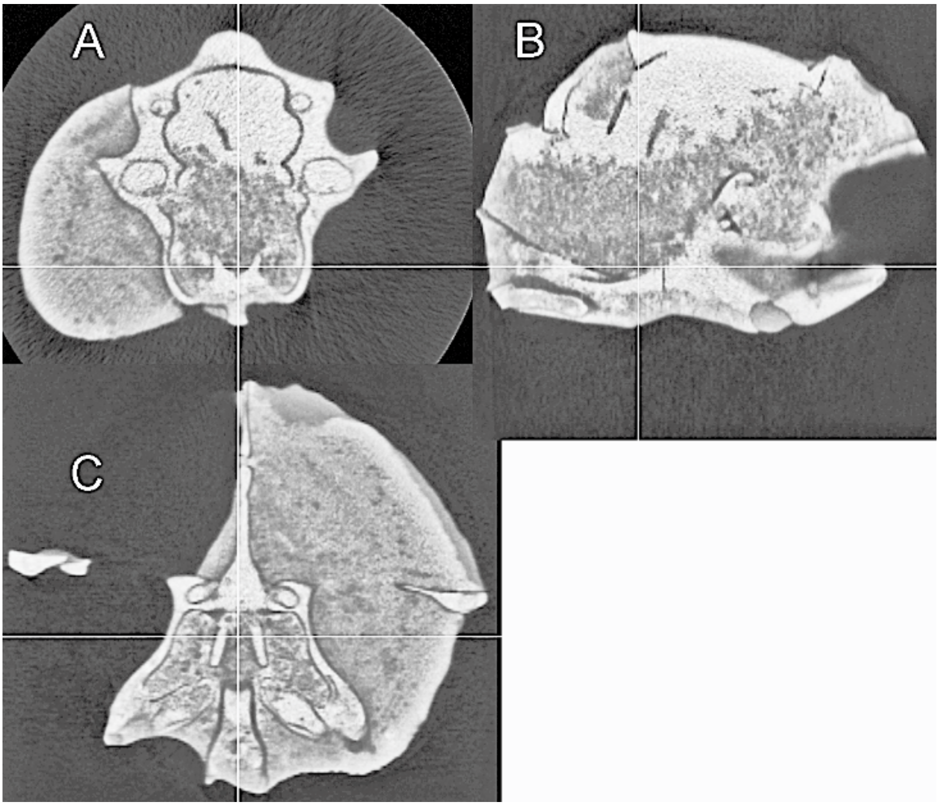

Fig. 43. "*Cobelodus*" CT scan, three-slice mode (digital reslicing of original transverse CT scan slices), showing orthographic views of the glossopharyngeal canal and surrounding cartilage. **A**, transverse slice; **B**, sagittal slice; **C**, horizontal slice. White lines correspond to x-y-z axes. Compare horizontal slice with figs. 37 and 38.

(though understandable, since their comparison was limited to platybasic Paleozoic elasmobranchs in which paired aortic canals are present; e.g., *Cladodoides wildungensis*, *Tamiobatis vetustus*; Gross, 1937; Romer, 1964). Schaeffer (1981: fig. 13) presented an alternative interpretation of the basicranial circuit in *Cobelodus aculeatus* in which the posterior depressions supposedly marked the entrance of the internal carotids rather than their exit, and the (paired) aortae were not enclosed by cartilage. The problem with both hypotheses is that the posterior collapse structures show no evidence of real openings in the cartilage. Furthermore, in specimens in which these collapse structures are weak or absent, there are no foramina behind the pair already noted (e.g., FMNH PF 7324; fig. 45). However, a second pair of foramina is present farther anteriorly within the smaller anterior collapse structure, anterolateral to the main pair. Comparison with "*Cobelodus*" suggests that the paired foramina described by Zangerl and Case (1976) probably housed the aortae shortly after they diverged, and the second pair farther anterolaterally probably housed the orbital arteries as they re-entered the basicranium (lda, ora; figs. 41, 44–46). As in "*Cobelodus*", there are no basicranial grooves for the internal carotids, suggesting that the basicranial circuit in *C. aculeatus* was similarly specialized (fig. 14).

Many of the compression fossils show a posterior median opening for the dorsal aorta, flanked by paired ventral paroccipital processes. Some specimens also show part of the basioccipital fovea (e.g., FMNH PF 7472; fig. 46). The lateral walls of the otic capsule are usually crushed in compression specimens, splitting along the external semicircu-

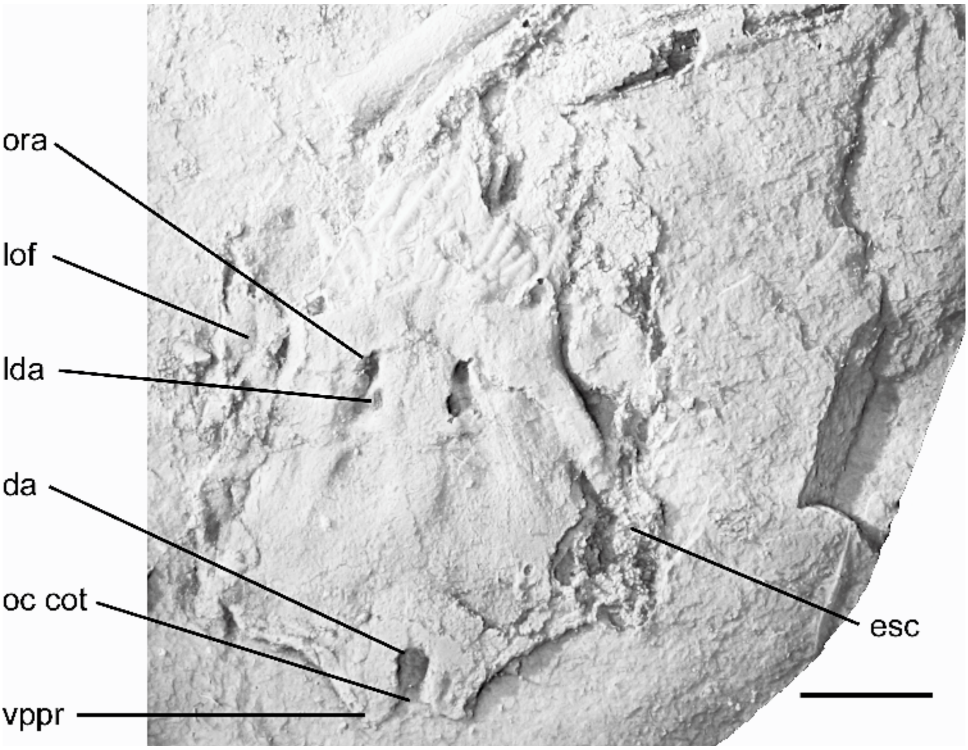

Fig. 44. *Cobelodus aculeatus* FMNH PF 8011. Silicone peel of braincase ventral surface, anterior to top. Scale bar = 10 mm.

lar canal, but in the counterpart to FMNH PF 7345 (which provides a rare opportunity to examine the dorsal surface of the braincase) there is evidence of a periotic process like that in "*Cobelodus*" (fig. 47). The supraorbital shelf in this specimen is wider and extends farther anteriorly than in "*Cobelodus*", and there is a notch in the midorbital part of the supraorbital shelf (confirming the earlier observation of X-rays). In most of the compression specimens, prismatic calcification of the otic capsules is usually broken and the individual tesserae can be scattered, possibly explaining why the periotic process is rarely observed.

It is concluded that the general morphology of the braincase in *Cobelodus aculeatus* and "*Cobelodus*" was probably similar, but diagenetic compaction of compression fossils has generated a suite of taphonomic artefacts (especially in the basicranium), obscuring or even obliterating many features. Crucially, the concretion specimen of *C. aculeatus* shows many similarities to "*Cobelodus*" in endocast morphology (once its orientation is properly established), showing that there was a deep dorsum sellae and an interorbital septum. X-rays and compression fossils also confirm the presence of a median dorsal aorta and a periotic process. Such unusual features indicate a close phylogenetic relationship and probably represent symmoriiform synapomorphies. *Cobelodus aculeatus* has a wider supraorbital shelf and a narrower suborbital shelf than "*Cobelodus*", suggesting that they are not conspecific and may not even be congeneric.

A new reconstruction of the braincase in *C. aculeatus* is presented here in which it is shown as tropibasic (fig. 48), somewhat different from previous interpretations, although Zangerl and Case (1976: 115) deserve credit for noting the presence of a narrow interorbital septum in their preliminary (un-

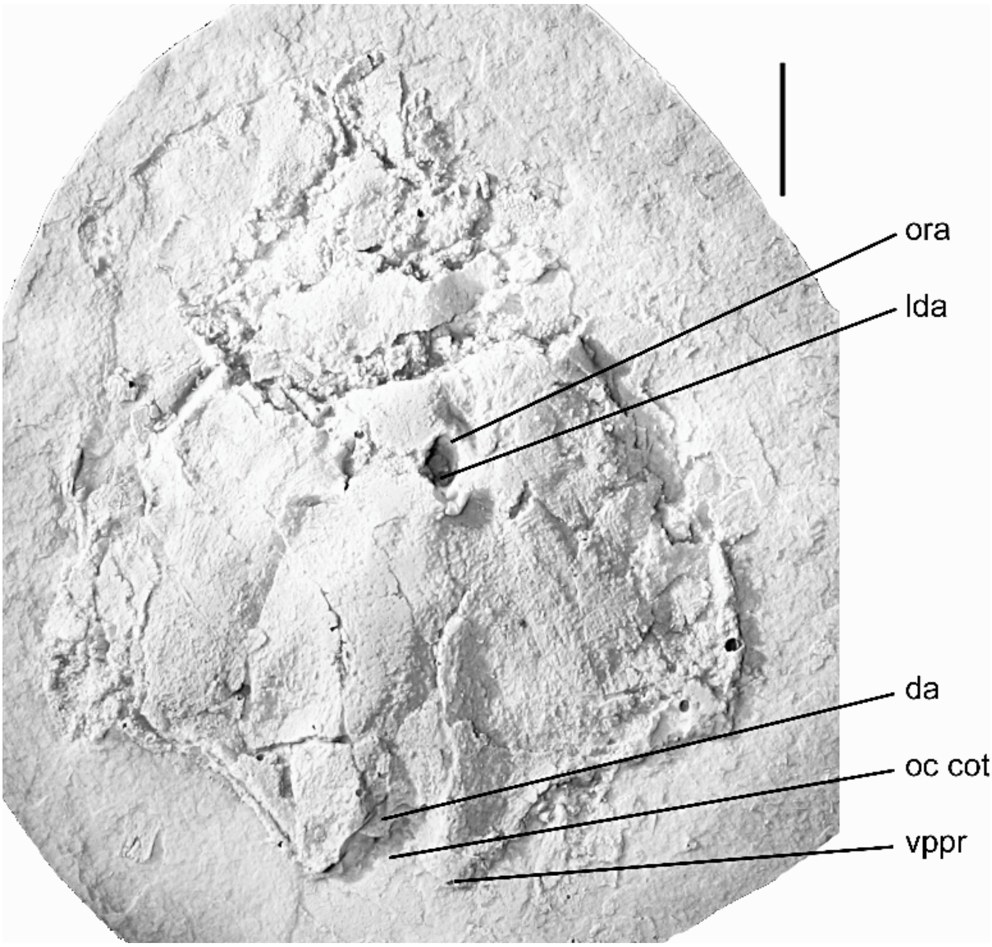

Fig. 45. *Cobelodus aculeatus* FMNH PF 7324. Silicone peel of braincase ventral surface, anterior to top. Scale bar = 10 mm.

published) reconstruction founded on X-rays and compression fossils. In hindsight, it was only their misinterpretation of the three-dimensional endocast discovered later that misled them into thinking *C. aculeatus* had a much wider interorbital region.

Since the cranial morphology in "*Cobelodus*" and *Cobelodus aculeatus* was probably very similar, it is likely that much of the cranial cartilage in "*Cobelodus*" is missing anteriorly, which would account for its somewhat squat appearance, the incomplete precerebral fontanelle, and lack of olfactory capsules (figs. 6–8). The supraorbital shelf is wider and better developed in *C. aculeatus*, and merges gradually with the postorbital arcade. By contrast, the arcade in "*Cobelodus*" is angled sharply outward from the supraorbital shelf, and forms a distinct lateral projection in dorsal view (cf. figs. 7, 48A). In dorsal view, the otic and occipital regions in *C. aculeatus* and "*Cobelodus*"are remarkably similar apart from the slightly more anteriorly positioned periotic process and the slightly longer occipital arch in *C. aculeatus*. Ventral views of the "*Cobelodus*" and *C. aculeatus* braincases are also similar (figs. 8, 48B), except that the orbital arteries were more completely enclosed by cartilage in *C. aculeatus*. Since the lateral view is conjectural in *C aculeatus* there is little point in comparing it with "*Cobelodus*".

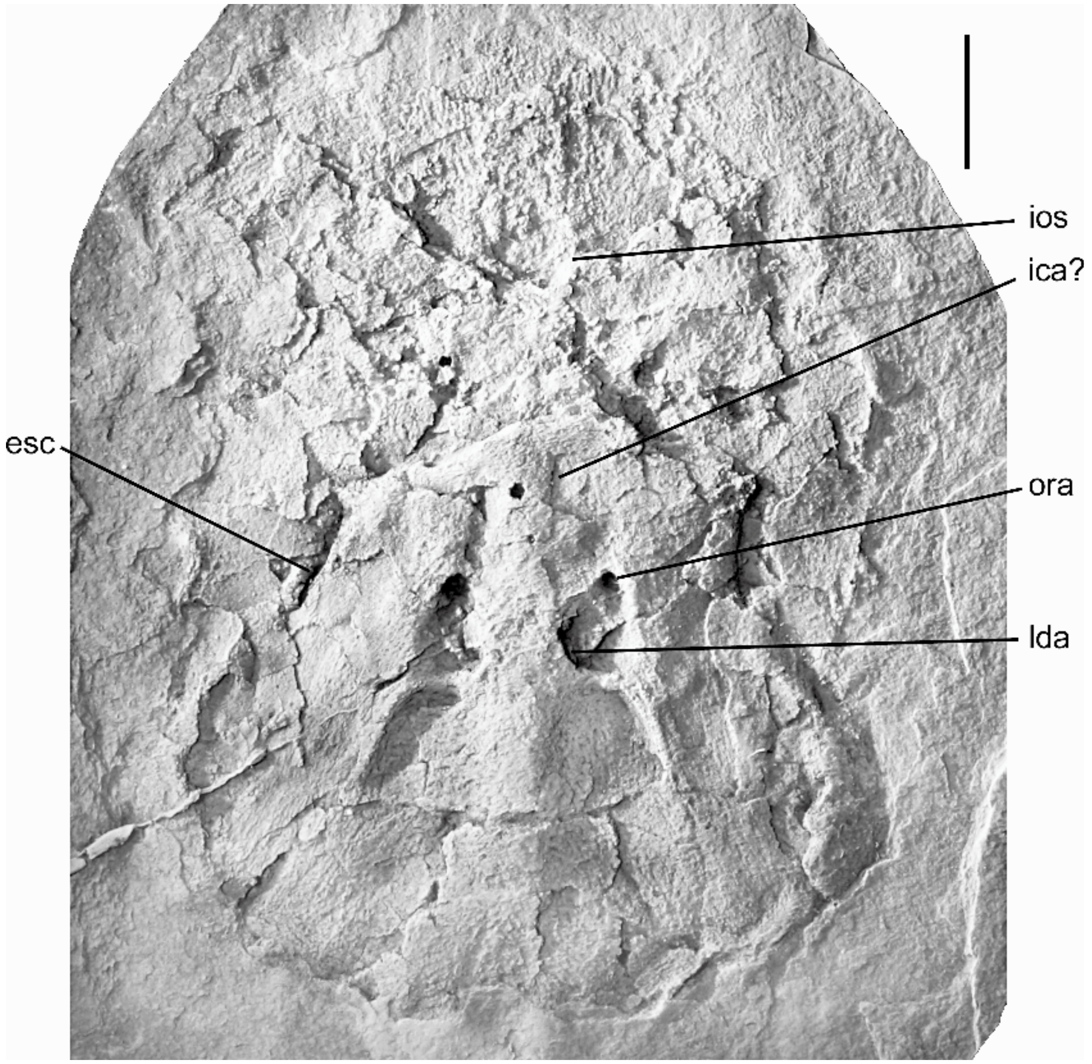

Fig. 46. *Cobelodus aculeatus* FMNH PF 7472. Silicone peel of braincase ventral surface, anterior to top. Scale bar = 10 mm.

SYMMORIUM RENIFORME COPE, 1893

MATERIAL EXAMINED: Holotype FMNH UF 574, plus X-rays; Court Creek, NE of Knoxville, Illinois; Mecca Quarry Shale, Liverpool cyclothem, Des Moines series, Westphalian Upper C, Pennsylvanian. Collected by F.R. Jelliffe, described by Cope (1893) and by Williams (1985); FMNH PF 2582, chondrocranium with rostrum; FMNH PF 2633, chondrocranium with rostrum, plus partial pectoral skeleton (both specimens X-rays only); Logan Quarry, Parke County, Indiana (Zangerl and Richardson, 1963); Logan Quarry Shale, Lower Wiley cyclothem (Staunton formation), Des Moines Series, Westphalian Upper C, Pennsylvanian; FMNH PF 8274, chondrocranium (X-ray only); Hajji Hollow, Wabash Township, Parke County, Indiana; Logan Quarry Shale, Lower Wiley cyclothem (Staunton formation), Des Moines Series, Westphalian Upper C, Pennsylvanian.

GENERAL REMARKS: This genus and species is founded on the disarticulated anterior part of a skeleton, plus numerous teeth clustered around the jaws (Cope, 1893).

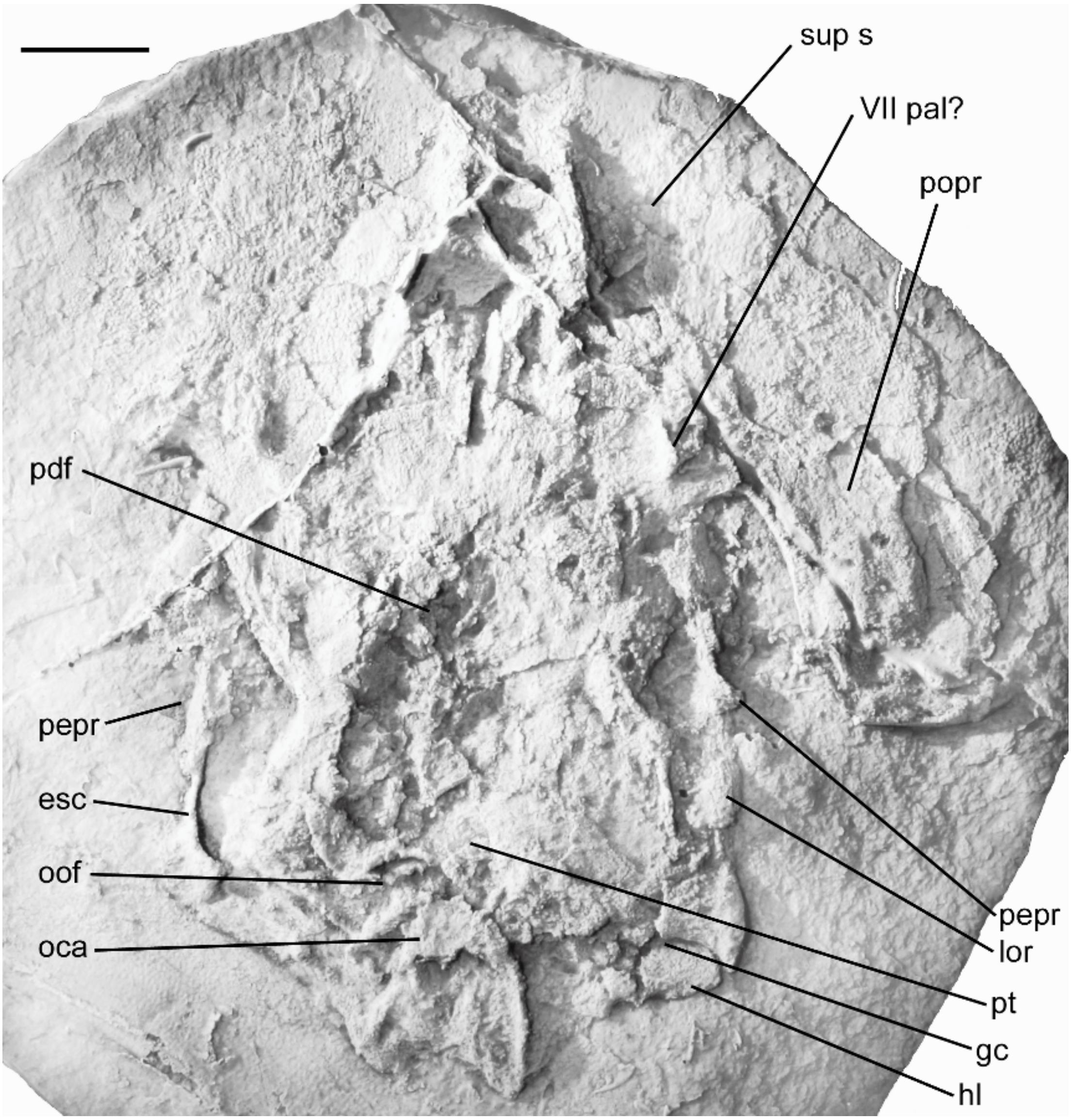

Fig. 47. *Cobelodus aculeatus* FMNH PF 7345. Silicone peel of braincase dorsal surface, anterior to top (same specimen as ventral view shown in fig. 37). Scale bar = 10 mm.

Williams (1985) referred several additional specimens to this species, although they differ from the holotype in overall tooth size and shape (Ginter, 2002). Nevertheless, morphologically intermediate teeth have now been found and these differences are now considered to be growth-related (M. Ginter, personal commun., Feb. 2006). Some large isolated teeth were also referred to *Symmorium reniforme* by Williams (1985), but these differ profoundly from the teeth in the holotype and are now referred to the ctenacanthiform genus *Glikmanius* (Ginter, 1998, 1999, 2002; Ginter et al., 2005), a form considered closely related to *Cladodus* (sensu Duffin and Ginter, 2006). The teeth in *S. reniforme* lack apical buttons, labiobasal projections, and a median labial concavity; instead, the upper side of the kidney-shaped tooth base has a long, low, crescent-shaped

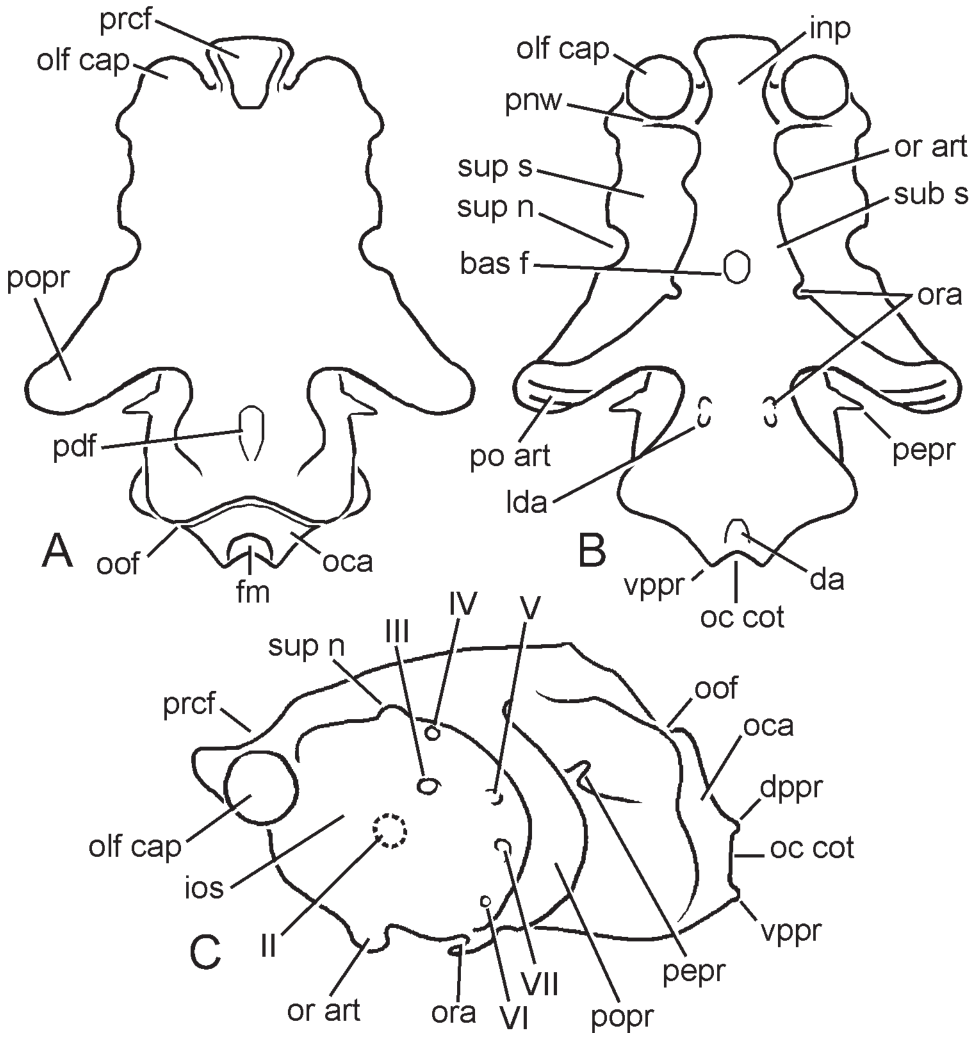

Fig. 48. Reconstruction of the braincase in *Cobelodus aculeatus*, interpreted as tropibasic following comparison with the digital reconstruction of the "*Cobelodus*" neurocranium. **A**, dorsal view; **B**, ventral view; **C**, lateral view. The "*Cobelodus*" reconstruction was used as a template, and the shape and proportions were adjusted from features identified in dorsal and ventral views in X-rays and compression fossils. In lateral view, the braincase depth and positions of foramina in the back of the orbit were established from the cranial endocast.

lingual ridge, the main cusp is flattened labiolingually, and there is a corresponding shallow, curved basal concavity. By contrast, *Glikmanius* teeth have a lingually directed base with two widely separated apical buttons, two corresponding labiobasal projections, and a median labial concavity between the projections.

DESCRIPTION: The braincase in *Symmorium reniforme* is not preserved in the holotype and can be observed only in X-rays of other specimens (listed above). In the most complete specimen (FMNH PF 2428), the head is preserved intact and has been compressed dorsoventrally, but the braincase cannot be distinguished from the underlying visceral skeleton. Williams (1985: 104) noted only that the otic region is short (approximately one-third the braincase length), that there is "a short, but well developed rostrum", and that the posterior process is "a stout, triangular projection and bears a thickened, transverse keel on its posterior border". As far as can be determined, however, the braincase resembles that of "*Cobelodus*" and may also have been tropibasic (especially since the palatoquadrate otic process is equally deep). Unfortunately, no direct indication of eye size can be established, because sclerotic cartilages are not preserved and the braincases are all dorsoventrally compressed. Consequently, it is not possible to confirm the presence of an interorbital septum (although one was probably present). No reconstruction of the braincase in *S. reniforme* will be presented here.

STETHACANTHULUS MECCAENSIS
(Williams, 1985)

MATERIAL EXAMINED (X-rays only): FMNH PF 2621, disarticulated chondrocranium and pectoral girdle; FMNH PF 8013, incomplete disarticulated skeleton (male individual according to Williams, 1985); Logan Quarry, Parke County, Indiana (Zangerl and Richardson, 1963); Logan Quarry Shale, Lower Wiley cyclothem (Staunton formation), Des Moines Series, Westphalian Upper C, Pennsylvanian; FMNH PF 7429, disarticulated chondrocranium and branchial arches (male individual according to Williams, 1985), Hesler Quarry, Wabash Township, Parke County, Indiana; Mecca Quarry Shale, Liverpool cyclothem, Des Moines series, Westphalian Upper C, Pennsylvanian; FMNH PF 8124, isolated chondrocranium referred to the species by Williams (1985); strip mine headwall north of Barrett Cemetery, Pike County, Indiana; Acaule Shale, Carbondale formation, Des Moines series, Westphalian Lower D, Pennsylvanian.

GENERAL REMARKS: Other symmoriiform shark remains from the Pennsylvanian black shales of central North America have been referred to the genus *Denaea* Pruvost, 1922 (in Fournier and Pruvost, 1922) and described as a new species (*D. meccaensis* in Williams, 1985: 88). While there is little doubt that *D. fournieri* (the type species) is a symmoriiform, its teeth differ in some important respects from those of the American form. The tooth base in *D. fournieri* has a single apical button and a corresponding labiobasal projection, and the tooth base narrows lingually. However, in "*Denaea*" *meccaensis* the tooth base lacks an apical button and a labiobasal projection, and is expanded lingually forming a broad plate with a lingual depression and basal prominence (Williams, 1985: fig. 7). Very similar teeth have been described from the Lower Permian (Sakmarian) of the Russian Arctic (as "*Denaea*" *decora*; Ivanov, 1999). It has been suggested that both "*D.*" *meccaensis* and "*D.*" *decora* should be assigned to a separate genus on the basis of these shared features and because of the unusual manner in which successive teeth articulate with each other (Ivanov, 1999).

Zangerl (1990) erected a new genus and species of stethacanthid symmoriiform, *Stethacanthulus longipeniculus*, based on a small, complete skeleton from the Acaule Shale (Petersburg Formation, Westphalian D) of Bethel Quarry, Indiana. About 32 other specimens were also referred to this taxon, although all are either badly mutilated individuals and gastric residues possibly containing the remains of more than one taxon. Very few features of its skeletal anatomy were described, and little can be discerned from the original X-rays. Crucially, Zangerl (1990) went to great lengths to point out that the "cladodont" teeth in this form were indistinguishable from those of "*Denaea*" *meccaensis*. However, he also believed that relatively large "fanglike" teeth were also present in *S. longipeniculus*, noting their similarity both to the upper "fanglike teeth" in *Cobelodus aculeatus* and to "*Cladodus pattersoni*" denticles forming the "brush" and head denticle patches in fossils referred to *Stethacanthus altonensis* by Williams (1985). Such fanglike teeth are not present in specimens referred to "*D.*" *meccaensis*; however, it should be noted that Zangerl (1990) based his description of these "teeth" on macerated or coprolitic specimens, rather than on the holotype of *S. longipeniculus*. Consequently, it is not clear whether these "teeth" are present in the holotype of *S. longipeniculus*, or that they represent teeth at all (they could be head or "brush" denticles). The only remaining differences between "*D.*" *meccaensis* and *S. longipeniculus* are: (1) the supposed absence of a dorsal spine in the former; and (2) the comparatively long palatoquadrate otic process in the latter. Both of these differences could represent sexual dimorphism (it is also possible that palatoquadrate proportions changed during growth) and neither of them provides compelling evidence that two genera are represented. Consequently, "*D.*" *meccaensis* and "*D.*" *decora* are referred here to the genus *Stethacanthulus*, since it is the first generic name available for sharks with this characteristic tooth morphology. The species *longipeniculus* is provisionally placed in synonymy with *meccaensis*, pending the discovery of more complete specimens that might allow them to be separated.

DESCRIPTION: The braincase in *Stethacanthulus meccaensis* is known only from a few compression specimens. However, unlike in *Cobelodus aculeatus*, the braincase is preserved in different orientations, some being dorsoventrally compressed while others are seen more or less in lateral view (Williams, 1985: fig. 3). The gross morphology of the braincase is similar to that of "*Cobelodus*" and *Cobelodus aculeatus*, but its otic region is extremely compact and comparatively short. In ventral view, the cranium is slightly expanded posteriorly, and there is evidence of a pair of basicranial foramina just behind the postorbital arcade, possibly corresponding to those housing the orbital arteries in "*Cobelodus*". The postorbital arcade is delicate and surrounds a large jugular canal as in "*Cobelodus*", and has an articular facet for the palatoquadrate ventrolaterally. The occipital cotylus is very narrow, and is flanked ventrally and perhaps dorsally by paroccipital processes. Traces of the hypotic lamina are present at the posterolateral margins of the otic capsules, suggesting the presence of a wide glossopharyngeal canal.

The orbital region is strikingly similar to that in "*Cobelodus*", with a deep interorbital septum (sometimes showing a large oval fenestra; fig. 49A). X-rays clearly show a concentration of radio-opaque material in the dorsal part of the orbit, suggesting that the cranial cavity and its surrounding cartilage lay in above the interorbital septum, i.e., the braincase is tropibasic. In fact, Williams (1985: 91 and fig. 6) alluded to this possibility in his reconstruction of the braincase (slightly modified here; fig. 49B, C), but did not discuss its significance despite commenting on the presence of the interorbital fenestra. The depth of the orbit in laterally compressed specimens and the dimensions of sclerotic cartilages suggest that the eye in *Stethacanthulus meccaensis* was extremely large, with a maximum diameter greater then the depth of the braincase. The eyes were presumably large, filling the orbits and bulging from each side of the head. The supraorbital shelf in larger specimens contains a deep, concave midorbital recess similar to that seen in some specimens of *Cobelodus aculeatus* (figs. 39, 41), but this is absent in smaller individuals.

LATE PENNSYLVANIAN SYMMORIIFORMS FROM NEW MEXICO

GENERAL REMARKS: Zidek (1992) described two symmoriiform sharks from the Kinney Brick Co. Quarry, Manzanita Mountains, Bernalillo County, New Mexico (Pine Shadow member, Wild Cow formation, late Missourian or early Virgilian, Upper Pennsylvanian). One of these (NMMNH P-19182) is an almost complete skeleton, approximately 45 cm long, lacking only the anterior part of the chondrocranium and dorsal part of the tail. Zidek (1992) referred this specimen to *Cobelodus aculeatus* on the basis that it has monocuspid teeth similar to the supposed palatoquadrate teeth of *C. aculeatus* described by Zangerl and Case (1976). However, no multicuspid teeth seem to be present, and the supposed teeth may be denticles from the top of the head (see earlier comments regarding the dentition in *C. aculeatus*). The other specimen (NMMNH P-19180) is less complete and lacks teeth, but includes part of the occipital region as well as parts of the visceral arches, pectoral endoskeleton, vertebral column, and dorsal fin. Both specimens undoubtedly represent symmoriiform sharks and may represent a single species, but neither can be referred convincingly to *C. aculeatus*.

CRANIAL MORPHOLOGY: The otico-occipital region is preserved in NMNH P-19182,

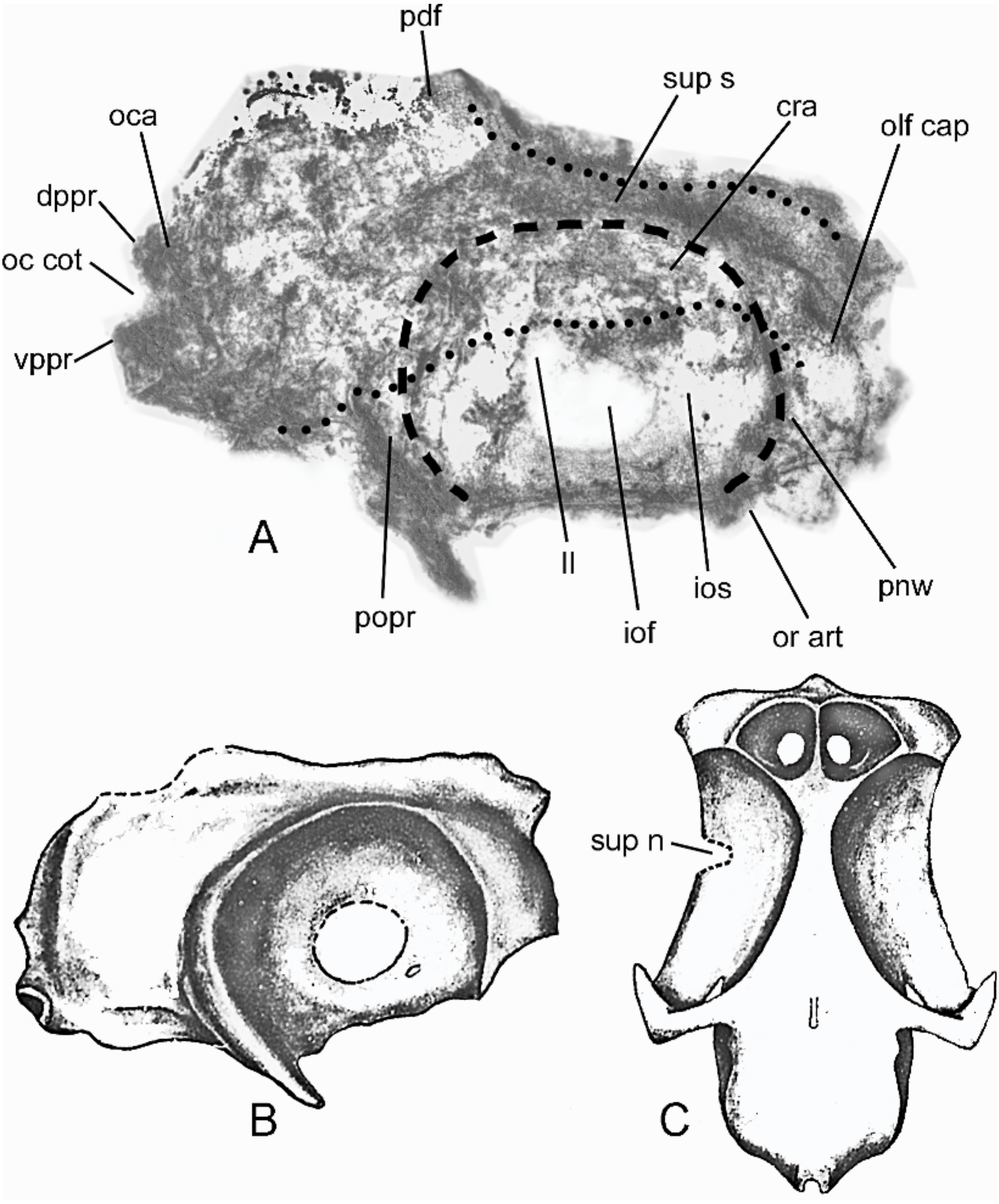

Fig. 49. *Stethacanthulus meccaensis* FMNH PF 2621. **A**, braincase in oblique dorsolateral view, positive image from X-ray, anterior to right; **B**, **C**, reconstruction of braincase (after Williams, 1985); **B**, lateral view; **C**, ventral view. Note interorbital septum and fenestra in lateral view and midorbital notch in dorsal view. Dotted line defines cranial cavity, dashed line defines orbit.

but few morphological features are discernible and Zidek's (1992) interpretation is based on the erroneous reconstruction of *Cobelodus aculeatus* from Zangerl and Case (1976). Nevertheless, several features can be identified that agree with both *C. aculeatus* and "*Cobelodus*", including: a narrow occipital cotylus with pronounced paired paroccipital processes, a large but anteroposteriorly short postorbital arcade surrounding a wide jugular canal, and paired depressions on either side of the ventral midline (presumably collapse structures in the hypotic lamina beneath the glossopharyngeal canal, as in *C. aculeatus* compression fossils). Zidek's (1992: fig. 4B) reconstruction of the basicranium showed paired basicranial foramina (supposedly for lateral aortae) plus a median opening supposedly for internal carotids, but these are probably collapse structures. The braincase of NMMNH P-19182 therefore displays some symmoriiform features shared by *C. aculeatus* and "*Cobelodus*" and it may have been tropibasic although this cannot be verified. No reconstruction of the braincase is presented here.

DENAEA FOURNIERI Pruvost
(in Fournier and Pruvost, 1922)

GENERAL REMARKS: Based solely on Fournier and Pruvost's (1922) somewhat inadequate description, *Denaea fournieri* seems to have a short, high braincase including a very large, round orbit. The shape of the palatoquadrate resembles that of other symmoriiforms in having a very narrow anterior moiety below the orbit, and a much deeper otic process posteriorly. The braincase of *D. fournieri* is tropibasic, with deep orbits and a narrow ethmoid region (in preparation). No reconstruction of the braincase is presented here.

AKMONISTION ZANGERLI
Coates and Sequeira, 2001a

GENERAL REMARKS: Spectacular skeletal remains of a "stethacanthid" shark have been recovered from the Manse Burn Formation (Serpukhovian, Lower Carboniferous) of Bearsden, Scotland (Wood, 1982). The braincase in this form was first described by Coates and Sequeira (1998), who referred it to *Stethacanthus* sp. Unfortunately, *Stethacanthus* is founded upon isolated dorsal spines whose diagnostic characters are of uncertain taxonomic value. Coates and Sequeira (2001a) referred the Bearsden material to a new genus and species *Akmonistion zangerli*, which was diagnosed on the basis of alleged differences from *Stethacanthus* in the spine-brush complex (especially the presence of a rodlike element within the brush), the arrangement of radials in the tail and paired fins, and the structure of the neurocranium. However, its teeth seem identical to those referred elsewhere to *Stethacanthus* (e.g., Lund, 1974; Ginter, 1999).

CRANIAL MORPHOLOGY: Coates and Sequeira (1998, 2001a) reconstructed the braincase in *A. zangerli* as platybasic (fig. 50) based on four specimens, all of which are flattened to some degree and their original depth cannot be observed directly (although none is compressed as much as the Pennsylvanian sharks from North American black shales). Coates and Sequeira (1998: fig. 2) illustrated several oblique sections through one of these braincases, but only two of them reach the orbit and neither passes through the interorbital region. From their description it is not possible to determine whether an interorbital septum like that of "*Cobelodus*" was originally present, nor whether the basicranial fenestra opened into the floor of the orbit as in "*Cobelodus*".

Similarities between the braincases of *Akmonistion zangerli*, "*Cobelodus*", and *C. aculeatus* include: the large size of the orbits; compact and boxlike otic region (unlike in *Cladodoides*, *Tamiobatis vetustus*, and *Orthacanthus*, where the otic region is elongated and the orbital region is comparatively short); presence of a median aortic canal, extending from below the occipital cotylus and dividing just behind the postorbital arcade before leaving the basicranium; and dorsal otic ridges are weak or absent. In addition, the roof of the braincase in *Akmonistion* is elevated posteriorly, on either side of the posterior dorsal fontanelle, although it does not seem to form a dorsal "chimney" as in "*Cobelodus*". The depth of the palatoquadrate otic process in *Akmonistion* is less than in *C. aculeatus* but is still considerable, suggesting that the depth of the orbit may be greater than shown in the reconstruction.

The suborbital shelf in *Akmonistion* is more extensive than in "*Cobelodus*" and forms a continuous floor to the orbit. The supraorbital shelf is more extensive anteroposteriorly than in "*Cobelodus*" and forms a broad platform extending to the broad postnasal wall, but it apparently lacks a mid-

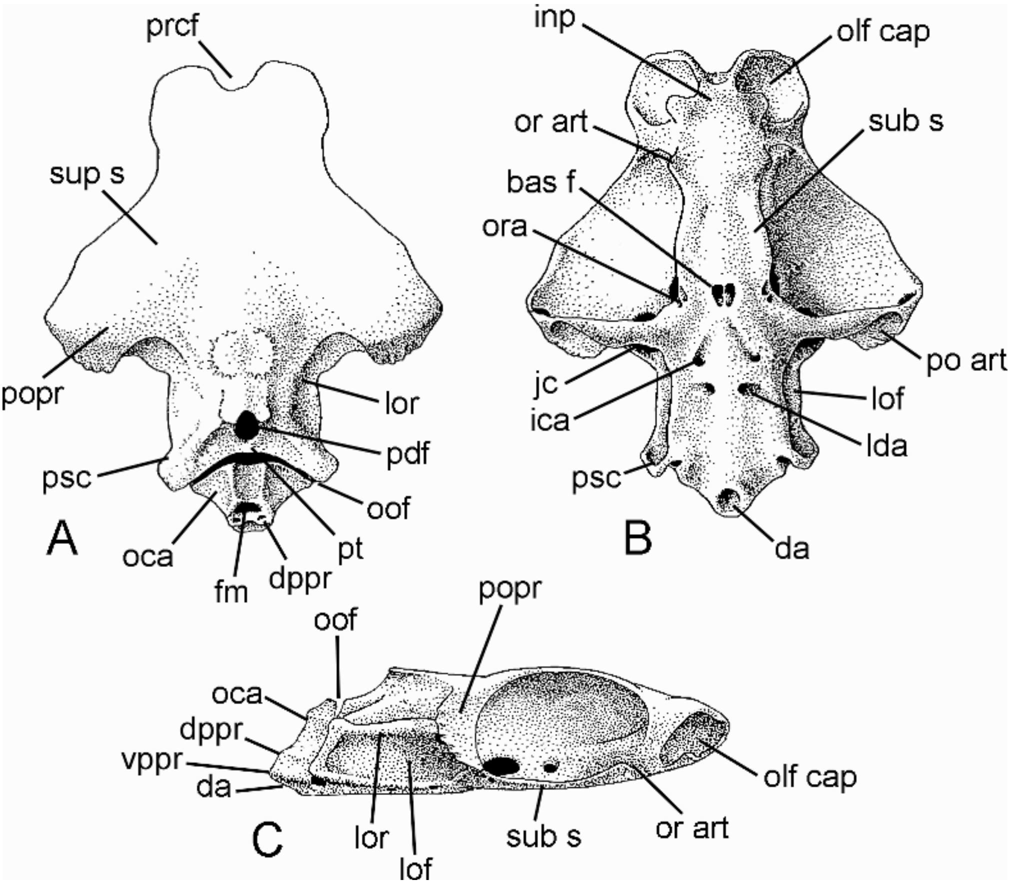

Fig. 50. *Akmonistion zangerli*. Reconstruction of braincase from Coates and Sequeira (1998), with abbreviations changed to agree with those used in the present work. **A**, dorsal view; **B**, ventral view; **C**, lateral view, right side.

orbital notch as in *Cobelodus aculeatus* and *Stethacanthulus meccaensis*. The supraorbital shelf of *Akmonistion* is wider than in *C. aculeatus*, although in both forms it expands posteriorly to meet the postorbital process. A jugular canal is undoubtedly present in *A. zangerli* although its size has not been accurately determined. The otic region in *A. zangerli* is parallel-sided rather than "waisted" as in "*Cobelodus*" and *C. aculeatus*. Consequently, in ventral view the lateral otic fossa in *A. zangerli* can be seen running along the entire length of the otic region (fig. 50B). By contrast, in "*Cobelodus*" and *C. aculeatus*, the hypotic lamina expands posteriorly and obscures the lateral otic fossa in ventral view (cf. figs. 8, 48B). Sections through the otic region in *A. zangerli* suggest that a strong lateral otic ridge extended along most of the lateral capsular wall, and there is no evidence of a periotic process. Coates and Sequeira (1998) depict the posterior dorsal fontanelle in *A. zangerli* posterior to the crus commune, a difference not only from "*Cobelodus*" and *C. aculeatus* but also from platybasic sharks such as *Cladodoides* and *Orthacanthus* (where the fontanelle is flanked by the left and right crus commune). In modern elasmobranchs, the endolymphatic fossa (considered homologous to the posterior dorsal fontanelle; Maisey, 2001b, 2004b) is also located between the upper part of the posterior semicircular canal rather than behind it (although a crus commune is absent; e.g., *Notorynchus*, *Squalus*). The location of the posterior fontanelle in *A. zangerli* is therefore unusual for elasmobranchs, but the posterior dorsal fontanelle also lies posterior to the crus commune in some early actinopterygians (e.g., *Mimia*; Gardiner, 1984a: fig. 26).

The arterial circuit in *Akmonistion zangerli* as interpreted by Coates and Sequeira (1998) is clearly at odds with the arrangement hypothesized here in "*Cobelodus*", and *C. aculeatus*. In all these forms, however, the dorsal aorta was unpaired where it entered the basicranium and divided before it emerged from the cartilage. *Akmonistion zangerli* and *C. aculeatus* are also similar in having only two pairs of basicranial foramina. According to Coates and Sequeira (1998), the posterior pair contained only the efferent hyoidean artery in *A. zangerli*, but the corresponding foramina in *C. aculeatus* probably contained the lateral aorta (figs. 41, 44–46).

The presence of internal carotid arteries in *Akmonisition* is suggested by paired basicranial grooves that converge behind the basicranial fenestrae (Coates and Sequeira, 1998: fig. 3). Faint depressions occupy a corresponding position in some specimens of *Cobelodus aculeatus* (fig. 46). Coates and Sequeira (1998) suggested that the efferent pseudobranchials in *A. zangerli* exited via separate foramina, a different arrangement from that postulated in "*Cobelodus*".

"*STETHACANTHUS*"

General Remarks: The genus *Stethacanthus* (type species *S. altonensis*) is founded on isolated but distinctive dorsal spines from the Mississippian of North America (Newberry, 1889). The spine in *Akmonistion* is nevertheless virtually identical to those of *Stethacanthus*, suggesting that spine morphology is a poor criterion for recognizing genera. The earliest endoskeletal remains referred to *S. altonensis* (also representing the earliest symmoriiform fossils) are from the Famennian (late Devonian) Cleveland Shale of Ohio (Williams, 1985). The majority of fossils referred to *Stethacanthus* are of Mississippian age, including some specimens with a braincase, e.g., a laterally compressed head from the Waverly Black Shale (AMNH 1734) referred to *S. altonensis* (Zangerl, 1981; Williams, 1985), and three specimens from the Bear Gulch Limestone of Montana (Serpukhovian, Namurian E2b, Upper Mississippian; MV 2830, CM 23654, CM 37680; Lund, 1974, 1985b), the stratigraphic equivalent of *Akmonistion* from Scotland. Lund (1974) identified MV 2830 as a male individual and considered that CM 23654 represented a female, but subsequently commented that its "clasper cartilages are unknown" (Lund, 1985b: 2). He originally referred both specimens to *S. altonensis*, but subsequently referred CM 23654 to *S.* cf. *S. productus* (Lund, 1985b). The stratigraphically youngest skeletal fossils that have been referred to *S. altonensis* are from the Logan Quarry Shale of Indiana (Desmoisnian, Westphalian Upper C, Pennsylvanian; Williams, 1985).

Lund (1974) and Williams (1985) considered that many of the nominal species of *Stethacanthus* founded on isolated dorsal spines may be synonymous, and suspected that differences between them are attributable either to taphonomic effects or to individual variation. The teeth of *Stethacanthus* have a characteristic cusp and basal plate morphology (M. Ginter, personal commun., February, 2006). The median cusp of the tooth is moderately thick in Bear Gulch specimens referred to *Stethacanthus* (Lund, 1974: fig. 11a; note, however, that isolated teeth referred to *Stethacanthus* in Lund [1985b: fig. 8] are probably not even symmoriiform; Ginter et al., 2005). The median cusp is also thick in teeth associated with a partial skeleton with a "stethacanthid" spine-brush complex from Oklahoma, referred by Zidek (1993) to *S.* cf. *S. altonensis*, as well as in *Gutturensis nielsoni* and *Akmonistion zangerli* (Sequeira and Coates, 2000: fig. 6; Coates and Sequeira, 2001a: fig. 4). The teeth in AMNH 1734 have a slightly more slender median cusp and relatively longer lateral cusps than in the aforementioned specimens, but these differences may represent variation related to age or position in the jaw. Williams (1985) referred some Upper Mississippian teeth from the Sunbury Shale to *Stethacanthus*, but did not figure the teeth of the Pennsylvanian specimen (FMNH PF 2207).

Cranial Morphology: Lund's (1974, 1985b) illustrations of braincases referred to *Stethacanthus* are reproduced here (fig. 51;

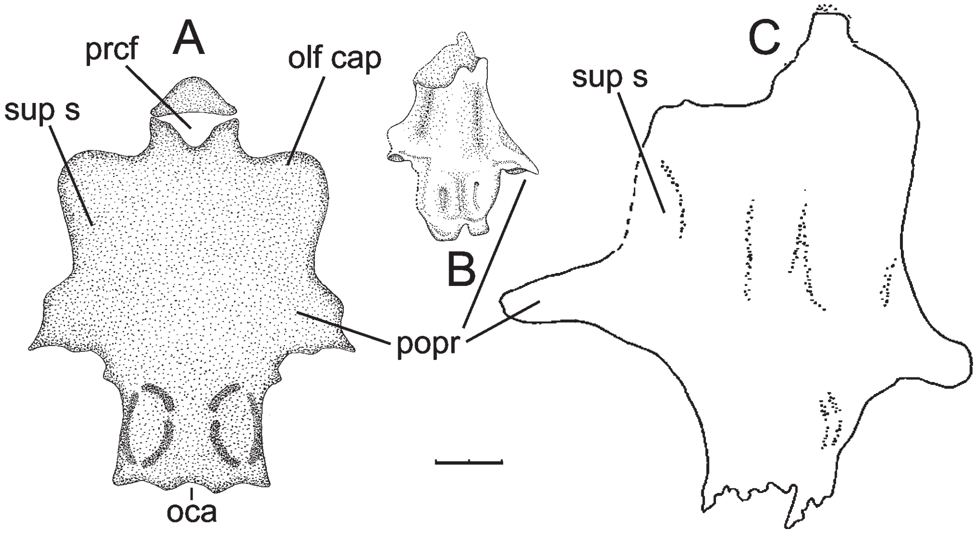

Fig. 51. Outline dorsal views of the braincase in three specimens that have been referred to *Stethacanthus*, all from the Bear Gulch Limestone (Chesterian, late Pennsylvanian). **A**, Specimen referred to *S. altonensis*, MV 2830 (from Lund, 1974: fig. 3); **B**, specimen referred to *S.* cf. *S. altonensis* (from Lund, 1985: fig. 4); **C**, specimen referred to *S.* cf. *S. productus* (from Lund, 1985: fig. 1). Anterior to top. The original illustrations have been adjusted to approximately the same scale (scale bar = 10 mm). See text for details.

note that the illustrations have been scaled according to information in the original papers and annotated to agree with other figures in the present work). The information content of these specimens is low and only their dorsal surfaces can be compared. There is an enormous disparity in size between these individuals; the braincase in CM 37680 is about half the length of that in MV 2830 and one third that of CM23654. Also, the smallest specimen has narrower supraorbital shelves than the others (possibly an age-related feature, since the shelf appears late in modern elasmobranch ontogeny and frequently does not attain its full extent until maturity; Holmgren, 1940). Otherwise, the specimens are similar in overall morphology and proportions, with a short otico-occipital region and relatively longer orbital region. As illustrated by Lund (1974, 1985b), there is no indication of a persistent otico-occipital fissure, but the shape of the posterior margin of MV 2830 suggests that the occipital cotylus is flanked by large, paired glossopharyngeal canals comparable to those in "*Cobelodus*".

AMNH 1734 (fig. 52) is a laterally compressed symmoriiform head from the Waverly Black Shale (early Mississippian), referred by Zangerl (1981) and Williams (1985) to *Stethacanthus altonensis*. The postcranial skeleton is not preserved and it is unknown whether this individual possessed a "stethacanthid" spine-brush complex, but the top of the head is covered by a thick-set patch of "*Lambdodus*" denticles arranged geometrically in alternating rows. The large orbit size in this specimen is reminiscent of "*Cobelodus*", suggesting that an interorbital septum is present (although it is extremely difficult to find traces of cartilage beneath the dense teeth and denticles filling the orbit, and CT-scanning was uninformative).

FMNH PF 2207 is an articulated symmoriiform from the Pennsylvanian of Indiana (fig. 53). The specimen includes a spine-brush complex and teeth that are identical to those referred elsewhere to *Stethacanthus*, which led Williams (1985) to refer this specimen to *Stethacanthus altonenis*. Although the orbits are large, few other features can be recognized in X-rays Nevertheless, the outline of the braincase is similar to that of "*Cobelodus*". A large, circular shadow within the orbit in the X-ray is provisionally interpreted as sclerotic cartilage, but there is no evidence

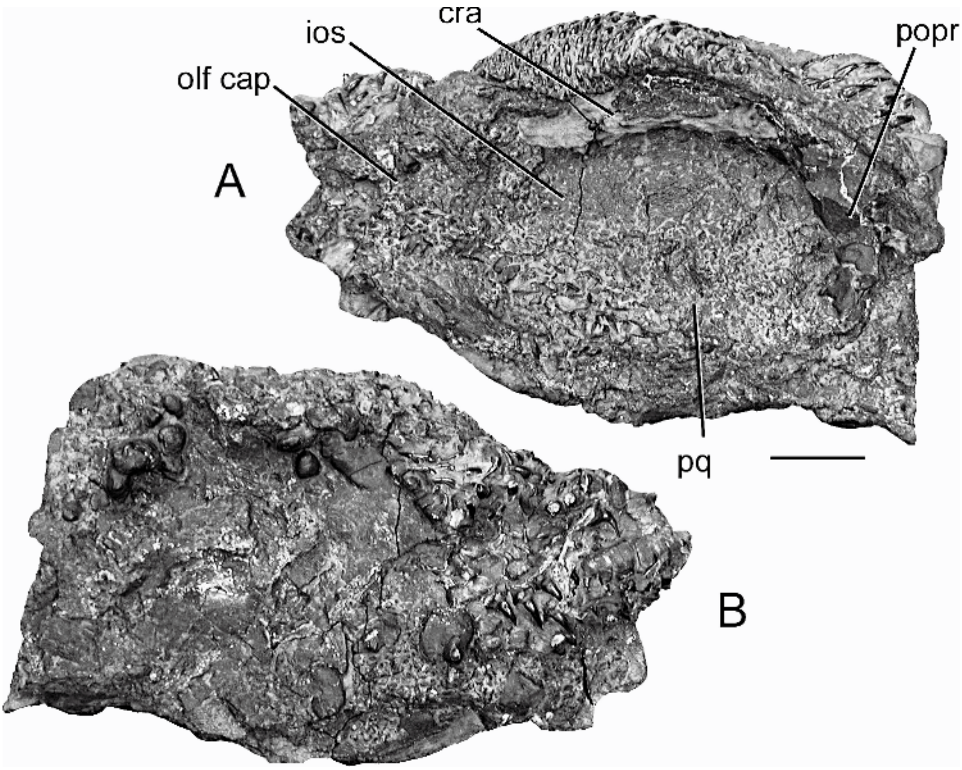

Fig. 52. Lateral view of AMNH 1734, a complete head referred to *Stethacanthus altonensis*, from the Sunbury Shale (= "Waverly Black Shale", Tournaisian, Lower Mississippian) of Ohio. **A**, left side; **B**, right side. The specimen has a deep, round orbit, a deep postorbital otic process, and a slender palatine ramus. Scale bar = 10 mm.

of separate ossifications as in falcatids (see below).

Coates and Sequeira (2001a: 439) considered that the morphology of the braincase in *Akmonistion zangerli* differed "significantly" from specimens referred to *Stethacanthus* (including AMNH 1734 and FMNH PF 2207), but many of the supposed differences are equivocal. For example, although they claimed that the postorbital process in *Akmonistion* projects "farther from the main body of the neurocranium" than in the Bear Gulch specimens (ibid: 440), *Akmonistion* seems to be intermediate between MV 2830 and CM23654 in this respect (figs. 50, 51). They also suggested that the supraorbital shelf was "more extensive" in *Akmonistion*, but it seems no larger than in MV 2830 or CM23654. The posterior dorsal fontanelle in *Akmonistion* is supposedly wider and better defined than in other "stethacanthids", but this feature was not illustrated or described by Lund (1974, 1985b) and is unknown in other material referred to *Stethacanthus*. The only remaining cranial feature by which Coates and Sequeira (2001a) distinguished *Akmonistion* from *Stethacanthus* is the supposedly narrower span of the olfactory capsules in the former. The ethmoidal region certainly appears wider in MV 2830 and CM23654, but its overall breadth is not a reliable indicator of the distance between the capsules or the width of the internasal septum, as shown by *Cobelodus aculeatus* and *Stethacanthulus meccaensis* (figs. 39, 49). The ethmoidal region is broad in both those forms, but in *C. aculeatus* the capsules are positioned at the lateral extremities of the ethmoid region whereas in *S. meccaensis* they lie closer to the midline (unfortunately, the arrangement of the olfactory capsules cannot be compared in material referred to *Stetha-*

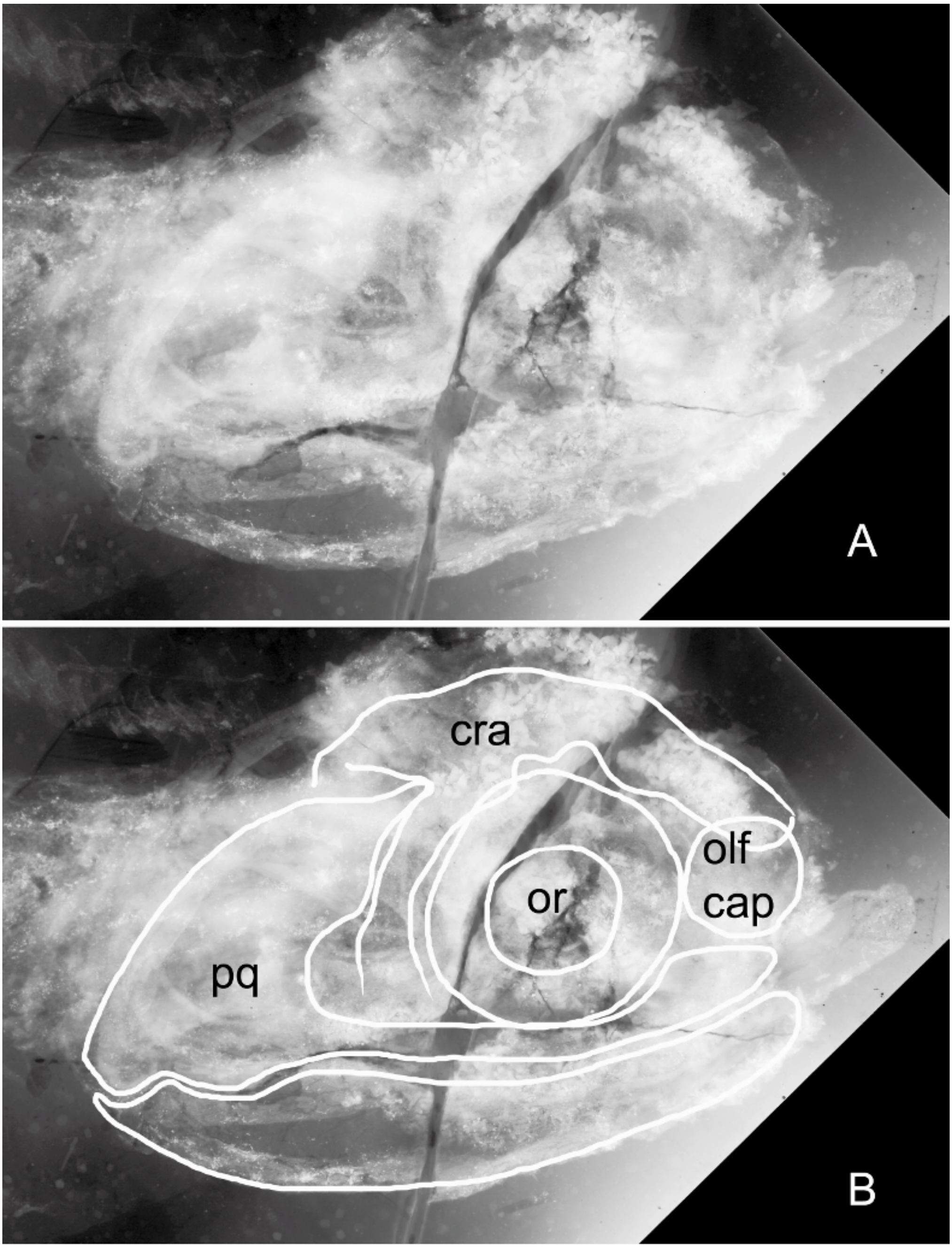

Fig. 53. **A**, X-ray of the head in FMNH PF 2207, an almost complete skeleton referred to *Stethacanthus altonensis*, from the Logan Quarry Shale (Desmoinesnian, Westphalian Upper C, Pennsylvanian), Parke County, Indiana. **B**, same view, with outlines of the orbit, braincase, olfactory capsule, palatoquadrate, and Meckel's cartilage outlined in white. Note the extremely deep postorbital arcade, the large, round orbit, the deep palatoquadrate postorbital flange, and the comparatively slender palatine ramus below the orbit. Anterior to right.

canthus). The putative differences in cranial morphology between *Akmonistion* and *Stethacanthus* proposed by Coates and Sequeira (2001a) need to be verified from better material.

DWYKASELACHUS OOSTHUISENI
Oelofsen, 1986

General Remarks: *Dwykaselachus oosthuiseni* is founded on a single specimen of a chondrichthyan braincase (SAM K5840), from the Prince Albert Shale Formation in Cape Province, South Africa (Artinsian-Sakmarian, Lower Permian; Oelofsen, 1986). The specimen is well preserved in three dimensions as a hollow cast within a radiolarian-rich nodule. From Oelofsen's (1986) description, it is not possible to resolve the systematic position of *Dwykaselachus* satisfactorily although it may represent a symmoriiform (making it the youngest example known from cranial material). Unfortunately, as described, its features represent a curious anatomical mixture unknown in any other shark, and it was not possible to obtain the specimen for investigation. Therefore, the inclusion of *Dwykaselachus* in this work is highly provisional and the following remarks are inconclusive, but the affinities of this enigmatic Permian shark may nevertheless be closer to symmoriiforms than to modern elasmobranchs.

Cranial Morphology: The overall shape of the braincase in *Dwykaselachus* is reminiscent of "*Cobelodus*", especially the broad postorbital arcade, the short and narrow otic region with a narrow "waist" immediately behind the postorbital arcade, and the extremely large orbits. The chordal part of the basicranium is exposed as far as the prominent dorsum sellae. In front of this is a median opening, interpreted by Oelofsen (1986) as the hypophyseal fossa. He identified traces of paired canals (supposedly for internal carotid arteries) in the fossa, as well as paired grooves for lateral dorsal aortae on the ventral surface of the basicranium farther posteriorly. He also interpreted the glossopharyngeal nerve as leaving the basicranium beneath the otic capsules, an extremely unusual position for a shark (Oelofsen, 1986: fig. 10). Comparison of his illustrations with the "*Cobelodus*" braincase suggests that the glossopharyngeal nerve in *Dwykaselachus* passed between the cranial cavity and otic capsule and then above a wide hypotic lamina below the occipital arch. The feature identified by Oelofsen (1986) as the floor of the saccular chamber may instead be the dorsal surface of the hypotic lamina below the capsule, and the passage he identified as a glossopharyngeal foramen may have allowed that nerve to enter an extensive canal below the capsule, as in "*Cobelodus*".

The labyrinth in *Dwykaselachus* shares an interesting plesiomorphic feature with "*Cobelodus*" and platybasic Paleozoic sharks such as *Cladodoides*, namely, the presence of a crus between the anterior and posterior semicircular canals (Oelofsen, 1986: fig. 12). Although this feature has little phylogenetic significance, at least it shows that *Dwykaselachus* did not possess the specialized inner ear morphology that characterizes modern elasmobranchs and hybodonts (Maisey, 2001b; Maisey et al., 2004). The posterior dorsal fontanelle in *Dwykaselachus* is small and rounded, and is located at the highest part of the cranial roof, as in "*Cobelodus*" (Oelofsen, 1986: fig. 40). The region presumably formed by the posterior tectum is long, again as in "*Cobelodus*".

Oelofsen (1986) identified paired occipital condyles in *Dwykaselachus*, and claimed this was a synapomorphy with modern sharks. However, the "condyles" may instead be paired epioccipital processes like those of "*Cobelodus*" (although it cannot be determined from his illustrations whether these are dorsal or ventral in position). The position of the posterior ampullae can be determined, but from the published figures it is unclear whether a persistent otico-occipital fissure was present. *Dwykaselachus* apparently lacks a lateral otic process, but there is no evidence of a periotic process like that in "*Cobelodus*".

The postorbital arcade in *Dwykaselachus* is wide and deep, with a large central jugular canal (though apparently smaller than in "*Cobelodus*"; see Oelofsen, 1986: fig. 7). There is a canal in the ventral part of the arcade, lateral to the jugular canal, which possibly housed the buccal branch of the trigeminal nerve. Oelofsen (1986: fig. 3) reconstructed *Dwykaselachus* with a postorbital articulation low on the ventrolateral part of the postorbital arcade as in "*Cobelodus*" (i.e., on cartilage presumably formed in the lateral commissure), but did not describe or illustrate the articular facet.

The interorbital region in *Dwykaselachus* is narrow, although Oelofsen (1986: figs. 3, 4) interpreted the braincase as platybasic. However, there could be an interorbital septum below the main cranial cavity at the level of the postorbital arcade (Oelofsen, 1986: fig. 7). Furthermore, as Oelofsen (1986: 116) noted, *Dwykaselachus* resembles *Cobelodus aculeatus* (and "*Cobelodus*") in lacking a suborbital shelf. *Dwykaselachus* possesses an extensive transverse postnasal wall, anterior to which the paired olfactory capsules are located fairly close to the midline.

Oelofsen (1986: fig. 13) suggested that *Dwykaselachus* was closely related to *Synechodus* and modern elasmobranchs, based on several putative synapomorphies including: paired occipital condyles; a "true" rostrum; location of the occipital arch wedged between the otic capsules; short "parietal" fossa; and "adult hypophyseal duct closed externally". However, the "condyles" may be homologous to the epioccipital processes in "*Cobelodus*", a prominent rostrum is present in falcatid symmoriiforms (although it is usually uncalcified), a "short" occipital region is common in symmoriiforms (and also occurs in basal chondrichthyans such as *Pucapampella*; Maisey and Anderson, 2001), and the hypophyseal region is closed off from the cranial cavity in "*Cobelodus*". Within the "hypophyseal duct", Oelofsen (1986: 122, fig. 9) identified a pair of laterally situated foramina supposedly within the floor of fenestra, although from his illustration these appear to be in its roof (a similar arrangement to "*Cobelodus*"?).

FAMILY FALCATIDAE ZANGERL 1990

FALCATUS FALCATUS

(St. John and Worthen, 1883)

MATERIAL EXAMINED: MV 4793, well-preserved head, part and counterpart, laterally compressed; MV 5448, head and disarticulated visceral skeleton, part only, laterally compressed; MV 5392, anterior region of body including a large dorsal spine, and head preserved in lateral oblique view, part and counterpart; MV 6156, almost complete laterally compressed individual with dorsal spine and poorly preserved axial skeleton, part and counterpart; MV 6951, broken specimen of anterior part of body, with braincase in dorsoventral view, part and counterpart; MV 6956, almost complete individual with impression of large dorsal spine, laterally compressed, part only; MV 7689, complete individual with well-developed dorsal spine, laterally compressed, part and counterpart; MV 7690, complete individual with small (presumably immature) dorsal spine, laterally compressed, part and counterpart; all from Fergus County, Montana; Bear Gulch Limestone, Bear Gulch member, Heath Formation, Upper Chesterian, Namurian E2b, Upper Mississippian.

GENERAL REMARKS: Lund (1985a) erected the genus *Falcatus* for a species originally referred to *Physonemus* (*P. falcatus* St. John and Worthen, 1883), and described several fairly complete specimens from the Bear Gulch Limestone of Montana (Serpukhovian, Namurian E2b, Upper Mississippian). Zangerl (1990) considered *Falcatus* and *Damocles* (discussed below) sufficiently distinct from other "stethacanthids" to warrant placing them in a separate Family Falcatidae.

The braincase is preserved in many specimens of *Falcatus falcatus*, in a variety of orientations that collectively provide a good idea of its overall shape and morphology (figs. 54–56). A peculiar recurved dorsal spine is present just behind the head, but in *Falcatus* the spine is not associated with a "brush complex" of fin rays and denticles like that of *Stethacanthus*. Instead, the dorsal spine supports a rodlike structure composed of long, hollow tubes. These tubes seem to consist of fused fin rays that Lund (1985a) considered homologous with the "brush" in *Stethacanthus* (disputed by Coates and Sequeira, 2001a). Lund (1985a) presented convincing evidence that the spine-brush complex is present only in male *F. falcatus*, and only in individuals above 124 mm standard length. *F. falcatus* is a comparatively small shark, the largest individuals being about 140–150 mm in length. The teeth of *F.*

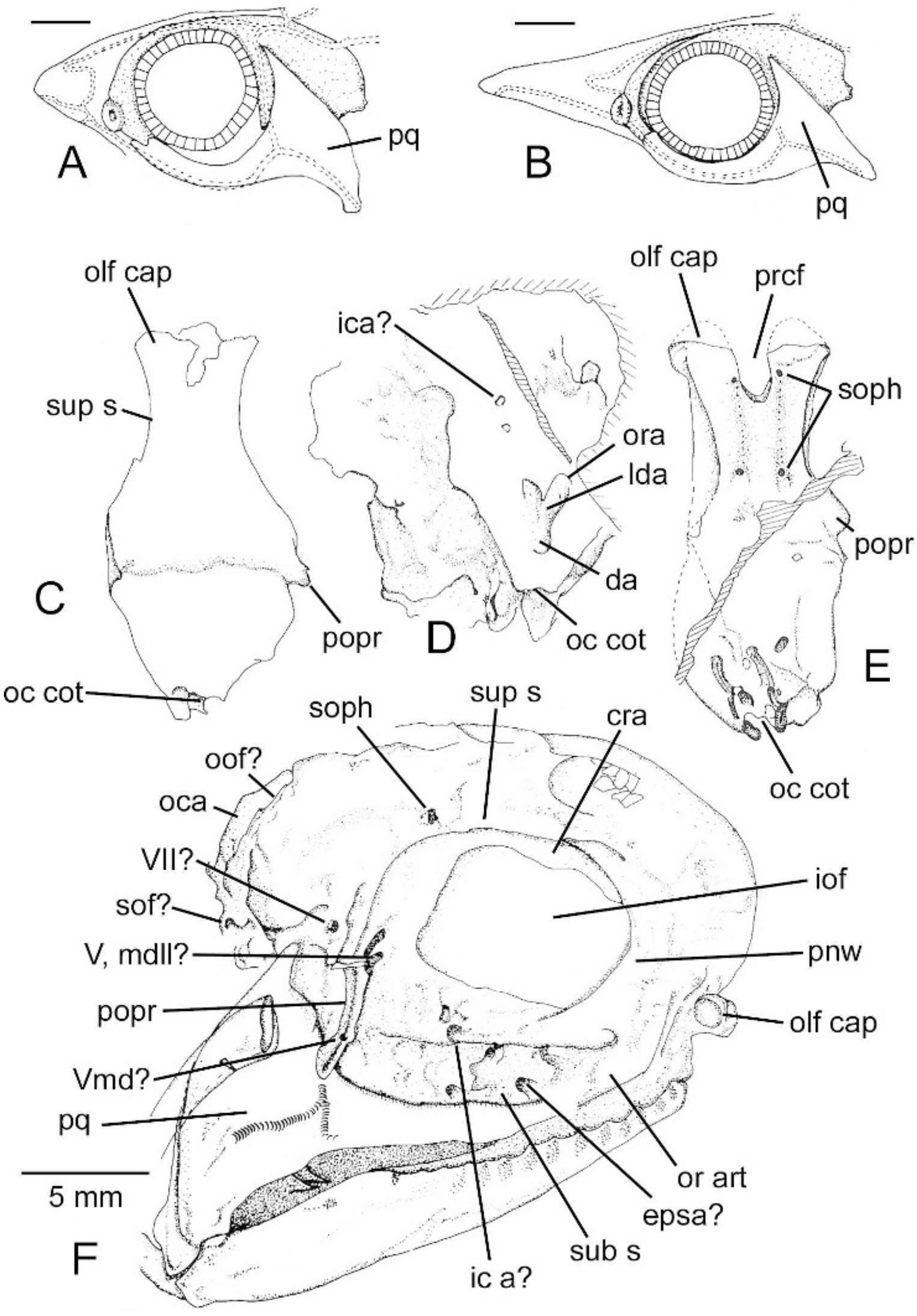

Fig. 54. Features of the head and braincase in *Falcatus falcatus*, from the Bear Gulch Limestone (Chesterian, late Pennsylvanian). All illustrations from Lund (1985a), with annotations changed to agree with those used in this work. **A**, MV 5386, lateral view of braincase and palatoquadrate; **B**, MV 5385, lateral view of braincase and palatoquadrate; **C**, CM 23677, dorsal view of braincase; **D**, MV 6951, ventral view of braincase; **E**, MV 6951, dorsal view of braincase. **F**, MV 5392b, lateral view of head skeleton. 5 mm scale bar shown in A, B, F; no scale was originally provided for C–E.

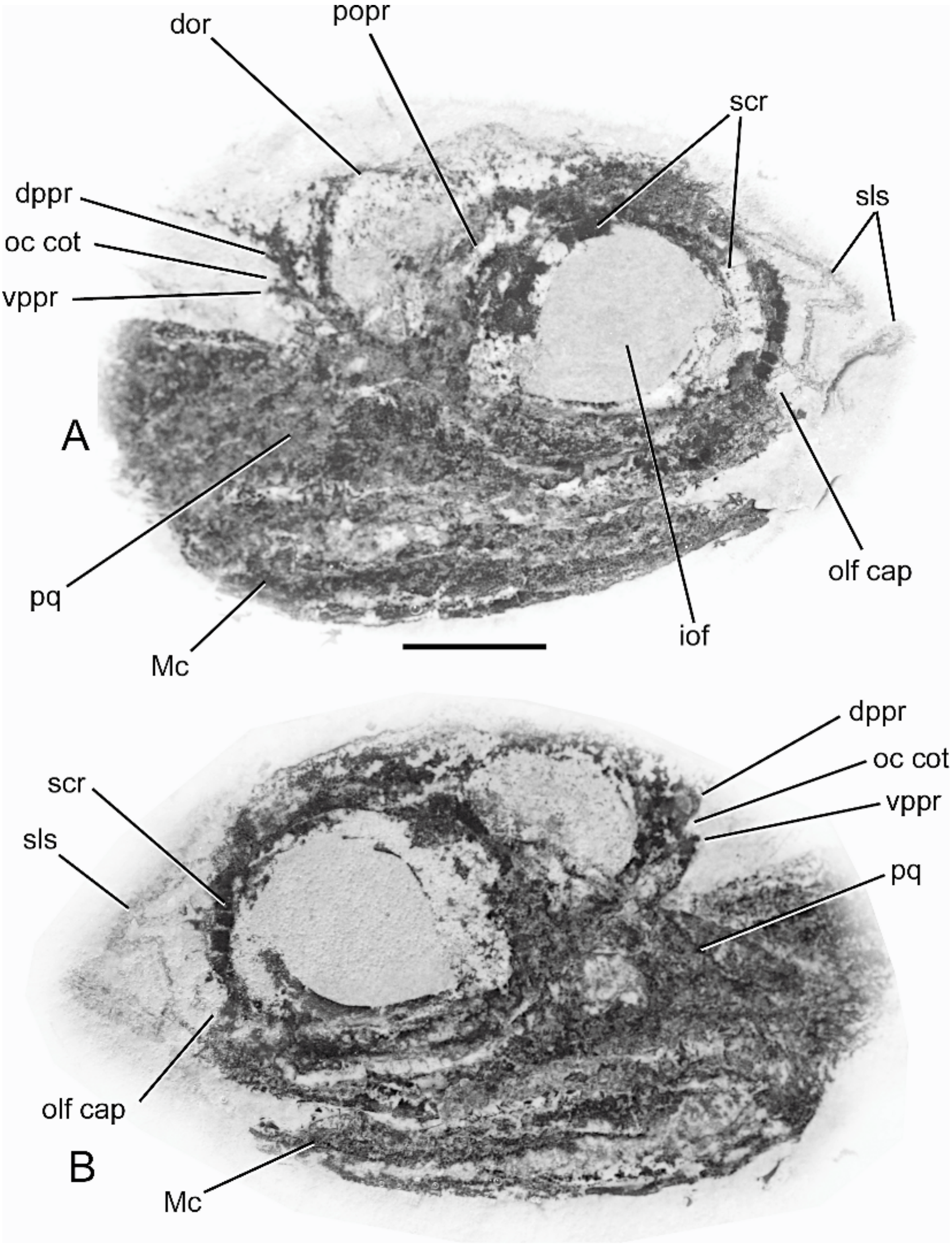

Fig. 55. *Falcatus falcatus* MV 4793, part and counterpart, Bear Gulch Limestone. Head in lateral view (original specimen, uncoated). Anterior to right in A, to left in B. Scale bar = 5 mm.

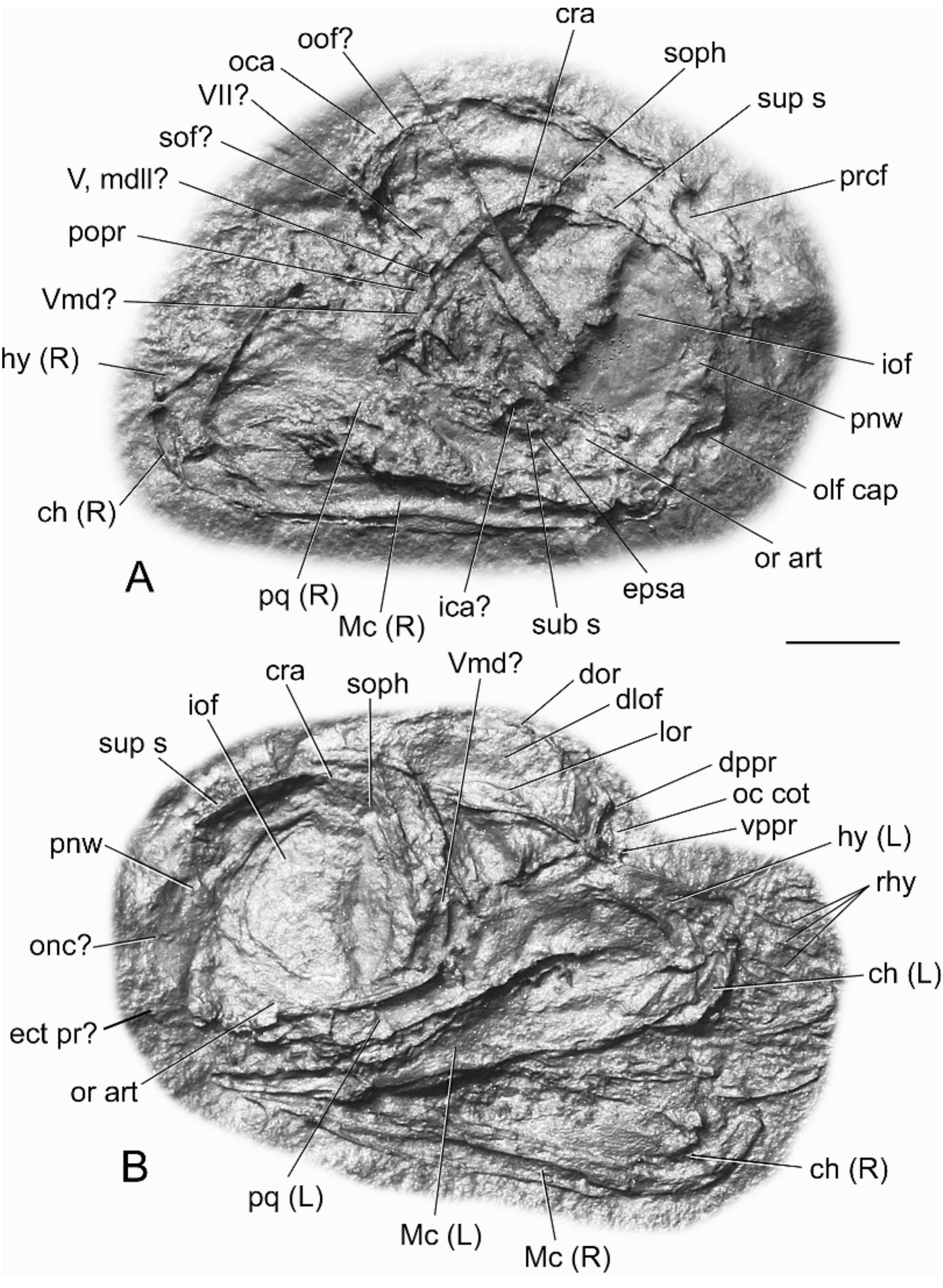

Fig. 56. *Falcatus falcatus* MV 5392, part and counterpart, Bear Gulch Limestone. Head. **A**, dorsolateral view, right side; **B**, ventrolateral view, left side. From silicone peels, blackened with graphite. Scale bar = 5 mm.

falcatus are extremely small and resemble those referred to *Stethacanthus* in their multicuspid "cladodont" morphology, but are otherwise poorly known.

DESCRIPTION: Lateral views of the braincase show a deep, round orbit. The postorbital flange of the palatoquadrate is particularly deep, but the palatine ramus is slender (as in the *Stethacanthus* specimens described earlier). Large eye size is confirmed by the presence of a ring of "sclerotics" (sensu Lund, 1985a) consisting of numerous plates extending around the margin of the orbit (fig. 55). This ring extends ventrally as far as the palatine part of the palatoquadrate (which is concave below the orbit), and in some specimens the eye itself may be represented by dark (choroid?) pigment that almost completely fills the orbit. The hard tissue forming the sclerotic plates was described as a "smooth, dense, glossy mineralization lacking any evidence either of fusion of denticles or of Tome's processes" (Lund, 1985a: 17), and was interpreted as acellular bone. The ring presumably lay at the corneal-scleral limbus of the eye, suggesting that it is homologous to the ring of scleral ossicles of osteichthyans, rather than to the scleral cartilage that supports the eyeball in gnathostomes generally (see discussion below).

In MV 5392, compression of the fossil has flattened the left postnasal wall anteriorly so that it covers and obscures the olfactory capsule (fig. 56B). Unlike in "*Cobelodus*", the postnasal wall is strongly calcified and forms a continuous surface that defines the front of the orbit. This surface is penetrated by a foramen centrally, possibly indicating the position of the orbitonasal canal (which marks the location of fusion between the orbital cartilage and orbitonasal lamina in modern gnathostomes; De Beer, 1937). The postnasal wall extends as a short ventrolaterally directed process that may correspond to the ectethmoid process (formed in cartilage lateral to the orbitonasal canal in modern elasmobranchs; Holmgren, 1940; Maisey, 1983, 2004b; Coates and Sequeira, 1998; Maisey et al., 2004). In other *Falcatus* specimens, impressions of denticles associated with sensory canals show that the rostrum extended a considerable distance anterior to the postnasal wall and the olfactory capsules, especially in males (it may have been shorter in females), but there is no evidence that the cartilage forming the snout was calcified.

The dorsal surface of the braincase was apparently narrower in *Falcatus falcatus* than in *Cobelodus aculeatus*, *Stethacanthulus meccaensis*, or *Akmonistion zangerli*, with only a narrow supraorbital shelf (indicated by a row of pores for nerve ramules supplying the supraorbital sensory canal; e.g., MV 6951, CM 23677; fig. 48C, E). In this respect, the braincase of *Falcatus* resembles smaller individuals referred to *Stethacanthus* (cf. fig. 51), suggesting that either they were not fully developed or *Falcatus* retained the juvenile condition into adulthood. Lund (1985a) found no evidence of a large posterior dorsal fontanelle in *Falcatus*, and suggested that there may have been have been only small, paired openings for the endolymphatic ducts (although these were not identified). The olfactory capsules in *F. falcatus* lie close to the midline on either side of a deep recess in the roof of the braincase (probably marking the position of the precerebral fontanelle).

According to Lund (1985a), the ventral surface of the braincase has a strong internasal keel and a very narrow interorbital region, and lacks suborbital shelves as well as a basicranial fenestra. In the floor of the otic region of MV 6951, however, he noted a Y-shaped groove, with the arms of the Y diverging anteriorly and each containing a foramen (fig. 54D). Lund (1985a) hypothesized that these grooves contained the lateral aortae, and it is possible that the groove marks the course of a median aorta, which diverged into paired lateral aortae anteriorly, as in "*Cobelodus*", *Cobelodus aculeatus*, and *Akmonistion zangerli*, since the stem of the Y extends along much of the otic region and terminates a short distance in front of the occipital cotylus. The dorsal aorta in *F. falcatus* may therefore have been enclosed by cartilage only beneath the occipital arch, emerging farther anteriorly before giving rise to the internal carotid, orbital and efferent hyoidean arteries. The foramina associated with the arms of the Y-shaped groove may have housed the orbital arteries on their way to the orbits. Lund (1985a: fig. 9) also noted the presence of small basicranial foramina farther anteriorly (presumably below the orbit). These may be homologous to the paired openings in "*Cobelodus*" that connect the basicranial fenestra to the orbit, perhaps allowing the internal carotids to enter the orbits as postulated earlier. Lund (1985a: 8) claimed that there is a marked basal angle in *Falcatus*, but this is not evident in the illustrations and there is no evidence of one in the material examined. The anteroposterior profile of the basicranium is similar to that in "*Cobelodus*", where a basal angle is absent.

Lund (1985a) noted a large uncalcified interorbital fenestra in *Falcatus*. This was probably bridged in life by a membranous septum and suggests that the cranial cavity in *Falcatus* did not extend ventrally as far as the basicranium (i.e., that its braincase was tropibasic, as in "*Cobelodus*"). A suborbital shelf (supposedly absent according to Lund, 1985a) may be represented by an area of cartilage located ventral to the large interorbital fenestra. Lund (1985a) identified foramina for the orbital artery and palatine ramus posteriorly in the floor of the orbit, as well as foramina for the optic and olfactory nerves farther anteriorly. However, if the cranial cavity was confined to the dorsal part of the orbit as in "*Cobelodus*", these openings could not have communicated with the cranial cavity. A silicone peel of MV 5392B shows at least one prominent opening within the floor of the orbit, corresponding to the canal connecting the basicranial fenestra and the orbit in "*Cobelodus*" and suggesting that the internal carotid entered the orbit in similar fashion (cf. figs. 14, 15, 56). Openings identified by Lund (1985a) as optic and olfactory foramina are positioned adjacent to a slightly thickened part of the basicranium. Comparison with "*Cobelodus*" suggests that one of these openings probably contained the efferent pseudobranchial artery, and that the thickened area adjacent to it represents the orbital articulation. In that case, the embryonic polar cartilage in *Falcatus* may have been as extensive as in "*Cobelodus*". Lund (1985a: 9, fig. 7) observed a "notch and ventral facet on the ventral surface of the ethmoid region for the ethmoid articulation of the palatoquadrate" in MV 4750, and suggested that the palatoquadrate was strongly braced against the braincase anteriorly. Although the opening identified by Lund (1985a) as the olfactory foramen lies only a short distance behind the capsule, the olfactory nerve could not have exited here if the braincase was tropibasic, but may instead have passed through the antorbital wall farther dorsally.

Other foramina identified by Lund (1985a) in the posterior wall of the orbit of *F. falcatus* seem to match those in "*Cobelodus*", apart from a foramen interpreted by Lund (1985a) as the jugular canal. Comparison with "*Cobelodus*" suggests that this opening probably contained the hyoidean ramus of the facial nerve.

The postorbital arcade in MV 5392 is slender but continuous, forming a delicate rim to the posterior part of the orbit between the sclerotic ring and the palatoquadrate postorbital flange (fig. 56). A canal running through the arcade was interpreted by Lund (1985a: fig. 10) as containing the "nerve for infraorbital lateral line canal" (i.e., the buccal ramus of the anterodorsal lateral line nerve). A similar canal is present in the postorbital arcade of "*Cobelodus*" (see above) and *Cladodoides* (Gross, 1937; Maisey, 2005), and may have housed the buccal maxillary complex and/or the mandibular ramus of the trigeminal nerve.

In MV 5392, the occipital arch appears to be separated from the otic capsule by a persistent otico-occipital fissure (identified as a "nuchal crest" by Lund, 1985a). A foramen in the lower part of the occipital region may have contained a spino-occipital nerve rather than the glossopharyngeal nerve as Lund (1985a) suggested, since this nerve occupies a wide glossopharyngeal canal between the floor of the otic capsule and the hypotic lamina in "*Cobelodus*" and other Paleozoic sharks (e.g., *Cladodoides*, *Tamiobatis*, *Orthacanthus*). In chondrichthyans, a separate glossopharyngeal canal is present in hybodonts and modern elasmobranchs (in which the hypotic lamina has fused to the overlying capsular wall) and in chimaeroids (in which the hypotic lamina is not expanded beneath the otic capsule and the nerve passes through the basicranium ventrally, as in osteichthyans). This reinterpretation of the glossopharyngeal nerve passing through a persistent metotic fissure in *F. falcatus* is important, because it was coded as *not* doing so in *Falcatus* and *Damocles* by Coates and Sequeira (2001b). In their phylogenetic analysis, this feature represented a reversal and helped unite these forms with holocephalans (which were coded in an identical fashion, although the relationship of the glossopharyngeal nerve to the basicranium differs in chimaeroids and sharks; in the former, there is no hypotic lamina or metotic fissure, whereas in the latter the fissure is closed secondarily during ontogeny and the hypotic lamina fuses to the floor of the otic capsule; De Beer, 1937).

The palatoquadrate in *Falcatus* is closely associated with the entire posterolateral margin of the postorbital arcade (Lund, 1985a). The palatoquadrate attachment behind the orbit may have been strengthened by ligaments or extensive connective tissue, suggesting that the original postorbital articulation was weak (and possibly rigid). The palatoquadrates reach the ethmoid region anteriorly, but the jaws are not "terminal", terminating instead on the ventral surface of the head below the snout (as in many modern elasmobranchs). Presence of an elongate snout has been used to distinguish falcatids from other symmoriiforms (Zangerl, 1990), but the original extent of the rostrum in the latter may have been underestimated because it is extremely rare for parts of the braincase anterior to the orbit to be preserved in fossil sharks.

DAMOCLES SERRATUS Lund, 1986

MATERIAL EXAMINED: MV 5449, complete small individual lacking a dorsal spine, with the head in ventrolateral view, and a twisted caudal skeleton, part and counterpart; MV 6158, dorsal spine in lateral view, associated with scattered dermal denticles, part and counterpart; MV 7685, small curled skeleton with well-preserved head and detached dorsal spine lying across caudal fin, part and counterpart; all from Fergus County, Montana; Bear Gulch Limestone, Bear Gulch member, Heath formation, Upper Chesterian, Namurian E2b, Upper Mississippian.

GENERAL REMARKS: *Damocles serratus* is the second falcatid symmoriiform described from the Bear Gulch Limestone of Montana (Lund, 1986). Fewer specimens are known than for *Falcatus falcatus* and its skeletal anatomy is less completely known. No females have been identified satisfactorily, although one specimen of uncertain gender lacks a dorsal spine (MV 5449). Where present, the spine resembles that of *Falcatus*, but it is not associated with a *Stethacanthus*-like "brush" or a *Falcatus*-like dorsal rod (although this could be fused to the distal part of the spine). Lund (1986) described the teeth of *D. serratus* as similar to those of *F. falcatus*, although they may have a shallower lingual torus. *Damocles* teeth may also lack an apical button (as in *Stethacanthulus*), but it has not been determined whether this feature was absent or present in *Falcatus*.

DESCRIPTION: The braincase in *Damocles serratus* is known from only a few specimens, all of which are preserved in lateral or ventrolateral views (fig. 57). The postnasal wall is short and poorly calcified. As in *Falcatus falcatus*, ringlike denticles mark the course of the cephalic sensory line system and reveal that the snout extended a considerable distance in front of the jaws although there is no evidence of cartilage mineralization in the rostrum (Lund, 1986: fig. 5). There is a large, round orbit and the otic region is short. No features of the orbital wall are known, but a large sclerotic ring is present and consists of numerous small plates as in *F. falcatus*. The postorbital arcade is delicate and short anteroposteriorly. Lund (1986) suggested that variation in the length of the otic region in *D. serratus* may be growth related, although in MV 7685 and CM 35472 (which are apparently closely matched in size) there is considerable discrepancy in the relative length of the otic region. The occipital arch was short. It is unknown whether there was a persistent otico-occipital fissure.

Articulated specimens of *Damocles* show that the otic process of the palatoquadrate made extensive contact with the postorbital arcade, suggesting that the jaw firmly attached by ligaments and other connective tissue although the postorbital articulation (on the ventrolateral surface of the arcade) was quite small. Lund (1986: fig. 4) reconstructed the orbital attachment of the palatoquadrate as robust as in *Falcatus*.

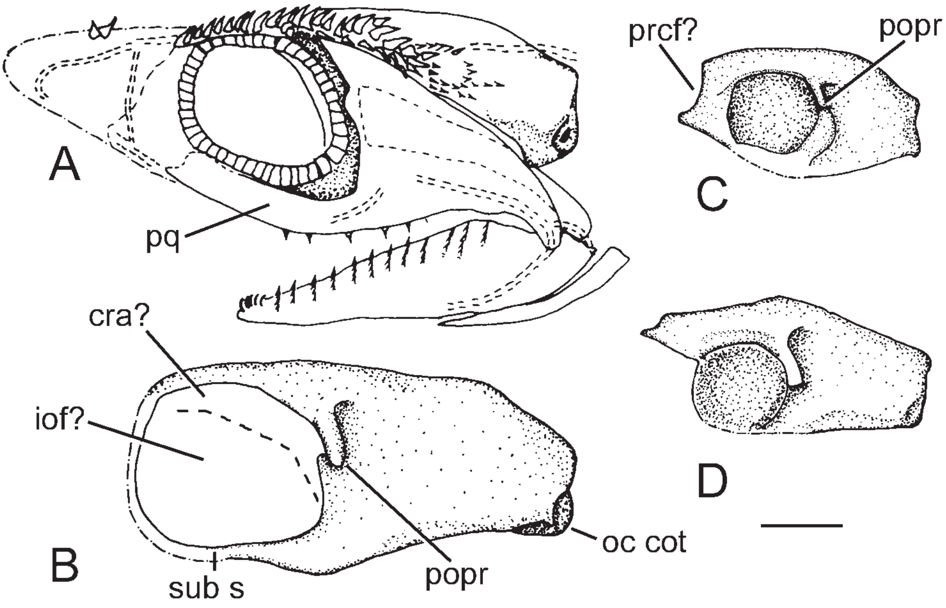

Fig. 57. Features of the head and braincase in *Damocles serratus*, from the Bear Gulch Limestone (Chesterian, late Pennsylvanian). All illustrations from Lund (1986) with annotations changed to agree with those used in this work and adjusted for scale. **A**, **B**, CM 35473. **A**, lateral view of head skeleton; **B**, lateral view of braincase. **C**, MV 7685, lateral view of braincase; **D**, CM 35472 (holotype), lateral view of braincase. Scale bar = 5 mm (illustrations have been scaled according to information in original publication).

ORDER CLADOSELACHIDA DEAN 1909
FAMILY CLADOSELACHIDAE DEAN 1894

CLADOSELACHE Dean, 1894

General Remarks: A comprehensive revision of the well known late Devonian shark *Cladoselache* is beyond the scope of the present work; it will merely be noted here that the systematics of *Cladoselache* are currently in disarray. The late Michael Williams (Cleveland Museum of Natural History) left notebooks in which he considered that Cleveland Shale *Cladoselache* represents two different but closely related genera, distinguishable mainly on the basis of postcranial features. However, until his unpublished findings can be analyzed and properly documented, *Cladoselache* is provisionally retained as a single genus.

Some investigators have separated *Cladoselache* from other sharks at ordinal level (e.g., Dean, 1909; Zangerl, 1981), whereas others have classified it alongside forms that are included here in the Symmoriiformes (e.g., *Denaea*; Glikman, 1967). More recently, Coates and Sequeira (2001b) have presented competing phylogenetic analyses in which *Cladoselache* either is a plesiomorphic sister taxon to all symmoriiforms or is nested within a clade comprising symmoriiforms plus holocephalans. Although some morphological characters of the braincase were included in their analyses, these did not impact the alternative phylogenetic positions of *Cladoselache* they postulated.

In addition to the Cleveland Shale material, parts of a well-preserved three-dimensional cladoselachian shark have been described from the Chattanooga Shale of Tennessee (Maisey, 1989). Although that specimen has provided important information about the visceral skeleton and musculature in cladoselachians, its cranium is poorly preserved and relatively uninformative.

Cranial Morphology: The braincase in *Cladoselache* is known mainly from two Cleveland Museum specimens described by Harris (1938), both of which were identified as *C. kepleri* (figs. 58, 59). These and other specimens were extensively prepared by

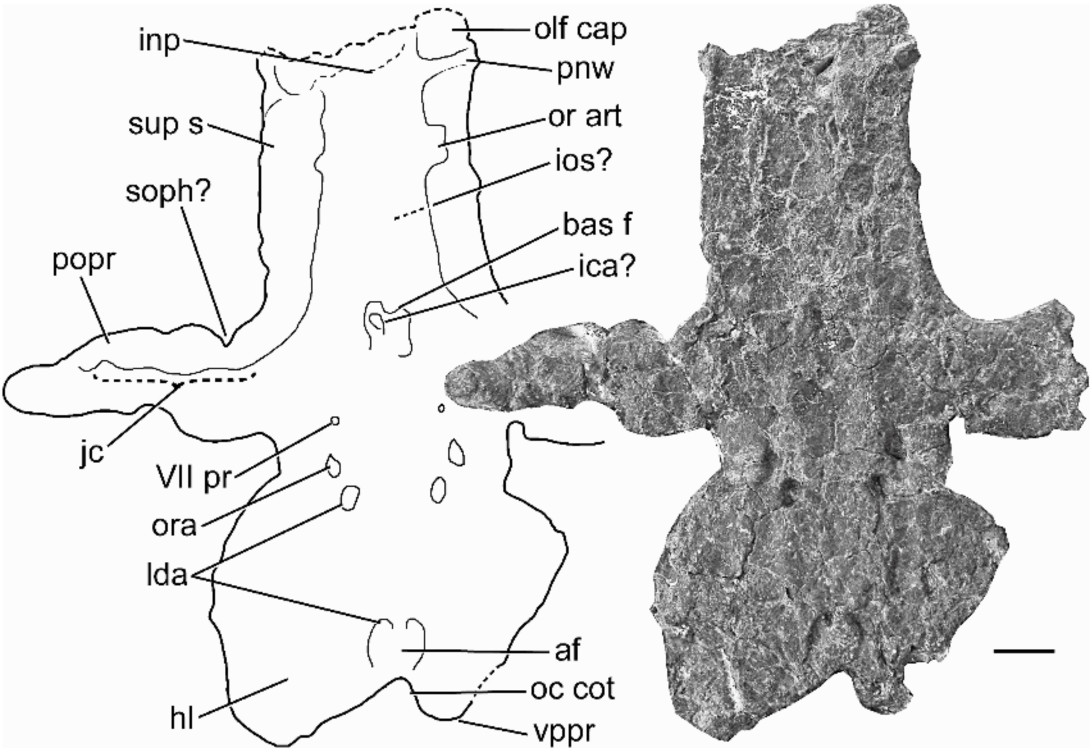

Fig. 58. *Cladoselache kepleri*, CMNH 5769, Cleveland Shale (late Devonian), Berea, Ohio. Ventral view of braincase. Scale bar = 10 mm.

Williams as part of an intended revision of *Cladoselache*, and now provide much more information on its cranial morphology. Unfortunately, all the specimens of *Cladoselache* in which the braincase is exposed are compressed dorsoventrally, and the original depth of the cranium is therefore difficult to estimate (as in *Cobelodus aculeatus*, *Akmonistion*, and *Stethacanthus*). Well-preserved palatoquadrates of *Cladoselache* have a shallower otic process than in most symmoriiforms, suggesting that the orbit was not as deep as in those forms.

Several features of the braincase are remarkably similar in *Cladoselache* and symmoriiforms. One feature of particular interest is the presence of a single median fossa for the dorsal aorta below the occipital region. This fossa can be seen in at least two specimens (CMNH 5769, 5611; figs. 58, 60), and shows that the dorsal aorta was either unpaired as it entered the basicranium, or that paired vessels shared a single opening. Unlike in "*Cobelodus*", however, the aorta apparently divided almost immediately on entering the basicranium, since the fossa in CMNH 5769 contains a pair of openings that presumably contained paired aortae. The aortic pattern in *Cladoselache* and symmoriiforms differs from that in Paleozoic sharks such as *Tamiobatis*, *Cladodoides*, and *Orthacanthus*, in which the aortae had already separated behind the occiput and the paired aortic canals are widely spaced.

The arrangement of basicranial foramina in the floor of the otic region is also very similar in *Cladoselache*, "*Cobelodus*", and *Cobelodus aculeatus*. The canals for the lateral aortae emerge a short distance behind the postorbital arcade (at which point each aorta presumably gave rise to an internal carotid, orbital and efferent hyoidean branch, because the foramen for the orbital artery lies but a short distance from the aortic foramen). By contrast, in Paleozoic sharks such as *Tamiobatis*, *Cladodoides*, and *Orthacanthus*, the foramen for the lateral aorta and its

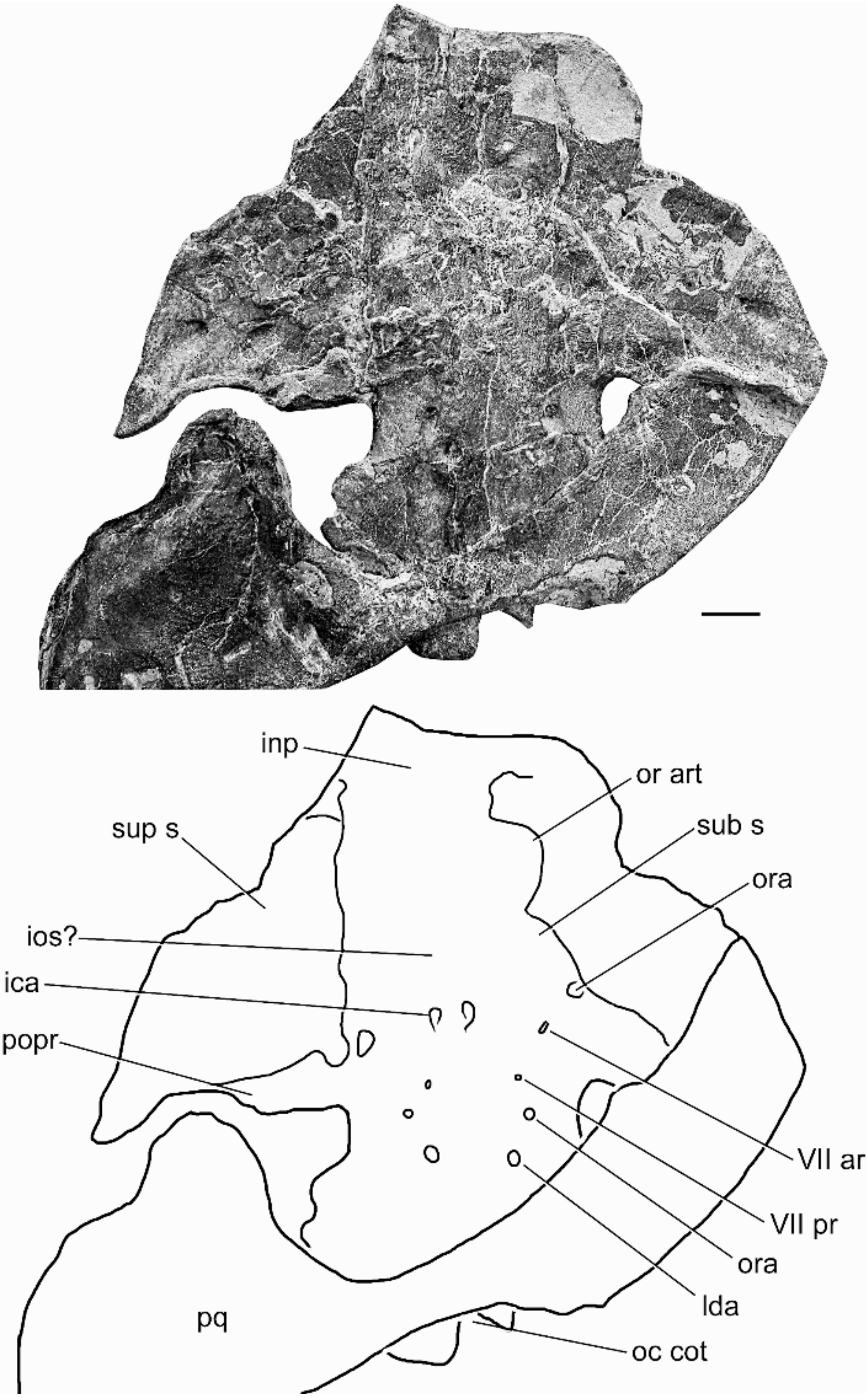

Fig. 59. *Cladoselache kepleri*, CMNH 6233, Cleveland Shale, Berea, Ohio. Ventral view of braincase partly overlain by palatoquadrate. Scale bar = 10 mm.

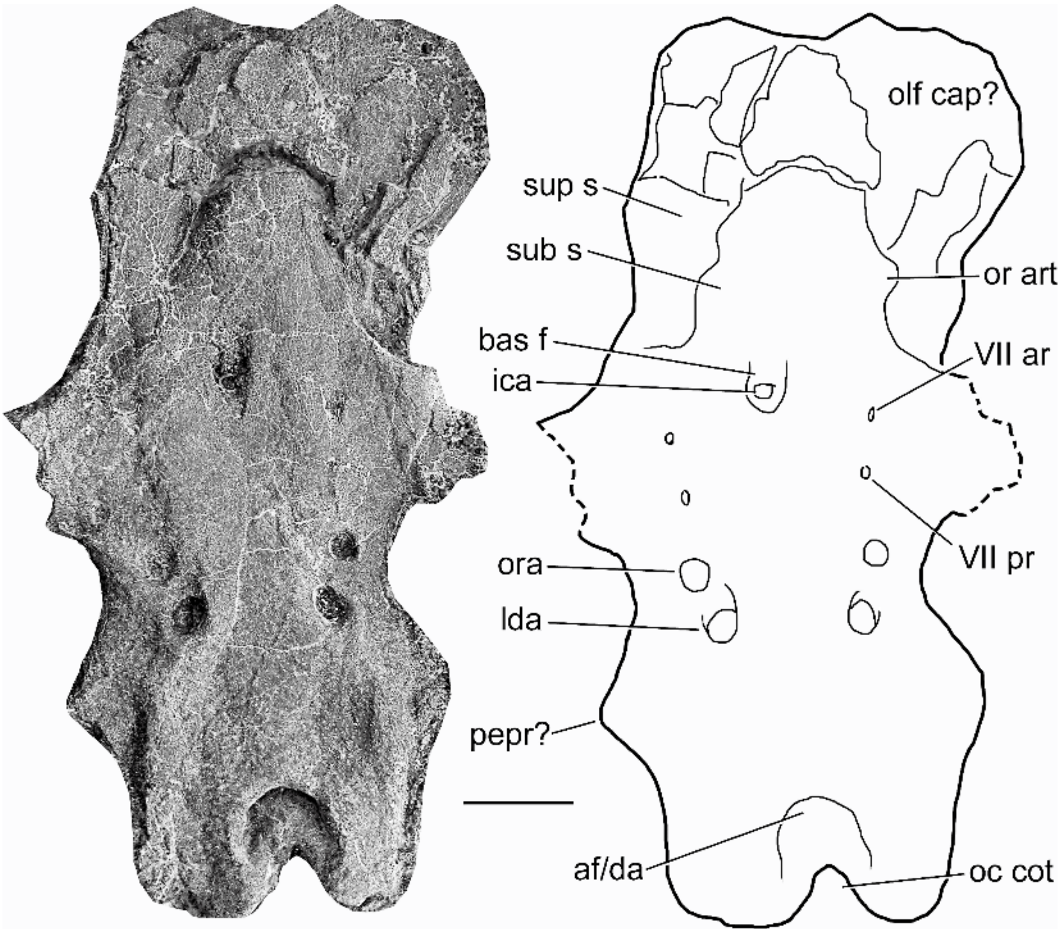

Fig. 60. *Cladoselache* sp., CMNH 5611, Cleveland Shale, Berea, Ohio. Ventral view of braincase lacking postorbital processes. Scale bar = 10 mm.

orbital artery are farther apart, presumably leaving more of the arteries exposed beneath the braincase.

Other unusual features of the braincase shared by *Cladoselache* and symmoriiforms include: presence of a distinct "waist", or narrowing of the otic region behind the postorbital arcade; absence of a lateral otic process; an extremely wide but anteroposteriorly short postorbital arcade; an expansive jugular canal (e.g., CMNH 5769; fig. 58); and possibly the presence of a periotic process (e.g., CMNH 5611; fig. 60).

The dorsal surface of the braincase in *Cladoselache* has not been described previously, but parts of it are visible in CMNH 6233 (fig. 61). Features of interest include the presence of a notch in the lateral margin of the supraorbital shelf, similar to that found in *Cobelodus aculeatus* and *Stethacanthulus meccaensis*, a small median opening probably for the pineal organ, and a short occipital arch separated from the otic region by an otico-occipital fissure (the arch is either incomplete or was uncalcified dorsally). In this specimen, the roof of the otic region, the medial capsular walls, and the semicircular canals are either uncalcified or missing. The floor of the medullary region is therefore exposed, but the posterior dorsal fontanelle (which presumably lay above this area) cannot be observed.

A wide hypotic lamina is present (fig. 58), an important similarity with other elasmo-

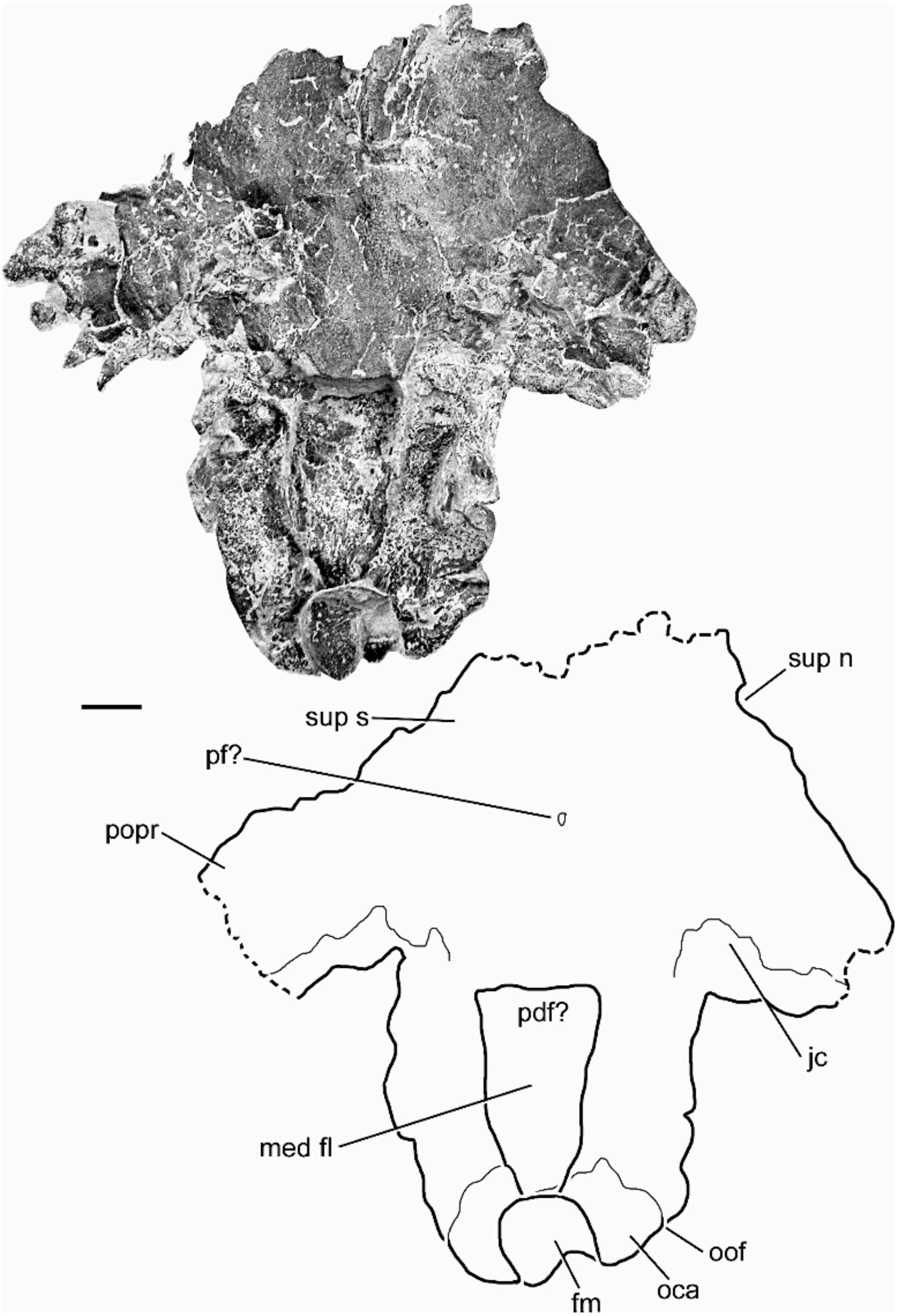

Fig. 61. *Cladoselache kepleri*, CMNH 6233, Cleveland Shale, Berea, Ohio. Dorsal view of braincase (opposite side of specimen shown in Fig. 55). Scale bar = 10 mm.

branchs. There is no evidence of a glossopharyngeal foramen in the basicranium, and the nerve probably left the braincase via the otico-occipital fissure. The otic region in *Cladoselache* and symmoriiforms is much shorter than in *Tamiobatis*, *Cladodoides*, and *Orthacanthus*. In addition, the occipital cotylus in *Cladoselache* and symmoriiforms is narrow from side to side, whereas it is much wider in forms such as *Tamiobatis*, *Cladodoides*, and *Orthacanthus*. The phylogenetic significance of these features is unclear because of their wider occurrence in other gnathostomes. Within chondrichthyans, however, a wide occipital cotylus and widely spaced aortic canals are unusual features that may represent apomorphic characters (possibly correlated with elongation of the otic region).

Cladoselache has separate, paired foramina for the anterior and posterior ramules of the palatine ramus. A separate foramen for the posterior ramule is also present in *Cladodoides* and perhaps in *Tamiobatis vetustus* (Maisey, 2005: figs. 5, 35). However, in "*Cobelodus*" the passages for both palatine ramules open into the roof of the groove for the orbital artery (fig. 8), and a similar arrangement is possible in *Cobelodus aculeatus*, because there is no evidence of separate foramina for these ramules despite the fact that the orbital artery was enclosed by a canal. Both palatine ramules in *C aculeatus* may have accompanied the orbital artery throughout its canal, and may have accompanied the orbital artery within its groove in "*Cobelodus*". The presence of separate foramina for the palatine ramules therefore distinguishes *Cladoselache* from symmoriiforms.

A median basicranial fenestra and paired internal carotid foramina are present in *Cladoselache*, although it is not possible to determine whether these openings communicated with the cranial cavity or opened into the orbit as in "*Cobelodus*". There is a broad suborbital shelf, extending anteriorly as far as the orbital articulation. This articular surface may indicate the posterior end of the embryonic trabecular cartilage, as inferred in "*Cobelodus*" and *Cladodoides* (Maisey, 2004a, 2005), suggesting that the polar cartilage made an extensive contribution to the basicranium in *Cladoselache*.

While *Cladoselache* appears to share several apomorphic cranial features with symmoriiforms, no definitive evidence of an interorbital septum has been detected (although one could be represented by a faint ridge in CMNH 5769; fig. 58). Some doubt therefore exists whether its braincase was tropibasic or platybasic. *Cladoselache* has customarily been classified in a separate family or even order (e.g., Dean, 1894, 1909; Zangerl, 1981), but the observations presented here suggest that such a remote classification is unjustified and instead support the phylogenetic hypothesis that *Cladoselache* is closely related to symmoriiforms (Coates and Sequeira, 2001b).

DISCUSSION

Tropibasia in Symmoriiforms

For many years, the only Paleozoic sharks in which the braincase was well known were *Tamiobatis*, *Cladodoides*, and *Orthacanthus* (Eastman, 1897; Gross, 1937, 1938; Romer, 1964; Schaeffer, 1981; Maisey, 2005). All these forms have fundamentally identical cranial morphology, with a platybasic chondrocranium, wide ethmoidal and orbital regions, a stout postorbital process surrounding a moderately wide jugular canal, an elongate otic region in which the lateral otic process contains part of the posterior semicircular canal, and a moderately long occipital region separated from the rest of the braincase dorsally by a persistent otico-occipital fissure.

A few previous investigators nevertheless suspected the presence of an interorbital septum in symmoriiforms (e.g., Zangerl and Case, 1976; Williams, 1985). Zangerl and Case (1976: 120) stated that in their original (unpublished) reconstruction of the braincase in *Cobelodus aculeatus* (based entirely on compression fossils studied by means of stereo X-rays) "the medial walls of the orbits were assumed to be close to the sagittal plane, or actually formed an interorbital septum." Evidently it was their subsequent misinterpretation of the three-dimensionally preserved specimen found afterward (FMNH PF 3090; figs. 37, 38) that caused them to change their interpretation and to place the orbits on either side of the cranial cavity in a "conventional" platybasic arrangement. Without the almost perfectly preserved three-dimensional "*Cobelodus*" braincase, it would be extremely difficult even now to recognize a deep interorbital septum in compression fossils of *C. aculeatus*.

Despite the impossibility of making ontogenetic observations in fossils, it can still be inferred on the basis of morphological features that the embryonic orbital cartilage in "*Cobelodus*" probably contributed to the entire upper half of the orbit and had a membranous or blastemic connection with the trabeculae at the approximate level of the optic foramen (fig. 2A). The orbital cartilages were entirely fused at the ventral midline, forming an interorbital septum that was poorly chondrified centrally but strongly calcified where it met the polar cartilage and parachordals. Although the position and extent of the embryonic trabeculae can only be inferred, the fact that the bucco-hypophyseal fenestra is separated from the cranial cavity suggests that the trabeculae were fused along much of the midline, probably forming an extensive trabecula communis to which the orbital cartilages were also fused. Thus, in "*Cobelodus*", the adult tropibasic condition probably arose from a tropitrabic embryonic one. The preoptic pila was incompletely calcified in "*Cobelodus*", but was apparently better developed in *Falcatus* and *Stethacanthulus*, where there is broad contact between the septum and postnasal wall. Farther posteriorly in the orbit, cartilage extending between the optic and ophthalmic foramina in part probably represents the metoptic pila. The ophthalmic foramen lies immediately above the optic pedicel centrally in the orbit, and the oculomotor foramen lies farther posteriorly above and even slightly behind the pedicel attachment area (forming the base of the antotic pila in modern elasmobranchs; see De Beer, 1931, 1937; Holmgren, 1940; El-Toubi, 1949).

Cartilage extending behind the pedicel includes the facial and trigeminal foramina, and is therefore regarded here as having formed in tissues derived both from the antotic pila and from secondary chondrification of the embryonic prootic fissure between the pila and the otic capsule (including the prefacial commissure). In "*Cobelodus*", the polar cartilage probably contributed to approximately one-third of the orbit floor, i.e., it was slightly less extensive than in *Cladodoides* (fig. 2B). The pituitary vein presumably lay within an extracranial subpituitary space between the posterior ends of the trabecular-polar cartilage and the parachordals as in other gnathostomes (Allis, 1928).

The positions of the efferent pseudobranchial artery, optic pedicel, and pituitary vein in both "*Cobelodus*" and *Cladodoides* suggest that the polar cartilage made an extensive contribution to the braincase. By contrast, in modern elasmobranchs (and in gnathostomes generally), the polar cartilage is comparatively small and the trabeculae commonly extend into the posterior part of the orbit (fig. 1). Thus, despite many obvious differences between the neurocrania of "*Cobelodus*" and *Cladodoides*, early cranial development in both forms was apparently characterized by hypertrophy of the polar cartilage and confinement of the trabeculae to the anterior half of the orbit. Features that are typically located in the posterior part of the orbit in modern *Notorynchus* lie farther anteriorly in *Cladodoides* (e.g., the oculomotor foramen, bucco-hypophyseal chamber, optic pedicel, efferent pseudobranchial foramen, and palatobasal articulation; Maisey, 2005: fig. 27). "*Cobelodus*" resembles *Cladodoides* in all these respects, suggesting that hypertrophy of the polar cartilage and related forward displacement of features in the orbit is a derived developmental condition shared by *Cladodoides* and "*Cobelodus*".

These observations suggest that the unusual morphology of the neurocranium in "*Cobelodus*" resulted from at least two distinct evolutionary modifications to the presumably conserved pattern of cranial development seen in modern elasmobranchs. The first step involved hypertrophy of the polar cartilage, and probably arose in sharks in which the adult braincase was still morphologically platybasic (e.g., *Cladodoides*, *Tamiobatis*, *Cladodus*; Maisey, 2005; Ginter and Maisey, 2007). The second step (in symmoriiforms such as "*Cobelodus*") involved deepening and expansion of the orbit and development of an interorbital septum (presumably involving extensive fusion of the embryonic trabeculae to form a trabecula communis along the entire length of the orbit), accompanied by an anterior shift of the ventral arm of the lateral commissure (at least relative to its position in *Cladodoides*). Thus, hypertrophy of the polar cartilage may have been a precursor condition to the tropibasic adult condition in symmoriiforms. The combined effect of these ontogenetic changes apparently resulted in a crowding together of the embryonic metoptic and antotic pilae. Consequently, much of the interorbital septum in symmoriiforms was presumably supported by (or formed in) the polar cartilages on either side of the hypophyseal chamber, and also by cartilage derived from the antotic pila farther dorsally. The anterior part of the interorbital septum either did not chondrify or remained uncalcified, but was probably connected to the trabeculae by membranous tissue.

Comparison with Recent actinopterygians suggests that the tropibasic adult morphology found in symmoriiforms such as "*Cobelodus*" involved altered ontogenetic trajectories of the trabeculae, which became more extensively fused at the ventral midline and formed a trabecula communis that extended to meet the orbital cartilages (tropitrabic condition), resulting in the development of deep orbits that are barely separated medially (probably correlated with relatively large eye size and the related upward displacement of the brain). However, there are significant differences in the inferred extent of the antotic pila and polar cartilage of "*Cobelodus*" and in actinopterygians. In the latter, loss of the antotic pila and reduction or loss of the polar cartilage may be correlated with the development of the posterior myodome. By contrast, in "*Cobelodus*" the antotic pila is apparently retained (though possibly merged with the metoptic pila), and a posterior myodome is not developed. In addition, the polar cartilage in "*Cobelodus*" seems to have been much more extensive than in actinopterygians and osteichthyans generally.

The efferent pseudobranchial artery in osteichthyans does not traverse the space between the polar and trabecular cartilages as in elasmobranchs (De Beer, 1924, 1937; Holmgren, 1943), and an optic pedicel is absent in all modern osteichthyans. Unlike in elasmobranchs, therefore, these landmarks cannot be used to identify the former extent of the polar cartilage (although the site of the foramen for the pituitary vein may similarly indicate its posterior margin). A pedicel attachment site has been identified in several early osteichthyans (e.g., *Ligulalepis*, *Psarolepis*, *Achoania*, *Stylolepis*; Basden et al., 2000; Basden and Young, 2001; Zhu et al., 1999; Zhu et al., 2001; Zhu and Yu, 2002), immediately behind the optic foramen and anterodorsal to the foramen for the pituitary vein (fig. 62). Perhaps significantly, in early osteichthyans where the oculomotor foramen has been identified (e.g., *Psarolepis*, *Ligulalepis*; Yu, 1998; Basden and Young, 2001), it is positioned directly above the presumed pedicel attachment area (i.e., as in sharks). Despite the profoundly different course of the efferent pseudobranchial artery with respect to the polar and trabecular cartilages in elasmobranchs and osteichthyans, the topo-

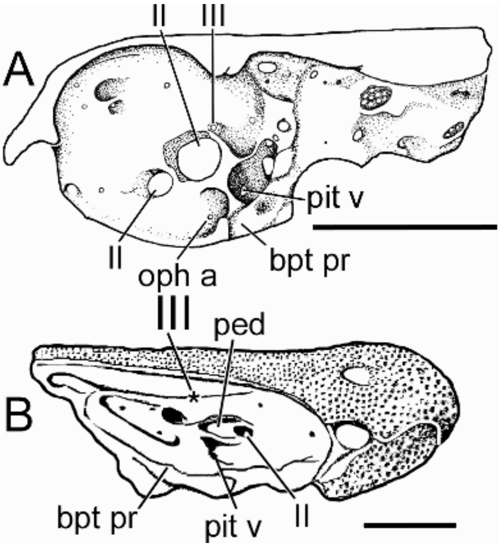

Fig. 62. Two early osteichthyan neurocrania in lateral view, showing positions of landmark features associated with the embryonic polar cartilage and antotic pila in modern gnathostomes. **A**, The primitive actinopterygian *Ligulalepis* sp., left side (after Basden and Young, 2001); **B**, The primitive sarcopterygian *Achoania jarviki*, right side of ethmosphenoid region (after Zhu et al., 2001; position of oculomotor foramen inferred from *Psarolepis romeri*, after Yu, 1998). Scale bars = 5 mm.

graphic and developmental relationships of the antotic pila and polar cartilage are remarkably similar. If the optic pedicel, polar cartilage, and trabeculae represent evolutionary novelties of the prechordal part of the neurocranium in gnathostomes, then fusion of the pedicel to the embryonic antotic pila just above the dorsal margin of the polar cartilage and immediately anterior to the basisphenoid pillar may represent a conserved gnathostome pattern that arose prior to the divergence of osteichthyans and chondrichthyans.

SCLERAL OSSICLES

Scleral ossicles are present in many osteichthyans (including tetrapods) as well as in placoderms, but ossicles are absent in modern chondrichthyans although the scleral cartilage may form a capsule (Walls, 1942). The only chondrichthyans in which scleral ossicles have been identified are extinct and all date from the Paleozoic (e.g., *Falcatus*, *Damocles*, *Cladoselache*), suggesting that these structures were lost early in chondrichthyan evolution and never reappeared. The absence of bone in the scleral capsule of chondrichthyans is in all probability related to the acquisition of tesselated endoskeletal calcification (replacing endoskeletal bone?), since the capsular cartilage is calcified prismatically (like much of the endoskeleton) in modern sharks such as *Lamna*. By contrast, the absence of capsular bone in most osteichthyans (other than teleosts; Franz-Odendaal and Hall, 2006) probably represents a true reduction in ossification.

In modern amniotes, scleral ossicles develop intramembranously in dermal (neural crest) tissue forming the scleral mesenchyme (Franz-Odendaal and Hall, 2006 and references therein), and the same developmental history can be postulated for these ossicles in chondrichthyans such as *Falcatus*. By contrast, the scleral cartilage is formed directly in ectomesenchymal tissue and can be cartilaginous (e.g., sarcopterygians, *Lamna*), membranous (e.g., actinopterygians), or bony (e.g., osteostracans, placoderms). The presence of scleral ossicles has been regarded as a gnathostome synapomorphy (Maisey, 1986; Donoghue et al., 2000), although today these structures occur only in osteichthyans (*Latimeria*, tetrapods and teleosts) and are absent in modern dipnoans (Kemp, 1999; Franz-Odendaal and Hall, 2006). Scleral ossicles are nevertheless present in many extinct basal sarcopterygians (Jessen, 1966; Schultze, 1973; Janvier, 1996) and actinopterygians (e.g., Edinger, 1929; Walls, 1942; Lund, 2000). Paradoxically, scleral ossicles in acanthodians seem to be restricted to a highly derived clade including *Cassidiceps* and acanthodiforms (Hanke and Wilson, 2004: character 2).

In some osteostracans and placoderms, the scleral cartilage forms an ossified cup surrounding the eye, to which a dermal sclerotic component is fused (e.g., *Tremataspis*, *Dicksonosteus*; Janvier, 1981, 1985, 1996; Burrow et al., 2005), but in many arthrodires (as well as in petalichthyids and antiarchs), the scleral cartilage was apparently unossified and separate ossicles are present (e.g., *Holonema*, *Brachydeirus*, *Dunkleosteus*, *Lunaspis*, *Bothriolepis*; Gross, 1932, 1961; Miles, 1971). Fusion between the scleral ossicles and cartilage therefore seems to be restricted phylogenetically to stem-group gnathostomes such as osteostracans and placoderms (it has not been recognized in any living or fossil crown-group gnathostome). This distribution led Franz-Odendaal and Hall (2006: fig. 5) to propose that a fully ossified capsule may represent the phylogenetically primitive gnathostome condition. However, it is far from clear whether the propensity for the optic capsule to be extensively and/or heavily ossified represents a cladistically primitive or derived condition, given its disjunct phylogenetic distribution within craniates (and especially among placoderms). In this regard, it is of interest that a strong developmental relationship exists between the scleral cartilage and the corneal-scleral limbus (where the ossicles are formed), because the scleral cartilages of teleosts and birds and the collagenous sclera of mammals first appear as a ring adjacent to the limbus before spreading posteriorly around the eye (Coulombre and Coulombre, 1958; Franz-Odendaal and Hall, 2006). A similar development can be postulated for placoderms and osteostracans, except that the scleral and capsular ossifications probably co-ossified at the

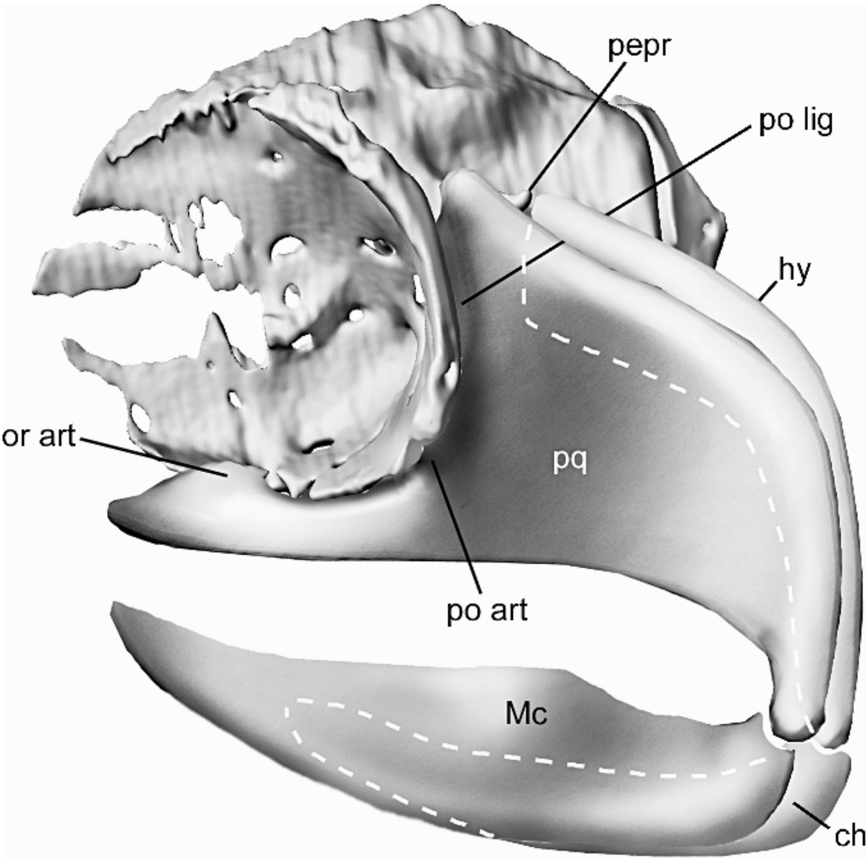

Fig. 63. "*Cobelodus*". Left side of head skeleton, with a reconstruction of the jaws and hyoid arch. No scale.

corneal-scleral limbus. Such co-ossification has a relatively restricted systematic distribution, and could therefore be secondary from both a developmental/ontogenetic *and* a phylogenetic perpective. Thus, absence of fusion between the scleral ossicles and cartilage may represent a highly conserved condition in crown group gnathostomes.

A RECONSTRUCTION OF THE JAWS IN "*COBELODUS*"

The three-dimensional "*Cobelodus*" cranium provides an opportunity to model a hypothetical set of mandibular and hyoid arches and replicate their original shape and orientation, using other symmoriiforms as a guide (fig. 63). Although the visceral skeleton is not preserved in "*Cobelodus*", the palatoquadrates of *Cobelodus aculeatus*, *Stethacanthulus meccaensis*, and *Symmorium reniforme* all have a high postorbital flange, suggesting a deep and round orbit as in "*Cobelodus*". Unfortunately, almost all the comparative material is flattened and distorted, obscuring the original curvature of the jaw ramus as well as the three-dimensional shape of individual cartilages.

The spatial dimensions and orientation of the orbital and postorbital articulations in the three-dimensional cranium provided the principal constraints for the reconstruction presented here. The curvature of the palatine rami and Meckel's cartilage below the ethmoid region was based on comparison with other elasmobranchs, but also followed the simple assumption that the tooth-bearing regions of both jaws had to be approximately parallel to each other in order for the teeth to occlude properly and provide a continuous biting surface (a factor that is overlooked in many previous reconstructions of extinct elasmobranchs). The outward swing of the jaw rami toward the mandibular joint was also based on comparison with other elasmobranchs, but in addition was constrained by the requirement of having the paired mandibular joints aligned along a single transverse axis of rotation. Flat templates were scaled and shaped according to these criteria, then photographed and digitally superimposed on a lateral view of the braincase.

In the reconstruction, with the postorbital and orbital articulations aligned, it is possible to fit the hyomandibula between the periotic process and mandibular joint (allowing for outward curvature of the jaw ramus), although the absence of a definite hyomandibular facet and variation in the position of the hyomandibular head in articulated symmoriiform fossils makes its position in "*Cobelodus*" highly conjectural (hyomandibular support for the mandibular arch in symmoriiforms is itself a controversial matter; see below). In "*Cobelodus*", the mandibular joint lies some distance behind the occipital region, but the otic region is short and there is little space behind the orbit for the origin of maxillary levator or first dorsal constrictor musculature.

The postorbital articulation is said to be laterally directed in some symmoriiforms, suggesting that it was covered by part of the postorbital arcade (Zangerl and Case, 1976; Williams, 1985; Coates and Sequeira, 1998). However, in "*Cobelodus*", the postorbital articulation is clearly positioned on the posterior surface of the arcade, and it is difficult to imagine how it could meet the lateral surface of the palatoquadrate. If such a laterally directed surface was present in "*Cobelodus*", it may have formed a secondary articulation or an attachment surface for ligaments connecting the palatoquadrate to the postorbital arcade above their primary articulation, or it may have acted as an insertion for tendons running from an adductor γ muscle (if present). The palatoquadrate in *Falcatus* and *Damocles* probably made broad contact with the postorbital arcade and the attachment may have been reinforced by ligaments (figs. 54–57). In *Notorynchus*, ligaments holding the postorbital articulation preclude any anterior shifting of the jaws and no translation is possible, any motion being restricted to the plane of the articular surface (Luther, 1908; Wolfram, 1984). The same was probably true in Paleozoic sharks with a postorbital articulation, but motion may have been further restricted in "*Cobelodus*" and other symmoriiforms if additional ligamentous connections were present dorsal to the articulation (e.g., extending from the otic process to the vertical platform of the postorbital arcade).

Zangerl and Case (1976) determined that the palatoquadrate flange and the postorbital arcade in *Cobelodus aculeatus* were in close proximity to each other for a considerable distance above and below their actual articulation. The otic flange of the palatoquadrate therefore extends some distance above the primary articular surface. The articular surface for the palatoquadrate is also situated ventrolaterally in *Stethacanthulus meccaensis* (Williams, 1985: fig. 6), and includes a lateral "pocket" where it articulates with the postorbital arcade. The postorbital arcade in *Symmorium reniforme* is comparatively stout and triangular in dorsal view, with a thickened transverse keel on its posterior border (Williams, 1985). The arcade is also comparatively long anteroposteriorly in *Akmonistion zangerli* (Coates and Sequeira, 1998). A postorbital articulation was probably present in *Denaea fournieri*, but no details are known (Fournier and Pruvost, 1922).

A reconstruction of the main mandibular musculature is presented here (fig. 64). Some parts of the branchiomeric musculature are difficult to reconstruct in extinct sharks because the skeleton lacks muscle insertion sites like those of osteichthyans. Comparison with modern elasmobranchs (Luther, 1908; Wilga, 2005) is helpful only at a very general level, even in forms that superficially resemble early sharks (e.g., hexanchiforms, *Chlamydoselachus*, *Heterodontus*). In *Notorynchus*, the palatoquadrate levator and first dorsal constrictor originate at the level of the dorsal otic ridge (Luther, 1908; Daniel, 1934: fig. 92), and this was probably also the case in "*Cobelodus*". The palatoquadrate levator of *Notorynchus* originates on the lateral wall of the otic capsule just behind the postorbital process and in front of the spiracular canal. From here, the muscle descends anteriorly

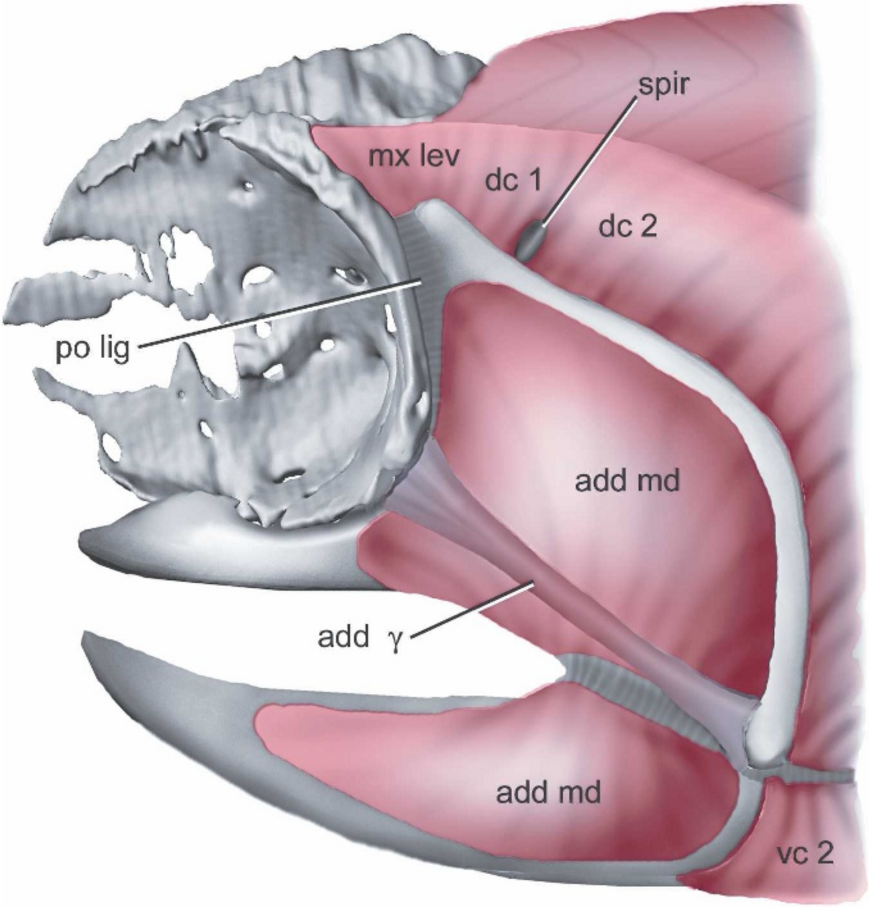

Fig. 64. "*Cobelodus*". Left side of head, with a reconstruction of main musculature associated with the jaws. No scale.

and meets the palatoquadrate in the posterior part of the orbit. The anterior extent of the palatoquadrate levator is constrained by the position of the mandibular ramus of the trigeminal nerve. In modern elasmobranchs, the ramus invariably passes in front of the palatoquadrate levator (Luther, 1908). In "*Cobelodus*", this ramus probably traverses the jugular canal and postorbital arcade, and it is therefore unlikely that the palatoquadrate levator extended into the orbit (the palatoquadrate levator lies also entirely behind the postorbital arcade in *Squatina*, where the ventral part of the lateral commissure is as strongly chondrified as in many Paleozoic sharks).

The shortness of the otic region in "*Cobelodus*" suggests that the second (hyomandibular levator) and subsequent dorsal constrictors probably originated entirely on a fascia of the dorsal epaxial musculature (in modern sharks, these generally arise from a fascia above the gill clefts as well as from the extrabranchial cartilages). A palatoquadrate spiracular notch has been reported in some symmoriiforms (Lund, 1985b), and it has therefore been assumed in the reconstruction that a spiracular canal was present between the first and second dorsal constrictors, oriented almost vertically between the palatoquadrate and periotic process and opening on the top of the head just behind the postorbital arcade.

The extent of the mandibular adductor musculature is fairly evident from the size and extent of the adductor fossa on the palatoquadrate and Meckel's cartilage. Most of the dorsal adductor muscle mass in "*Cobelodus*" presumably lay behind the postorbital arcade, and the dorsal (palatoquadrate) insertion area is much larger than the ventral (meckelian) one. Unfortunately, in "*Cobelodus*" there is no way to determine the presence or the extent of smaller muscles usually associated with the mandibular adductor in modern elasmobranchs (e.g., adductor γ or superficial adductor, preorbital/suborbital, labial levator). The inclusion of an adductor γ in the reconstruction is highly speculative. In *Notorynchus*, this muscle originates near the mandibular joint and is connected to the tip of the postorbital process by a tendon (Luther, 1908). According to Allis (1923), *Chlamydoselachus* has an adductor γ, but this is absent according to both Luther (1908) and Shirai (1992); the latter found only tendons and connective tissue in its expected position.

The preorbital muscle has been omitted from the reconstruction presented here although one may have been present. In primitive modern sharks, the preorbital muscle is not usually strong and commonly arises on the postnasal wall or ectethmoid process, inserting on the fascia of the main adductor muscle near the corner of the mouth (e.g., *Chlamydoselachus*). By contrast, in many dalatiiforms with a cutting-type dentition (sensu Cappetta, 1987), the muscle is massive and its origin has shifted posteriorly into the orbit (e.g., *Etmopterus*, *Squaliolus*). However, the preorbital muscle is absent in the highly specialized dalatiid *Trigonognathus* (which has an unusual clutching-type dentition and highly protrusible jaws; fig. 4C). In advanced modern lamniforms, the preorbital muscle has separate dorsal and ventral heads (Wilga, 2005). If a preorbital muscle was present in "*Cobelodus*", it is unlikely to have arisen on the interorbital region as in modern *Squaliolus*, or to have extended below the postorbital arcade to insert on the mandibular adductor or lower jaw, because such a course would have been obstructed by the ventral part of the postorbital arcade. Probably, any preorbital muscle would have been rather weak.

Other symmoriiforms display a slightly different postorbital arcade morphology from "*Cobelodus*", and may therefore have differed in the orientation and position of the postorbital articulation. In some forms, the postorbital articular fossa for the palatoquadrate has been described as being approximately midway along the arcade (e.g., *Damocles*, *Akmonistion*; Lund, 1986; Coates and Sequeira, 2001a: fig. 3). In others, the facet is apparently closer to the dorsal margin of the otic flange (e.g., CM 23654, referred to *Stethacanthus* cf. *S. productus*; Lund, 1985b: fig. 1). If such variation can be confirmed, it would suggest considerable variation in the origin, insertion, and distribution of the mandibular musculature that may reflect different feeding strategies and preferences in symmoriiforms.

The Anterior Palatoquadrate Articulation

A detailed discussion of the anterior palatoquadrate articulation has already been presented elsewhere (Maisey, 2005), and only a few points will be added here. Gegenbaur (1872) considered that the anterior articular surface in modern elasmobranchs corresponded to the palatobasal articulation in osteichthyans. However, Goodrich (1909: 414) suggested that the "orbito-palatine" articulation in modern hexanchiform sharks could either represent a palatobasal articulation (= "basal" articulation sensu Huxley, 1876) that had migrated anteriorly, or an anterior (palatine) articulation that had migrated posteriorly. While he considered the former view more plausible ("the fact that it articulates really with the basal or trabecular and not antorbital region of the skull is strong evidence that it is a true basal process"), he also noted: "the anterior articulation of the palatoquadrate seems to be very far forward in such early forms as the Acanthodii and Pleuracanthini .... Further study of the fossils may enable this point to be decided."

Watson's (1937) subsequent study seemed to settle the issue (at least for acanthodians). He considered that no basal process was present in sharks, and that the absence of a palatobasal articulation in elasmobranchs was an important difference from *Acanthodes*. He therefore distinguished the anterior process of elasmobranchs as an orbital process.

Miles (1965, 1973) reached essentially the same conclusion and interpreted *Acanthodes* with an osteichthyan-like palatobasal (basipterygoid) process. However, Holmgren (1943) and Jarvik (1977, 1980) argued that the articulation in *Acanthodes* is homologous with the orbital articulation in squaloids and hexanchiforms, but not to the palatobasal articulation of osteichthyans. On the other hand, De Beer (1931) and Gardiner (1984a) have both argued that the elasmobranch orbital and osteichthyan palatobasal articulations are morphological homologs (a view originally espoused by Huxley, 1876) because they have the same topographical relationship to the lateral head vein, the palatine ramus of the facial nerve, and the embryonic polar cartilage.

El-Toubi (1949: 262), defended Watson's (1937) position that no palatobasal articulation is present in sharks, and argued that the orbital process in *Squalus* changes its position relative to the trabecular cartilage during ontogeny and " does not articulate with a fixed point in all developmental stages". However, during earlier developmental stages when the palatoquadrate orbital process is located farther anteriorly, it has only blastemic connection to the cranium and lacks any real articulation. Although the palatoquadrate in *Squalus* and *Etmopterus* shifts posteriorly in ontogeny, the articular surface formed for it on the trabecular cartilage does not shift (Holmgren, 1940: figs. 55, 67, 79, 81), and is located at the posterior end of the trabeculae from its first inception (like the basitrabecular process in osteichthyans; Goodrich, 1930).

By contrast, the anterior palatoquadrate attachment in *Heterodontus* and galeomorphs is associated with the lateral or anterolateral part of the trabecular cartilage, and the palatoquadrate connects with the ethmoidal region (Holmgren, 1940). There is no corresponding articular surface in more advanced galeomorphs although ethmopalatine ligaments are often present (Wilga, 2005). In *Mitsukurina* and *Carcharias* these ligaments are paired, and in *Alopias* they are accompanied by an unpaired palatonasal ligament, but in other lamnids only a median ligament is present. However, these ethmopalatine and palatonasal ligaments are always connected to the anterior or antrolateral part of the trabecular region, farther anteriorly than the palatobasal articulation in other gnathostomes but corresponding topographically to the anterior articulation in *Heterodontus* and galeomorphs. Nevertheless, Wilga (2005: 114, fig. 6) inferred that the ethmopalatine ligament in galeomorphs is homologous to the sleeve-like ligament associated with the orbital articulation in hexanchiforms, despite the different positions of these attachments. The implied homology between these ligaments suggests that the orbital articulation was secondarily lost, but that the ligamentous part of the attachment become relocated farther anteriorly on the lateral margin of the trabeculae. However, even if the ethmopalatine attachment in galeomorphs is homologous only to the *ligamentous* part of the orbital articulation in orbitostylic sharks (and to the corresponding part of the palatobasal articulation in other gnathostomes), the ethmoidal articulation in *Heterodontus* and orectoloboids is most parsimoniously interpreted as a novel feature, perhaps correlated with their unusually massive and divided preorbital muscle that is oriented vertically and inserts onto Meckel's cartilage rather than on the mandibular adductor as in other sharks (Smith, 1942; Compagno, 1977; Motta and Wilga, 1999).

The Postorbital Articulation

In modern hexanchiform elasmobranchs, there is a postorbital articular surface on the primary postorbital process (fig. 65A–C). However, there is no continuous postorbital arcade and hexanchiforms lack a chondrified lateral commissure (Holmgren, 1941). By contrast, the postorbital articulation in many Paleozoic sharks is located farther ventrolaterally than in hexanchiforms, presumably on the distal part of the chondrified lateral commissure (fig. 65D, E). Furthermore, the articulation in hexanchiforms is lateral to the exit of the otic lateral line nerve (= classical "otic ramus of the trigeminal nerve") and dorsal to the lateral head vein whereas, in Paleozoic sharks such as "*Cobelodus*" and *Cladodoides*, the articulation is ventrolateral to the presumed position of the otic lateral line nerve and the lateral head vein.

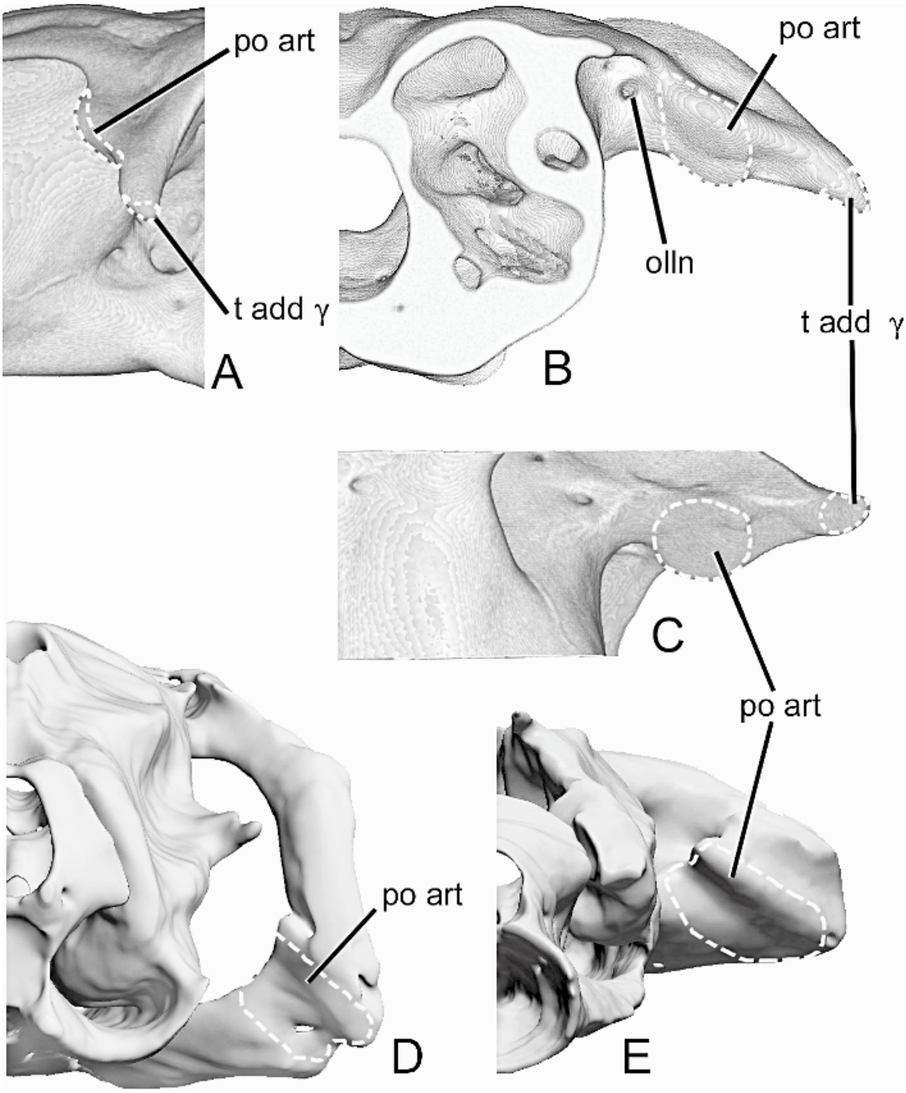

Fig. 65. Views of the right postorbital process showing the different position of the postorbital articulation in: **A**–**C**, *Notorynchus cepedianus*; **A**, lateral view (anterior to right); **B**, posterior view; **C**, ventral view (anterior to top) **D**, "*Cobelodus*", posterior view; **E**, *Cladodoides wildungensis*, posterior view. Not to scale.

Despite strong disagreement between phylogenetic hypotheses based on molecular and morphological analyses of crown group elasmobranchs (mainly involving the placement of batoids; Maisey et al., 2004), there is consensus that hexanchiforms (the only extant elasmobranchs with a postorbital articulation) do not lie at the base of the group. A postorbital articulation is also absent in hybodonts, the putative extinct sister group to modern elasmobranchs (Maisey et al., 2004). From a phylogenetic perspective, therefore, amphistyly (sensu Goodrich, 1909) in hexanchiforms appears to be a cladistically derived condition. The alternative possibility (that a postorbital articulation was primitively present in crown-group elasmobranchs and was lost independently numerous times in nonhexanchiforms) is considerably less parsimonious.

The postorbital articulation in hexanchiforms cannot therefore be considered primitive, based on morphological and phylogenetic evidence. This conclusion has important implications for those evolutionary hypotheses of jaw suspension in elasmobranchs in which the amphistylic condition in hexanchiforms has been regarded as a cladistically primitive condition from which other patterns supposedly arose (e.g., Wilga, 2005: fig. 7).

HYOMANDIBULAR INVOLVEMENT IN JAW SUSPENSION

In modern batoids and orbitostylic sharks (sensu Maisey, 1980), the hyomandibular facet is located on the posterolateral wall of the otic capsule, immediately in front of the exit of the glossopharyngeal nerve (in batoids and *Pristiophorus*, there are frequently two articular fossae for the hyomandibula; Holmgren, 1941). The hyomandibular facet sometimes extends farther anteriorly (e.g., *Squatina*), and occasionally extends along the entire otic region (e.g., *Orectolobus*). However, in *Heterodontus*, *Chiloscyllium*, and advanced galeomorphs, the facet occupies only the anterior part of the otic region (Holmgren, 1941).

The hyomandibular articulation in extinct sharks is usually located on the posterior part of the capsule and is often associated with the lateral otic process (e.g., *Orthacanthus*, *Tamiobatis vetustus*, "*Tamiobatis* sp.", *Egertonodus basanus*, *Tribodus limae*; Schaeffer, 1981; Maisey, 1983; Maisey and Carvalho, 1997). *Akmonistion* is so far the only symmoriiform in which a lateral otic process has been identified (Coates and Sequeira, 2001a). A more anterior position for the articulation has been suggested in *Tristychius arcuatus* (Dick, 1978: figs. 7, 9) and *Synechodus dubrisiensis* (Maisey, 1985).

"*Cobelodus*" lacks a distinct hyomandibular facet, suggesting that the hyomandibula may only have been attached by ligaments (possibly to the periotic process). In other symmoriiforms, a comparatively weak ligamentous connection is also suggested by the extremely variable position of the hyomandibular head. For example, in *Falcatus falcatus* and *Damocles serratus*, the hyomandibula extends as far as the postorbital arcade and is mesial to the palatoquadrate postorbital articulation (Lund, 1985a, 1986), a quite different configuration from that described in *Akmonistion* (Coates and Sequeira, 2001a). In *Cobelodus aculeatus*, the hyomandibular head has been described in various positions; according to Zangerl and Williams (1975), it reached the postorbital arcade, but according to Zangerl and Case (1976) it only extended about halfway along the side of the otic capsule.

There is considerable variation in the relative proportions of the hyomandibula and ceratohyal in symmoriiforms. It is only 50% as long as the ceratohyal in *Akmonistion zangerli* (Coates and Sequeira, 2001a: 443), but in *Cobelodus aculeatus* it is approximately 60% as long. However, according to Williams (1985: 98), the hyomandibula in *Stethacanthulus meccaensis* is much shorter (around 33% of ceratohyal length). The hyomandibula in both *Falcatus falcatus* and *Damocles serratus* is at least as long as the otic ramus of the palatoquadrate (Lund, 1885a: fig. 8; 1986: fig. 4). In *D. serratus*, the hyomandibula is considerably longer than the ceratohyal (the length of the ceratohyal has not been determined in *F. falcatus*). The hyomandibula extends at least halfway along the otic region in the Pennsylvanian Arkansas symmoriiforms (i.e., approximately as far as the periotic process in "*Cobelodus*"), but CT scans show that the hyomandibular head lies some distance from the neurocranium.

Collectively, these observations suggest that the hyomandibula in symmoriiforms was only attached loosely to the neurocranium and that the attachment position was more variable than in most elasmobranchs. A short hyomandibula obviously will not extend as far along the otic region as a longer one, but its attachment to the neurocranium is also governed in vivo by the angular relationship of the hyomandibula to the neurocranium, and by the width of the jaw ramus at the mandibular joint. If the jaws curved outward posteriorly (as in most modern elasmobranchs), even a comparatively long hyomandibula might reach only the posterior part of the otic region. Furthermore, if the hyomandibula was held in place by ligaments, it need not have extended the full distance between the mandibular joint and the ligamentous attachment site, and would easily become displaced during fossilization, possibly accounting for much of the positional variation.

It has been suggested that *Cobelodus aculeatus* was aphetohyoidean (with a full gill slit opened between the mandibular and the hyoid arches, as had been postulated earlier for *Acanthodes* by Watson, 1937), supposedly providing empirical support for Gegenbaur's (1872) theory that a fully developed hyoidean gill cleft represents a primitive evolutionary stage for gnathostomes (Zangerl and Williams, 1975; Zangerl and Case, 1976; Zangerl, 1981). However, the interpretations on which those proposals were based have been challenged both in *Acanthodes* (Miles, 1968) and in Paleozoic sharks (Maisey, 1984, 1989). Zangerl and Williams (1975) claimed that there was no connection between the epihyal and the mandibular joint in *C. aculeatus*; however, such a connection is also absent in modern hexanchiforms, which are clearly not aphetohyoidean and have a spiracle as well as a ligamentous connection between Meckel's cartilage and the ceratohyal (Devillers, 1958). Zangerl and Williams (1975) also considered that the relative dimensions of the mandibular and hyoid arch elements supported their aphetohyoid interpretation, but that argument has also been refuted (Maisey, 1989: 185). Nevertheless, a hyomandibular articulation has not been recognized in *Cobelodus aculeatus* (Zangerl and Williams, 1975; Zangerl and Case, 1976) and no strong evidence for one exists in "*Cobelodus*", although one may be present in other symmoriiforms (e.g., *Falcatus*, *Akmonistion*; Lund, 1985a; Coates and Sequeira, 1998). Furthermore, if the symmoriiform palatoquadrate referred to *Stethacanthus* by Lund (1985b: fig. 5) has a spiracular notch as he suggested, the hyoidean gill cleft was presumably reduced as in modern elasmobranchs.

It has also been argued that the hyoid arch in chimaeroids is "unmodified" (as interpreted by De Beer and Moy-Thomas, 1935) and that it provides neontological support for the aphetohyoid condition. In fact, this arch displays several specialized features (Maisey, 1984), including: the lateral rather than medial position of the "pharyngohyal" relative to the efferent artery (corresponding to the batoid pseudohyal; Watson, 1937); the "pharyngobranchial" is bypassed by the subspinalis muscle and has no insertion for any interpharyngobranchial muscle (Daniel, 1934); closure of the hyoidean gill slit and absence of a spiracular pseudobranch; absence of epihyal rays; and absence of hyoid adductor muscles. Additionally, the afferent vascular supply (and water flow) through the pseudobranch of gnathostomes is "reversed" (Laurent and Dunel-Erb, 1984), providing increased oxygenation of arterial blood flowing to the brain via the efferent pseudobranchial artery. Although the pseudobranch is absent in modern chimaeroids, the "pseudobranchial" artery provides the principal blood supply to the brain because the internal carotids are aborted during ontogeny; De Beer and Moy-Thomas, 1935). The hyoid arch in modern chimaeroids therefore displays a suite of apomorphic features contradicting its interpretation as "unmodified", and in some respects the hyoid arch of elasmobranchs is actually more primitive (e.g., presence of a pseudobranch, absence of a "pharyngohyal" lateral to the efferent artery). The relationship of the chimaeroid "pharyngohyal" to surrounding vessels and muscles strongly supports its interpretation as a morphological novelty. No conclusive evidence for an "unmodified" hyoid arch has been found in gnathostomes, and the aphetohyoid condition is entirely conjectural.

The posterior postorbital process in placoderms (e.g., *Dicksonosteus*; Goujet, 1984) is typically associated with attachment areas for the branchial arches, but the hyomandibular facet is positioned much farther anteriorly (on the anterior postorbital process). The osteichthyan parampullary process typically develops on the lateral wall of the posterior ampulla rather than over the external semicircular canal (Gardiner, 1984a). In modern and extinct osteichthyans, the first branchial arch often articulates with (or is attached by ligaments to) the parampullary process or the opisthotic (e.g., *Polypterus*, *Polyodon*, *Latimeria*, *Eusthenopteron*, *Kansasiella*, *Mimia*, *Styloichthys*; Jarvik, 1954; Poplin, 1974; Gardiner, 1984a; Zhu and Yu, 2002). The osteichthyan opisthotic forms in the ventrolateral wall of the otic capsule, surrounding the external semicircular canal as well as the lower part of the posterior canal (including the ampulla), and it also forms the posterior part of the hyomandibular facet. The posterior postorbital process in placoderms such as *Dicksonosteus* may be homologous to the parampullary process in osteichthyans, and it is also possible that this process (plus the area extending anteriorly to the hyomandibular facet) corresponds to the opisthotic in osteichthyans (Gardiner, 1984a). However, the posterior postorbital process in placoderms and the parampullary process in osteichthyans are not involved in hyomandibular support, and there is no compelling evidence to suggest homology between either of them and the periotic process in "*Cobelodus*", nor with the lateral otic process in *Tamiobatis* and *Orthacanthus*.

CONCLUSIONS

1. Tropitrabia and platytrabia are regarded as ontogenetic conditions that are frequently the precursors to the corresponding adult state (tropibasia and platybasia), but there are important exceptions. Ontogenetic data are unavailable for fossils and the majority of extant species of gnathostomes, but morphological features associated with platybasia and/or tropibasia may provide clues about the precursor ontogenetic condition.

2. The braincase in "*Cobelodus*" and some other Paleozoic symmoriiform sharks is morphologically tropibasic, but the extent to which this characterizes symmoriiforms generally is uncertain. The braincase of *Cobelodus aculeatus* was misinterpreted as platybasic by Zangerl and Case (1976). The braincase in most modern elasmobranchs is morphologically platybasic (although ventral downgrowths of cartilage below the embryonic trabeculae are present in some etmopterids), but may be tropibasic in *Squaliolus*. The extensive "medial area" of the anterior basicranium develops early in ontogeny; therefore, if it is regarded as part of the trabeculae, modern sharks may be characterized as tropitrabic. No morphological evidence of an interorbital septum can be recognized in placoderms, but the presence of separate paired ethmoidal ossifications in ptyctodonts suggests that there was a median preorbital cartilaginous area that may have formed in the trabecula communis.

3. The embryonic polar cartilage in "*Cobelodus*" appears to have contributed extensively to the prechordal basicranium, as in *Cladodoides*. Tropibasia in "*Cobelodus*" may therefore have been superimposed on an already unusual pattern of cranial morphology. Although tropibasia in osteichthyans (especially actinopterygians) is very similar to the pattern found in "*Cobelodus*", their polar cartilage is generally small or even absent.

4. The postorbital arcade in "*Cobelodus*" is unusual in several respects. The lateral commissure is extremely wide and surrounds a much larger jugular canal than in most other elasmobranchs. The ventral attachment of the arcade apparently extended to the ventrolateral border of the polar cartilage, instead of meeting the ventrolateral wall of the otic capsule as in modern elasmobranchs.

5. The basicranial arterial circuit in "*Cobelodus*" must have been considerably modified, because the internal carotids could not have communicated with the cranial cavity via the bucco-hypophyseal chamber. These arteries either were absent or they met the efferent pseudobranchials within the orbits before entering the cranium. Nevertheless, the arterial circuit inferred in "*Cobelodus*" represents a modification of the primitive elasmobranch pattern and differs profoundly from that of osteichthyans, in which the combined internal carotid/efferent pseudobranchial enters the cranial cavity via the basisphenoid pillar and not via the orbit.

6. The epiotic process in "*Cobelodus*" is located farther anteriorly than the lateral otic process of many other Paleozoic sharks. It is uncertain whether these processes are homologous to each other, although both may be associated with the hyomandibular attachment.

7. The labyrinth of the inner ear is similar to that of *Cladodoides*, modern chimaeroids, and osteichthyans, and lacks the specializations found in modern elasmobranchs and extinct hybodont sharks. In this respect, the inner ear in "*Cobelodus*" conforms to the generalized crown-group gnathostome condition.

8. The occipital region in "*Cobelodus*" is short, but contains the same number of

spino-occipital canals (five) as in *Cladodoides*, where the occipital region is much longer. The number of canals is probably underreported in most fossil sharks, but there is no obvious correlation between the length of the occipital region and the number of spino-occipital canals. The configuration of the occipital region in "*Cobelodus*" differs from that in *Cladodoides* and other Paleozoic sharks in several respects. Its occipital cotylus is comparatively small and is elevated above surrounding structures. The cotylus is also reinforced by paired dorsal and ventral paroccipital processes. Nevertheless, in "*Cobelodus*" there is a persistent otico-occipital fissure, regarded as a conserved crown-group gnathostome feature shared with several other Paleozoic chondrichthyans and with primitive osteichthyans.

9. Cranial endocasts of "*Cobelodus*" and *Cladodoides* suggest that the tegmentum was elongated above the dorsum sellae and the hypothalamus was displaced anteriorly. A comparatively straight mesencephalon is also inferred. Presence of a tight "S" in the mesencephalon around the posterior commissure is a potentially apomorphic character of modern elasmobranchs that may be shared with hybodonts and xenacanths.

10. The braincase in *Cladoselache* shares some apomorphic characters with "*Cobelodus*", although their phylogenetic significance is still uncertain, including: division of the dorsal aorta below or in front of the occipital region; comparatively anterior location of foramina for the lateral aortae between the postorbital processes; a distinct narrowing of the otic region behind the postorbital arcade; absence of a lateral otic process and (possibly) presence of a periotic process; an extremely wide but anteroposteriorly short postorbital arcade; and an expansive jugular canal. In addition, *Cladoselache*, *Cobelodus aculeatus*, and *Stethacanthulus meccaensis* possess an unusual notch in the lateral margin of the supraorbital shelf, although this seems to be absent in "*Cobelodus*" and several other symmoriiforms. However it has not been determined whether *Cladoselache* was tropibasic. *Cladoselache* has a wide hypotic lamina, an important but previously unrecognized character shared with other elasmobranchs. *Cladoselache* and symmoriiforms primitively share a comparatively short otic region and a narrow occipital cotylus. The wide occipital cotylus and widely spaced aortic canals in *Tamiobatis*, *Cladodoides*, and *Orthacanthus* may be apomorphic features of the otic region related to hypertrophy in width as well as length.

11. The postorbital articulation in hexanchiforms is probably a derived feature. The postorbital articulation in Paleozoic sharks is not located on the primary postorbital process as in hexanchiforms, but on cartilage presumably formed in the lateral commissure. In "*Cobelodus*", there is evidence of an additional attachment area (possibly for ligaments) on the posterolateral surface of the postorbital arcade, above the actual postorbital articulation. This may help explain previous reports of a laterally directed postorbital "articulation" in other symmoriiforms. Such extra bracing of the symmoriiform postorbital articulation is envisaged as a modification of the primitive postorbital articulation.

12. No hyomandibular facet has been identified in "*Cobelodus*", but this does not constitute evidence that it was aphetohyoidean (with a complete hyoidean gill slit and "unmodified" hyoid arch). Previous suggestions that symmoriiforms were aphetohyoidean are probably unfounded, although the epihyal in "*Cobelodus*" may have been only loosely bound to the cranium by ligaments (possibly attached to the periotic process).

13. The systematics and classification of symmoriiform sharks are in disarray. Symmoriiforms collectively are probably monophyletic, but the only group to present clearly apomorphic characters within the order is the family Falcatidae. The traditional distinction between "symmoriids" and "stethacanthids" is probably invalid, because it has never been convincingly demonstrated that "brushless" (presumably female) "stethacanthids" existed, or that "symmoriids" are anything but female "stethacanthids". Sex-linked dimorphism of the spine-brush complex has been demonstrated convincingly only in falcatids. The enigmatic Permian shark *Dwykaselachus* may be a symmoriiform rather than a close relative of modern sharks as suggested by Oelofsen (1986). The braincase in *Cladoselache* shares some unusual features

with "*Cobelodus*" that suggest a relationship with symmoriiforms.

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