

THE XENACANTH SHARK
NEUROCRANIUM, WITH COMMENTS
ON ELASMOBRANCH MONOPHYLY

BOBB SCHAEFFER

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 169 : ARTICLE 1 NEW YORK : 1981

THE XENACANTH SHARK
NEUROCRANIUM, WITH COMMENTS
ON ELASMOBRANCH MONOPHYLY

BOBB SCHAEFFER

*Curator Emeritus, Department of Vertebrate Paleontology
American Museum of Natural History*

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 169 : ARTICLE 1
NEW YORK : 1981

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 169, article 1, pages 1–66, figures 1–26, table 1

Issued September 10, 1981

Price: \$4.50 a copy

ISSN 0003-0090

CONTENTS

Abstract	4
Introduction	4
Acknowledgments	5
Abbreviations	6
Materials and Methods	7
Review of Xenacanth Systematics	8
Neurocranium of <i>Xenacanthus</i>	10
General Features	10
Ethmoid Region	12
Orbitotemporal Region	17
Otico-occipital Region	22
Basicranial Circulation	26
Endocast	30
Growth and Histology	32
<i>Tamiodontis</i> Neurocranium	35
“ <i>Cladodus</i> ” Neurocranium	43
Neurocrania from the Cleveland Shale and Neurocranial Proportions	45
Analysis of Neurocranial Characters	46
Neurocranial Characters and Levels of Monophyly	60
Literature Cited	62

ABSTRACT

The neurocranium of the shark *Xenacanthus* (*sensu lato*) from the early Permian of Texas shares derived characters with the neurocrania of various other Paleozoic shark genera, including *Tamiobatis*, "*Cladodus*," "*Ctenacanthus*," *Cladoselache*, and with *Hybodus* and the living neoselachians. These characters are consistent with the hypothesis that the above extinct and the

living taxa belong to the monophyletic group Elasmobranchii. *Xenacanthus* and *Tamiobatis* are proposed as sister taxa related to "*Cladodus*" and possibly to "*Ctenacanthus*" from the Cleveland shale. The details of *Xenacanthus* and *Tamiobatis* cranial morphology are based on three-dimensional specimens, both whole and sectioned.

INTRODUCTION

Because of generally poor preservation, the neurocranium of fossil sharks has played a minor role in providing characters for constructing hypotheses of relationship involving both extinct and living elasmobranch taxa. Neurocranial characters have been widely used, however, to propose relationships within the neoselachians (e.g., Compagno, 1973) but character conflicts are still evident, and further investigation is required including consideration of the cranial circulation and cranial nerve patterns. Detailed study of the few types of Paleozoic three-dimensional selachian braincases is mostly confined to the contributions of Gross (1937), Stensiö (1937), and Romer (1964). A rather obvious omission in this regard is the neurocranium of *Xenacanthus* (*sensu lato*), which is represented by many partial and nearly complete specimens from the Lower Permian rocks of Texas and Oklahoma.

During his more than four decades of fieldwork in the Texas Permian, A. S. Romer acquired many xenacanth braincase specimens, some with associated jaws and hyomandibulae. The restoration of the *Xenacanthus* skull in the several editions of his textbook (Romer, 1966) is based mostly on this material. Anticipating a complete description of the neurocranium, Romer supervised the serial grinding of five partial neurocrania using the "peel" method, the preparation of enlarged tracings of at least four of the peel series, and the construction of two wax plate models.

As this project was not completed at the time of Romer's death in 1973, I have at-

tempted to do so now thanks to the kindness of Dr. Farish Jenkins who permitted me to study the surviving peels, section drawings, and models preserved in the Museum of Comparative Zoology. Although Professor Romer made some tentative reconstructions of the xenacanth neurocranium, no manuscript by him has been found. Presumably this project was suspended prior to his research on the *Tamiobatis* neurocranium (Romer, 1964).

A key problem that became evident early in this study relates to the monophyly of the Elasmobranchii. Until recently the common ancestry of all "sharks" ranging from the Devonian to the Recent was rarely questioned. It is increasingly evident, however, that elasmobranch synapomorphies are by no means obvious, and that we cannot continue to talk about "Paleozoic elasmobranchs" unless this practice can be justified on the basis of derived characters that are shared with the living sharks (neoselachians). Accordingly, the braincase of *Xenacanthus*, along with that of certain other Paleozoic chondrichthyans, particularly *Tamiobatis* Eastman and "*Cladodus*" Agassiz, has been compared with the neurocrania of various neoselachians, with emphasis on those taxa for which adequate embryological data are available. For reasons of communication, however, terms such as "Chondrichthyes" (or "chondrichthyan"), "Elasmobranchii" (or "elasmobranch"), and "selachian" are used in various places in the text pending consideration of definition and relationship on pages 60–62.



FIG. 1. *Xenacanthus* sp. MCZ 12872. Associated neurocranium, jaws and partial hyoid arch. $\times 22$.

ACKNOWLEDGMENTS

I am indebted to a number of individuals and institutions for the loan of specimens,

fossil and Recent. These include Dr. James Atz and Dr. C. L. Smith, American Museum of Natural History; Dr. Michael Williams,

the Cleveland Museum of Natural History; Dr. John Bolt and Dr. Rainer Zangerl, Field Museum of Natural History; Mr. Gerard R. Case, Jersey City, N.J.; Dr. Farish A. Jenkins, Jr. and Mr. Chuck Schaff, Museum of Comparative Zoology, Harvard University; Dr. Nicholas Hotton, III and Mr. Robert Purdy, National Museum of Natural History, Washington, D.C.; Dr. Donald Baird, Princeton University; Dr. Leonard J. V. Compagno, Tiburon Center, San Francisco State University; Dr. Everett C. Olson, University of California, Los Angeles; and Dr. Wann Langston, Jr., University of Texas, Austin. Mr. Howard F. Barnett of Marion, Iowa has generously presented a second *Tamiobatis* neurocranium to the American Museum of Natural History.

The following have kindly supplied information or commented on the manuscript: Drs. Donald Baird, Leonard J. V. Compagno, John F. R. Dick, Malcolm Jollie, John Maisey, Everett C. Olson, Colin Patterson, Donn E. Rosen, Michael E. Williams and Rainer Zangerl, Mr. Gary D. Johnson and Mr. William Kohlberger.

I am particularly obliged to Ms. Lorraine Meeker for drafting numerous reconstructions of the xenacanth braincase, mostly from the serial grinding series. The final drawings, many of them composites based on these reconstructions, are the work of Mr. Juan C. Barbaris. The photographs were taken by Mr. Chester Tarka. Mr. Walter Sorensen prepared details of various specimens in order to locate foramina and other important characters.

ABBREVIATIONS

INSTITUTIONAL

AMNH, American Museum of Natural History
CMNH, Cleveland Museum of Natural History
FMNH, Field Museum of Natural History
MCZ, Museum of Comparative Zoology, Harvard University
NMNH, National Museum of Natural History
PUGM, Princeton University Geological Museum
UCLAVP, University of California, Los Angeles
UTVP, University of Texas

ANATOMICAL

aa, ampulla of anterior semicircular canal
ac, auditory capsule
acer, auricle of cerebellum
ah, ampulla of horizontal semicircular canal
arth, articular area for hyomandibula
artp, articular facet for palatoquadrate
asc, anterior vertical semicircular canal
ba, basilar artery
cbr, cerebrum
cer, cerebellum
da, dorsal aorta
dlof, dorsolateral otic fossa
dor, dorsal otic ridge
eha, efferent hyoidean artery
end, endolymphatic duct
endf, endolymphatic (parietal) fossa
epif, epiphysial foramen
epsa, efferent pseudobranchial artery
etha, ethmoid articulation
fepsa, foramen for efferent pseudobranchial artery
fhym, foramen for hyomandibular branch of VII
fhyp, hypophysial fenestra or fossa
fica, foramen for internal carotid artery
flda, foramen or canal for lateral dorsal aorta
fm, foramen magnum
foa, foramen or groove for orbital artery
focn, foramen or canal for occipitospinal nerve
foph, foramen for ophthalmic artery
fpal, foramen or canal for branch of palatine nerve or branch of orbital artery
fso, foramina for superficial ophthalmic nerves
hol, hypotic lamina
hsc, horizontal (lateral) semicircular canal
hym, hyomandibula
hym VII, hyomandibular branch of facial nerve
hyc, hypophysial cavity
ica, canal or groove for internal carotid artery
inf, infundibular cavity
jc, canal or groove for jugular vein (lateral head vein)
lag, lagena
lda, lateral dorsal aorta
lop, lateral otic (epiotic) process
lof, lateral otic fossa
lor, lateral otic ridge
med, medulla
nc, nasal capsule
not, notochordal space
occ, occipital condyle
ocf, occipital fossa
ocr, occipital crest
ocs, occipital segment

oof, otico-occipital fissure (embryonic metotic fissure)
 opa, optic artery
 opha, ophthalmic artery
 opl, optic lobe
 ora, orbital artery
 os, optic stalk depression
 pap, parachordal plate
 pf, precerebral (epiphysial) fontanelle or fossa
 plf, perilymphatic fenestra
 pro, preorbital (nasal, antorbital) process
 pop, postorbital process
 psc, posterior vertical semicircular canal
 pt, posterior tectum
 pv, pituitary vein
 rart, rostral articular area for palatoquadrate
 rf, rostral fenestra (basal communicating canal, subnasal fenestra)
 rob, orbital roof
 ros, rostrum

sac, sacculus
 scn, separate nasal calcification
 tfr, trigemino-facialis recess
 unc, uncalcified area
 ur, utricular recess
 ut, utriculus
 von, ventral otic notch
 vos, ventral otic shelf
 I, foramen or canal for olfactory tract
 II, foramen or canal for optic nerve and optic artery
 III, foramen or canal for oculomotor nerve
 IV, foramen or canal for trochlear nerve
 V, foramen or canal for trigeminal nerve
 VI, foramen or canal for abducens nerve
 VII, foramen or canal for facial nerve
 VIII, canal for auditory nerve
 IX, foramen or canal for glossopharyngeal nerve
 X, foramen or canal for vagus nerve

MATERIALS AND METHODS

The *Xenacanthus* neurocrania listed below have been chosen for study because they show specific morphological features in a relatively unaltered condition. Most specimens from the lower Permian rocks of Texas are fractured or compressed to such an extent that the surface details and internal features, including the foramina, are frequently obscured or eliminated. When necessary, preparation has been accomplished manually, with a vibro-tool, and by air abrasion. Matrix removal with dilute acetic acid has required caution as it attacks the calcified cartilage. Thioglycollic acid softens the matrix, but manual preparation is then required.

Detailed field data are not available for most of the neurocrania but are included where known. A general statement regarding the stratigraphic and geographic distribution of these braincases is included in the systematic section. The selected specimens are:

From the American Museum of Natural History: AMNH 7928, nearly complete, distorted neurocranium figured by Cope (1884); AMNH 7929, anterior part of neurocranium figured by Cope (1884); AMNH 7930, posterior part of neurocranium figured by Cope

(1884); AMNH 7246, nearly complete neurocranium, crushed, with paired foramina for internal carotids; AMNH 7247, orbitotemporal part of neurocranium; AMNH 7254, otico-occipital part of largest available specimen with estimated total length of 30 cm., sawed vertically through the endolymphatic fossa.

From the Museum of Comparative Zoology, Harvard University: MCZ 8944, nearly complete neurocranium; MCZ 12872, large, nearly complete neurocranium with associated palatoquadrates, mandibles, hyomandibulae and ceratohyals, from upper part of Admiral Formation, Black Flat, Archer County, Texas; MCZ 13377, nearly complete neurocranium, partly compressed; MCZ 13388, nearly complete neurocranium; MCA 13431, nearly complete neurocranium from Belle Plains Formation, near Dundee, Texas.

From the University of California, Los Angeles, UCLA VP 3155. From the Garber Formation in Oklahoma. This specimen has provided important information on the foramina, grooves, and canals in the basicranium.

From the Princeton University collection,

PU 22391. An incomplete braincase with a uniquely complete left orbit and postorbital process.

From the University of Texas, UTPV 40998-1 and 40998-2. Two weathered specimens showing basicranial details.

In regard to the serial grinding series, apparently five braincases were sectioned by the peel method. Following a note in Professor Romer's handwriting, these are designated as follows:

A. Transverse series of nearly complete neurocranium. This "Chicago" specimen was presumably in the original Walker Museum collection. Peels missing; series represented only by 90 enlarged tracings. Internal structures fragmented and poorly preserved.

B. Transverse series of otico-occipital region. Peels missing; series represented by 94

enlarged tracings and wax plate reconstruction. Preservation relatively good.

C. Horizontal (frontal) series of orbital region including postorbital processes. Peels missing; series represented by 40 enlarged tracings and a wax plate reconstruction. Preservation fair.

D. Horizontal series of nearly complete neurocranium including 59 peels and enlarged tracings. Most informative series; preservation relatively good.

E. Sagittal series of otico-occipital region with 80 peels; no tracings or wax model.

The peels, enlarged tracings, wax models, and graphic reconstructions are preserved in the Museum of Comparative Zoology, Harvard University.

The provenance and location of the *Tam-iobatis* and "*Cladodus*" neurocrania are given in the special sections on these specimens.

REVIEW OF XENACANTH SYSTEMATICS

Xenacanth braincases from the Lower Permian deposits of Texas and Oklahoma occur sporadically in lacustrine, flood plain, and channel deposits of the Wichita Group (Admiral, Belle Plains, and Clyde formations), in the overlying Clear Fork Group (Arroyo, Vale and Choza formations) of northern Texas, and in the Garber Formation (equivalent to the Arroyo) of southern Oklahoma (E. C. Olson, personal commun.). They are found occasionally in association with the jaws and upper segments of the hyoid arch. Isolated xenacanth teeth may be locally abundant and are sometimes attached to the palatoquadrate or the mandible. Cephalic spines, which are generally rare, have not been found in place on the neurocranium, and postcranial elements are unknown.

Cope (1884) provided the first description of the Texas xenacanth neurocrania based on some 12 specimens, one with associated jaws and a few teeth. He identified the braincase as elasmobranch and found the teeth remarkably like those of the recently described *Chlamydoselachus* Garman (1884) but also admitted that it showed a closer af-

finity with *Pleuracanthus* Agassiz (1837). Cope did, however, assign the Texas specimens to his genus *Didymodus*, which he had proposed in 1883 for some Pennsylvanian xenacanth remains to replace the preoccupied name *Diplodus* (Agassiz). Egerton (1857) had previously pointed out the apparent generic identity of the tooth forms called *Diplodus*, *Pleuracanthus*, and *Xenacanthus* (Beyrich, 1848).

Xenacanth (pleuracanth) taxonomy became badly confused in the several decades following Agassiz's (1837) original description of *Pleuracanthus*. More than a dozen names were assigned to isolated teeth, spines, denticles, and other bits of the skeleton ranging in age from the middle or late Devonian to the late Triassic. Some of this "tooth taxonomy" was clarified by the time of Woodward's (1889) catalogue, but systematic problems still exist at both generic and specific levels. Jordan (1923), among others, noted that the name *Pleuracanthus* is preoccupied. Excluding *Pleuracanthus*, he lists 17 names, including *Xenacanthus*, that at one time or another have been applied to xena-

canth remains. Comparison of recent taxonomic statements (Romer, 1966; Obruchev, 1967; Moy-Thomas and Miles, 1971) indicates that a critical review of all xenacanth remains is obviously needed.

Comprehensive papers by Reis (1879), Fritsch (1895) and Jaekel (1906) emphasized most of the unique derived characters of the pleuracanth skeleton, but did little to clarify the affinities of these distinctive fishes. Goodrich (1909) was so impressed with the separated halves of the pectoral girdle and the unconcentrated median fins that he provisionally separated the Pleuracanthodii from the Elasmobranchii (his Selachii plus Holocephali), Cladoselachii and Acanthodii, all of which he included in the Chondrichthyes. However, Moy-Thomas (1939) thought that the neurocranium is of "the typical elasmobranch kind," and there has been general agreement that the xenacanths are a monophyletic group of selachians of unknown affinity.

Returning to the Texas xenacanth material, Broili (1904) described a braincase in the Munich Museum with associated jaws, some teeth and hyoid elements under the name *Diacranodus* Garman (1885). Garman had noted that *Didymodus*, like *Diplodus*, is a synonym of *Xenacanthus*, and he proposed *Diacranodus* as a substitute name. Garman (1885, pp. 29–30) also improved on Cope's description of the neurocranium (from Cope's figures), and pointed out that the braincase is unsegmented and composed of calcified cartilage—in contrast to Cope's curious observation that it is divided into endochondral and dermal ossified elements. Broili added more details, including a lithograph of the Munich specimen in dorsal aspect with the left hyomandibular and the right palatoquadrate in articulation with the neurocranium. But aside from Hotton's (1952) study of the jaws, and Romer's figures of the neurocranium in his vertebrate paleontology text, there has been no publication on the Texas xenacanth head skeleton since Broili's contribution—which is rather odd in view of the fact that the Texas specimens represent the only three dimensional

braincases for the entire "*Xenacanthus*" complex. In this connection it may be noted that Fritsch's (1895) figures of the flattened Rothliegendes xenacanthid braincases are nearly incomprehensible (as are the actual specimens) except for the preorbital to postorbital proportions, which are similar to those of the Texas specimens.

On the basis of tooth form Cope (1884) recognized two species of *Didymodus* in the Texas Permian—*D. compressus* and *D. platypternus*. His series of 12 specimens, on which the original description of the neurocranium is based, were referred by him to *D. compressus*. In 1888, because of presumed differences with the Pennsylvanian "*Diplodus*" *compressus* (Newberry, 1856), Cope assigned these Texas specimens to a new species, *D. texensis*. In a more extended discussion of xenacanth tooth form Hotton (1952) has recognized *X. texensis* and *platypternus* as valid "tooth species," and he compares them with the teeth, plus cephalic spines and other skeletal characters of *Orthacanthus*, which he thinks is generically distinct from *Xenacanthus*. Lund (1969) has argued that *X. compressus* is really *Orthacanthus compressus* on the basis of tooth form and spine shape. Berman (1970) has recognized two previously described American Permian species of *Xenacanthus* and adds a third, *X. luedersensis*. G. D. Johnson (personal commun.), who is restudying European and American Pennsylvanian and the Permian xenacanth teeth, is inclined to support a dental distinction between *Xenacanthus* and *Orthacanthus*.

The differences in tooth form and to some extent spine shape (Zidek, 1978) expressed by the various taxonomic maneuvers discussed above are undoubtedly real. However, before we can expect reasonable stability in xenacanth systematics, I believe it will be necessary to reconstruct more or less complete upper and lower dentitions for each recognized taxon and to review all other skeletal characters that are present in both American and European forms to supplement the tooth evidence. Until some attempt of this sort has been made, I prefer to call the xenacanth from the Texas Permian sim-

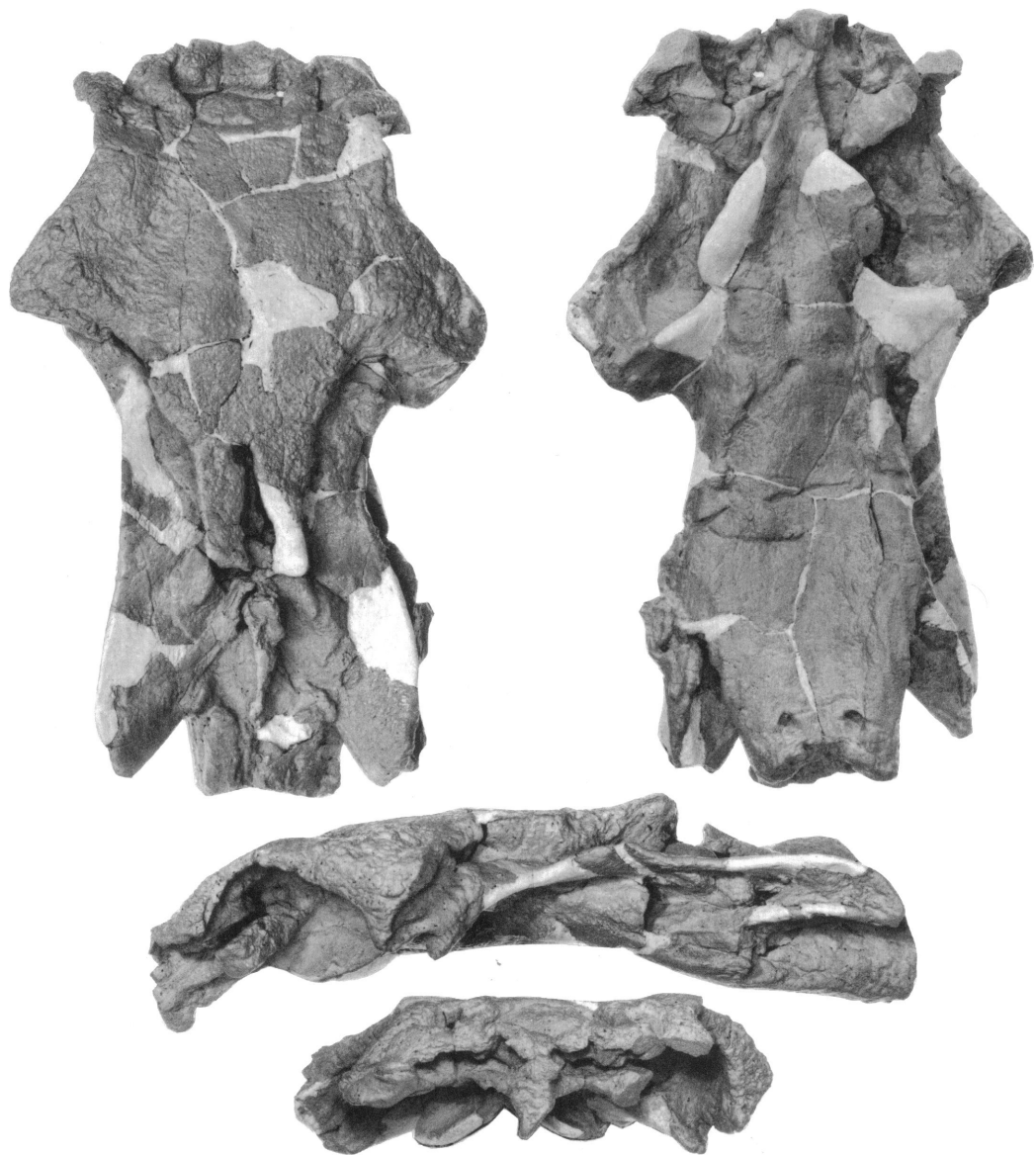


FIG. 2. *Xenacanthus* sp. MCZ 12872. Neurocranium in dorsal, ventral, lateral and anterior aspects. $\times .41$.

ply *Xenacanthus* sp. in agreement with Olson, 1965.

Systematic problems related to *Tamioba-*

tis, "*Cladodus*" and certain other Paleozoic genera are briefly discussed in the sections devoted to these taxa.

NEUROCRANIUM OF *XENOCANTHUS*

GENERAL FEATURES

Obvious characteristics of the relatively narrow xenacanth braincase are the length of the otic region and the prominence of the occipital segment (figs. 1-6). Together these

average more than half of the total braincase length regardless of overall braincase size. The occipital segment in neoselachians is typically wedged between the otic capsules. This is also the case in *Xenacanthus*, but the occipital block projects well behind the lat-

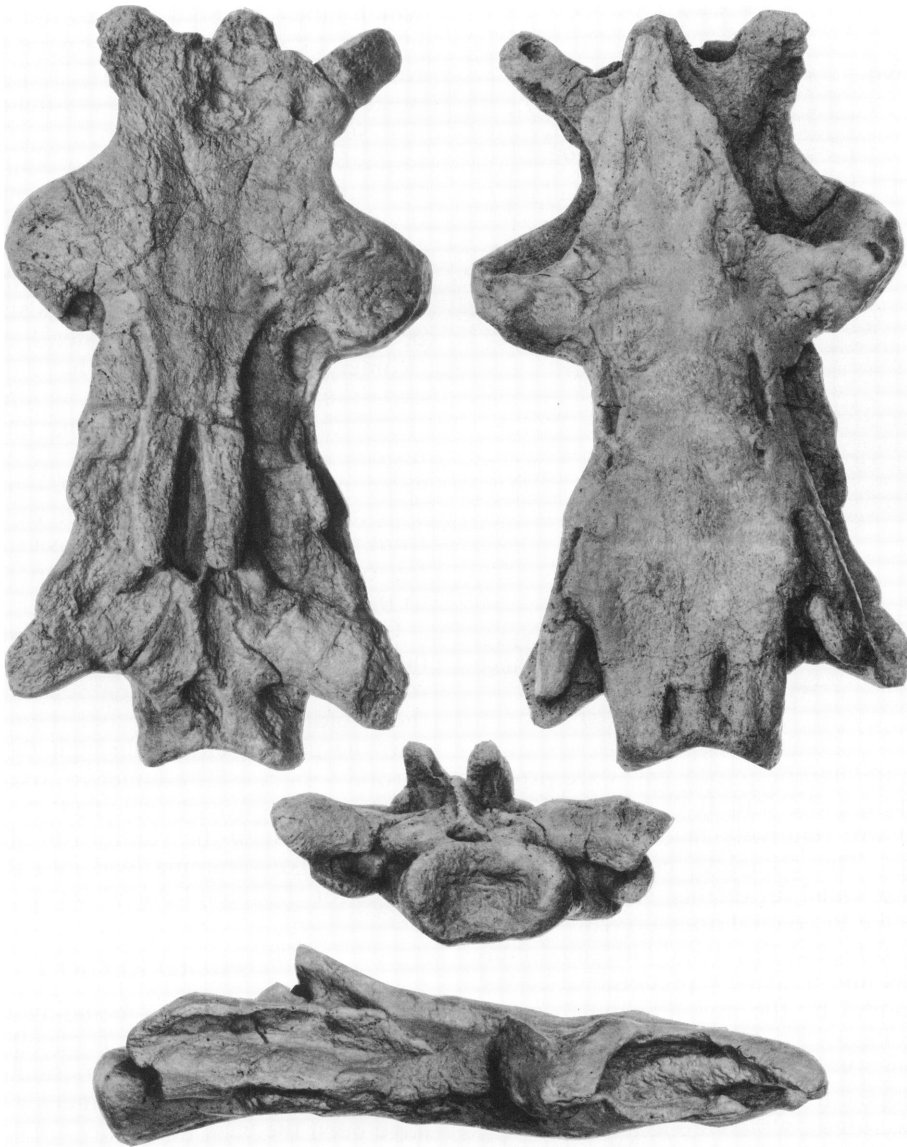


FIG. 3. *Xenacanthus* sp. MCZ 13388. Neurocranium in dorsal, ventral and lateral aspects. $\times .41$

eral otic processes as the narrowest region of the neurocranium. Persistent otico-occipital fissures, which partly separate the occipital block from the auditory capsules, extend posterolaterally from the endolymphatic fossa to the ventral surface of the braincase where they merge into the ventral otic notches that partly separate the lateral otic pro-

cesses from the continuous otico-occipital floor (figs. 2, 3, 5, 6, 9).

The rostral area, which is best preserved in MCZ 12872, projects somewhat beyond the calcified portions of the nasal capsules. There is also a median, ventrally directed rostral flange with an articular surface for the palatoquadrate (fig. 2). The antorbital, post-

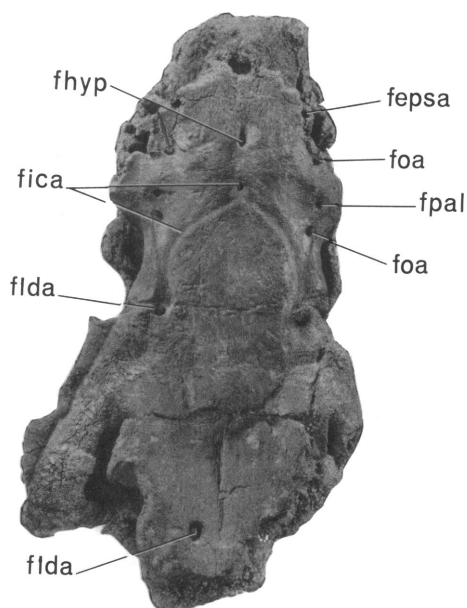


FIG. 4. *Xenacanthus* sp. UCLAVP 3155. Neurocranium in ventral aspect to show grooves and foramina. $\times 75$.

orbital, and lateral otic processes are prominent features; the lateral otic processes in particular are relatively larger than in neoselachians. The complete postorbital wall, with a large canal for the head vein, is palaeoniscoid-like in general appearance.

In dorsal aspect the ovoid anterior fontanelle leads into a shallow precerebral cavity that is floored by the dorsally domed internasal cartilage, much as in *Chlamydoselachus* (Allis, 1923, pl. ix). The roof of the otic region slopes toward the elevated, robust dorsal otic ridges, which are in turn undercut both laterally and posteriorly. The endolymphatic fossa, surrounding a slitlike opening into the cranial cavity, is situated in front of the occipital crest. Although no specimen from the Texas Permian has been found with the cephalic spine in place, it is probable that the scoop-shaped proximal end of the spine fitted over a rather ill-defined boss at the anterior end of the occipital segment.

The uncrushed orbit (figs. 5, 6) approximates a trapezoid in lateral aspect. It is bordered ventrally by the suborbital shelf,

which tapers abruptly toward the midline to join its counterpart in a blunt point below the rostrum. The postero-lateral surface of the postorbital process has a well-defined articular surface for the otic process of the palatoquadrate. Behind the postorbital process, the lateral surface of the otic region is subdivided by two strong horizontal ridges: the lateral otic ridge and the ventral otic shelf. The former houses the horizontal semicircular canal, whereas the latter is simply part of the cranial wall. The lateral otic fossa (Romer, 1964), which may have an incompletely calcified medial wall, is situated between these ridges. The robust lateral otic processes project sideways to about the same extent as the postorbital processes. The occipital segment, which is separated from the otic region except basicranially by the otico-occipital fissure, extends forward to the endolymphatic fossa.

Grooves and foramina on the ventral surface indicate the course of the internal carotid arteries between their separation from the lateral dorsal aortae and their entrance into the cranial cavity through the internal carotid foramen. The concave, ovoid occipital condyle is heavily calcified. A short distance anterior to the ventral rim of the condyle, slotlike foramina lead into the paired canals for the lateral dorsal aortae.

ETHMOID REGION

The ethmoid region, including the nasal capsules and the rostrum, is usually the last part of the neoselachian neurocranium to calcify (Benzer, 1944 and specimens). This may have been the case in *Xenacanthus*. Among the neurocrania available for this study, the nasal capsules and rostrum are best preserved in the largest specimens (MCZ 12872), which is about 27.5 cm. from the occipital condyles to the anterior termination of the trabecular plate. However, calcified parts of the ethmoid region are also present in much smaller specimens (NMNH 2444473—9.5 cm.; MCZ 55—11 cm.; AMNH 7928—16 cm.; MCZ 1388—21 cm.) and it is evident that the preorbital processes and the nasal capsules were at least partly covered with

thin layers of calcified prisms in braincases as small as 10 cm. in length.

Most major aspects of the xenacanth ethmoid region can be interpreted on the basis of a neoselachian model. The internasal plate (the part of the basicranium anterior to the hypophysial fenestra) flares laterally to form the suborbital (subocular) shelf (fig. 8C), but tapers to a blunt point below the preorbital processes where it merges anteriorly with the rostrum. There is no evidence of a nasal fontanelle in the calcified floor of the nasal cavity as described by de Beer (1937, p. 456) for neoselachians. The blunt, massive rostrum as preserved in MCZ 12872 (figs. 2, 5, 8A) probably extended somewhat beyond the olfactory capsules. As noted, it is fused below with the internasal plate, with the preorbital processes, and dorsally with the olfactory capsules. Unfortunately there are no certain clues regarding rostral ontogeny—that is, whether the rostrum developed as a separate chondrification (as in *Scyliorhinus*) or as a projection of the trabecular plate (as in *Squalus*). Nevertheless, its relationships to surrounding structures indicate homology with the neoselachian rostrum. One important difference from the neoselachian condition, however, is that the *Xenacanthus* rostrum has articular surfaces for the orbital ramus of the palatoquadrates, as confirmed by the associated upper jaws of MCZ 12872 (fig. 1).

The preorbital process (fig. 6, pro) projects obliquely forward from the internasal plate. It is partly separated from the ethmoid articular area (see discussion on palatoquadrate attachments, p. 56) and the more anterior tapered part of the plate by a well-defined, horizontal groove that runs from the anterior orbital rim forward to the rostrum and below the nasal capsule. The grooves and ridges on the medial horizontal lamina of the suborbital ramus of the palatoquadrate articulate with corresponding elevations and depressions on the upper surface of the ethmoid articulation (fig. 7, etha) as in "*Cladodus*" (Gross, 1938, fig. 2) and in *Cobelodus* (Zangerl and Case, 1976).

The ovoid margin of the anterior (precerebral) fontanelle is frequently evident (figs. 2,

3) but postmortem compression has usually eliminated the precerebral fossa—except in grinding series A, where it can be followed into the cerebral cavity (figs. 8, 14). There is no evidence of an epiphysial notch or foramen. The preorbital canal, through which the superficial ophthalmic nerve reaches the dorsal surface of the nasal capsule, opens into a shallow furrow next to the precerebral fontanelle (fig. 6).

In neoselachians (de Beer, 1937; Jollie, 1971) the preorbital process as well as the lateral, posterior, and in part the dorsal walls of the nasal capsule are formed by the lamina orbitonasalis, which projects anterolaterally from the trabecular plate. The internasal plate, also an outgrowth of the trabecular plate between the nasal capsules, forms the internasal septum, part of the nasal capsule roof, and in *Hybodus* (Maisey, personal commun.), *Chlamydoselachus* and the galoids, also the medial capsular wall.

The nasal capsules of *Xenacanthus* are close together (figs. 2, 5, 6), being separated only by the rather narrow internasal plate, which projects forward and ventrally as the rostrum. It is probable that the medial wall of the nasal capsules was formed only from the rostral internasal plate, which also contributed to the capsular roof along with the trabecular horns and the lamina orbitonasalis. The latter also formed part of the side, hind and ventral walls of the capsule. As noted by de Beer (1937, p. 61) these embryonic components form a short cylinder-like cavity around the large, irregular olfactory nerve. In *Xenacanthus* the roof of the capsule considerably overhangs its ventral border. The incurrent and excurrent narial openings must have been situated in the uncalcified or non-chondrified portion of the capsule and were probably directed ventrally as in the neoselachians. There is no indication of basal communicating canals (more aptly called subnasal or rostral fenestrae as they transmit neither nerves nor blood vessels), which are characteristic of the squaloids (Holmgren, 1941, p. 35) among the neoselachians (fig. 15) and which involved the development of secondary medial walls for the olfactory capsules (de Beer, 1937, pp. 54, 395).

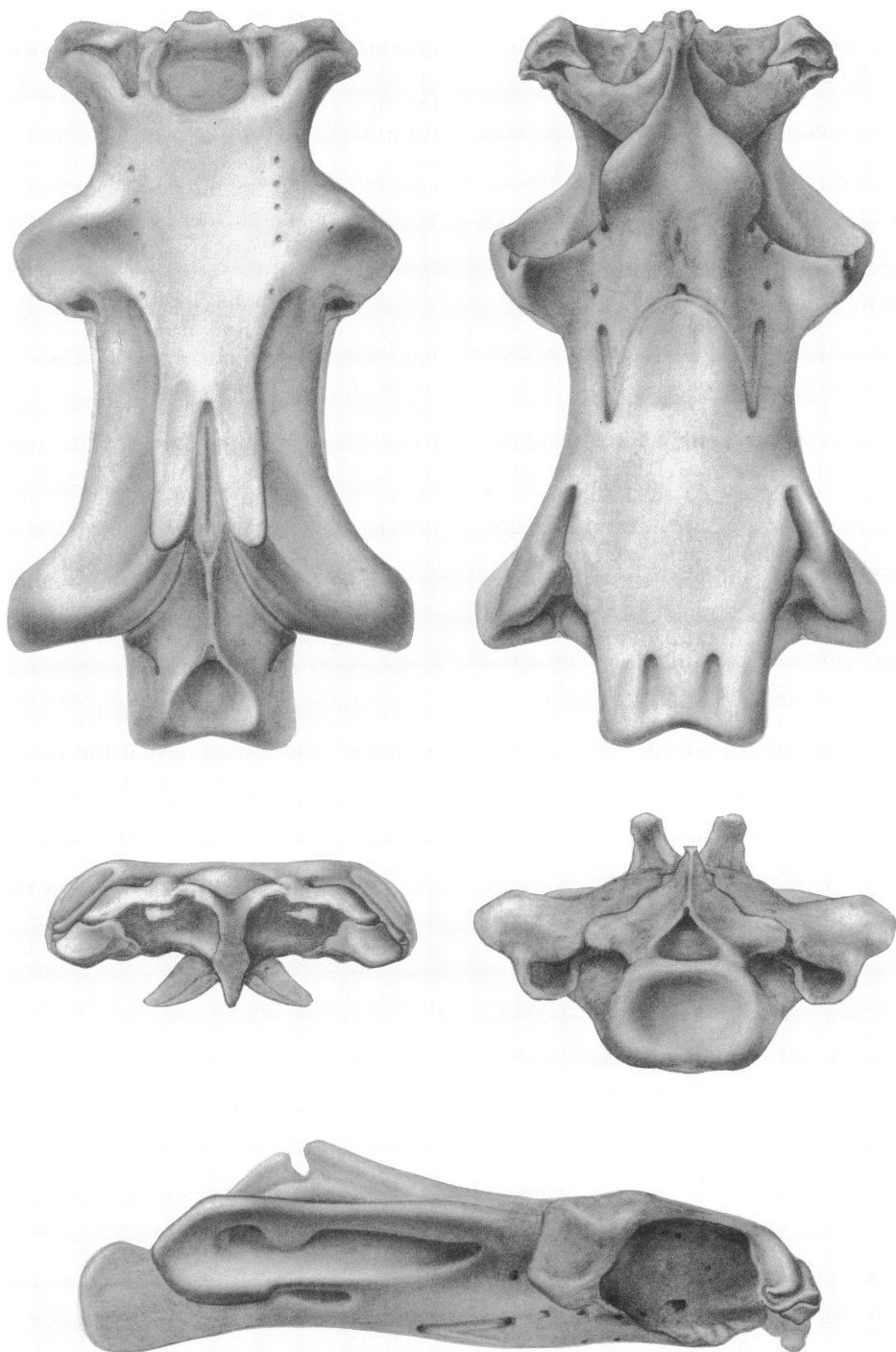


FIG. 5. *Xenacanthus* sp. Composite restoration of neurocranium in dorsal, ventral, rostral, occipital, and lateral aspects.

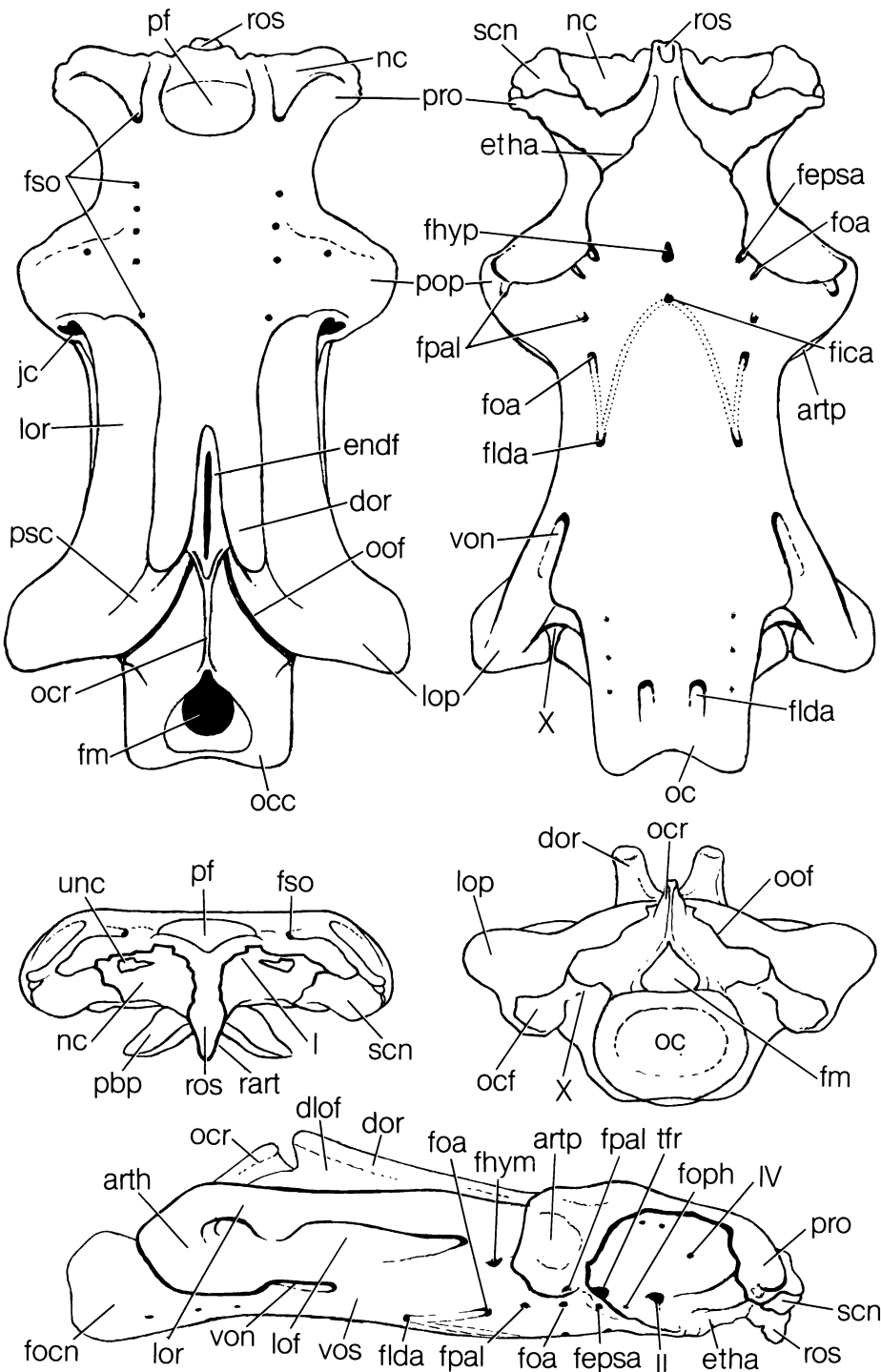


FIG. 6. *Xenacanthus* sp. Key diagrams for figure 5.

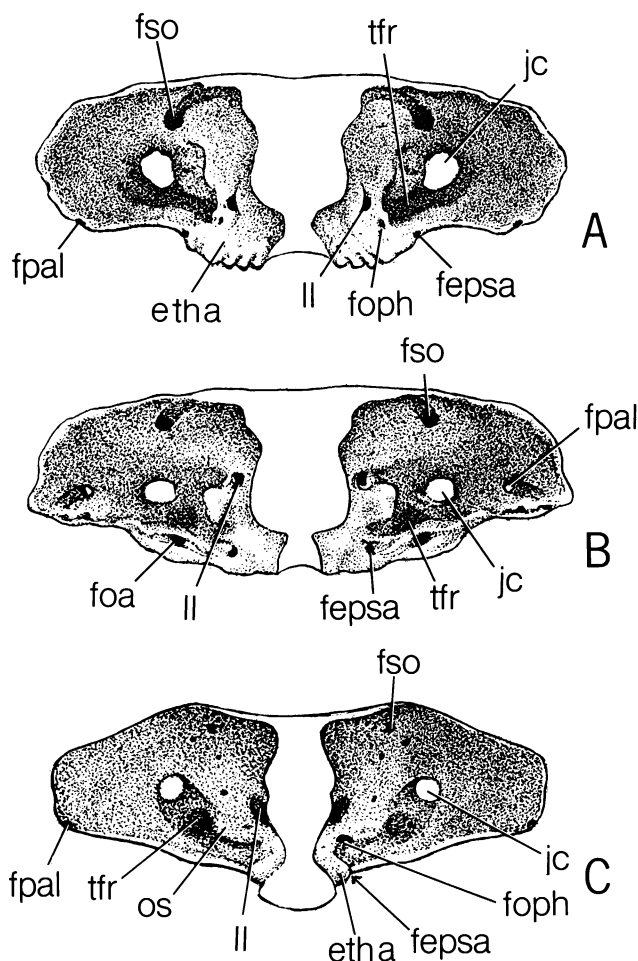


FIG. 7. Transverse section of neurocranium at level of postorbital wall. A. *Xenacanthus* sp. B. *Tamiobatis* sp. C. "*Cladodus*" *wildungensis*.

An explanation is not readily found for the apparent presence of a separate calcification on the anteroventral corner of the nasal capsule, which can be seen on the right capsule of MCZ 12872 (figs. 2, 5, 6). On the left capsule of the MCZ specimen, where this element is absent, the surfaces to which it would be attached are smooth and resemble contact areas. Based mostly on the descriptions of nasal capsule development in *Squalus* and *Scyliorhinus* (Holmgren, 1941 and de Beer, 1937), I suggest that it represents part of the nasal cartilage. In living sharks the

nasal cartilage develops independently of the capsule, and partly surrounds the narial fenestrae. It could be the same element as " 1_2 " and/or " 1_3 " in Parker's (1879) illustrations of the *Scyliorhinus* (*Scyllium*) skull. There is, however, no indication that it was involved in the subdivision of the narial fenestra into incurrent and excurrent apertures. It appears, however, that much of the dorsal, anterior and ventral walls of the nasal capsule in *Xenacanthus* were composed of uncalcified cartilage.

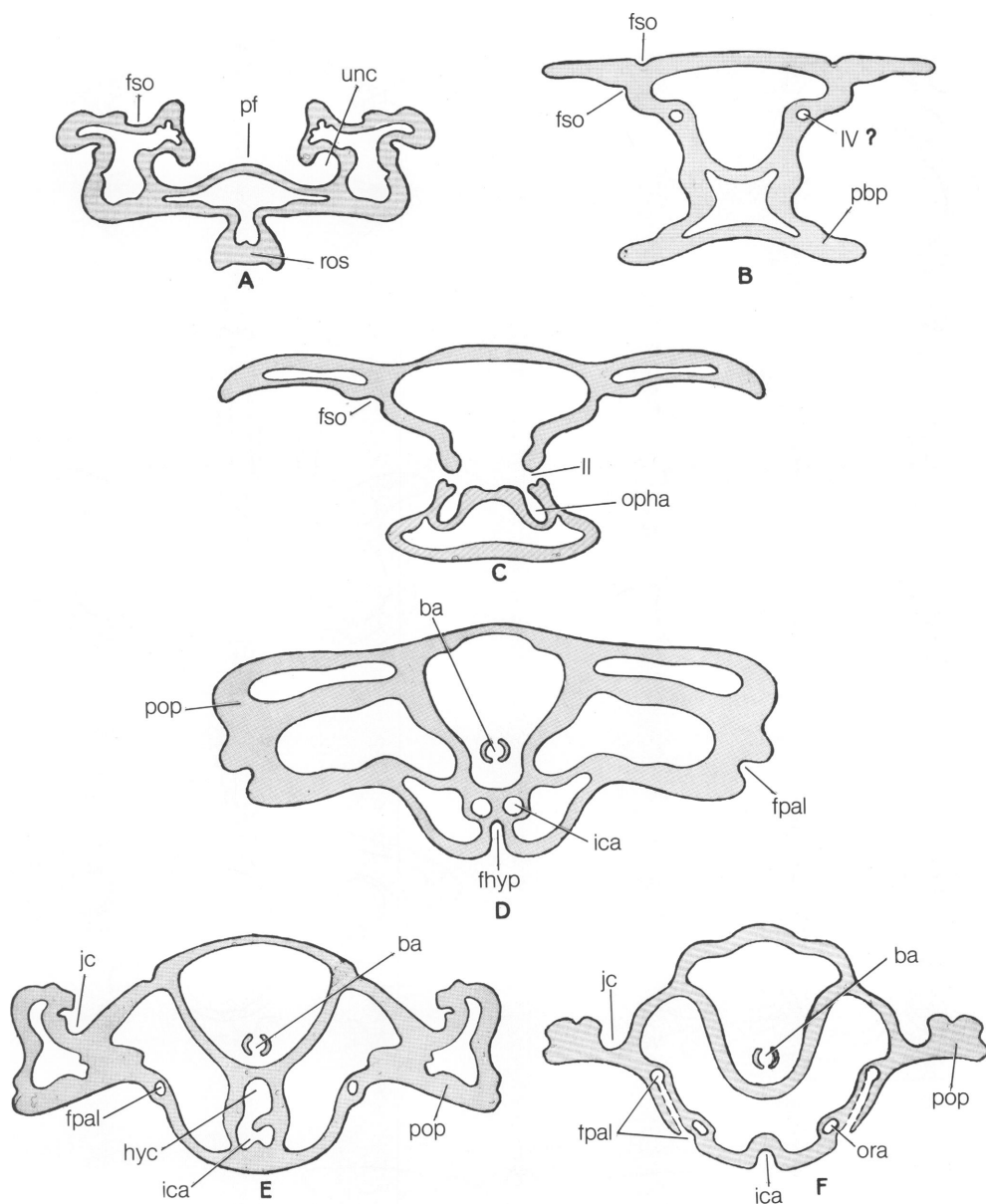


FIG. 8. *Xenacanthus* sp. Selected transverse sections through anterior part of neurocranium. Partly schematized and corrected for crushing. Based mostly on grinding series A and B.

ORBITOTEMPORAL REGION

The left orbit is preserved, relatively complete and undistorted, in one specimen (PUGM 22391 B) and has served for the restoration of the orbital area in figures 5 and 6.

Additional data for the orbital region were provided by the wax model based on grinding series C. In lateral aspect the orbit, as noted above, resembles a trapezoid with the vertical borders sloping somewhat anterior-

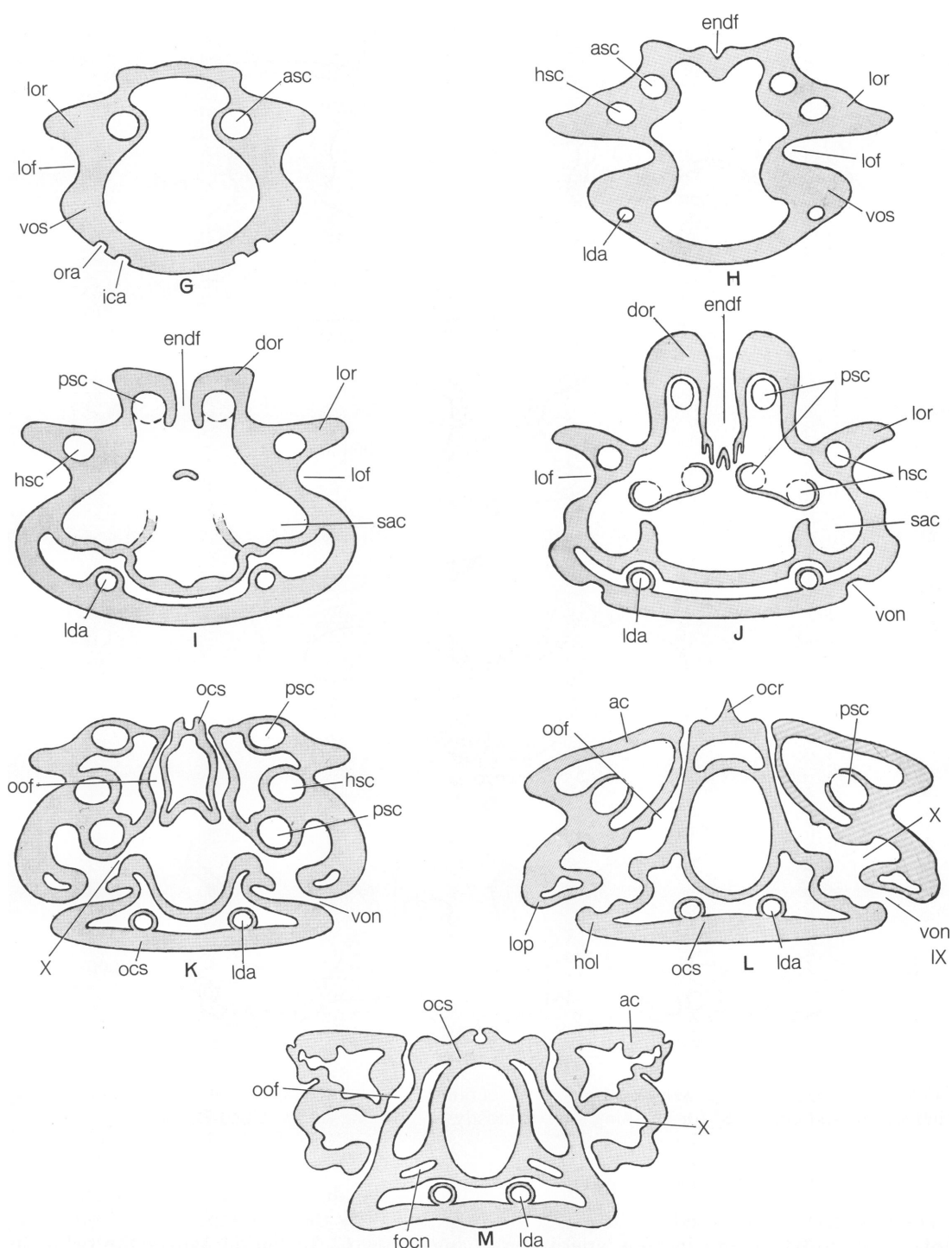


FIG. 9. *Xenacanthus* sp. Selected transverse sections through posterior part of neurocranium. Partly schematized and corrected for crushing. Based mostly on grinding series A and B.

ly. The roof, posterior wall and suborbital shelf are well developed. The suborbital shelf is characteristically incised at the level of the foramen for the efferent pseudobranchial artery, which is situated immediately below the edge of the shelf.

The anterior border of the orbit is defined by the rising pillar of the antorbital process, which is expanding dorsolaterally in relation to the olfactory capsules. Treatment with dilute formic acid has revealed the presence of a foramen in both orbits in the anterodorsal corner just below the gutter for the superficial ophthalmic nerve. This is too high to be the opening for the orbitonasal canal, but it may be the foramen for the deep ophthalmic nerve. The major foramina for the superficial ophthalmic nerve are at the anterior and posterior ends of the groove at the junction of the roof and medial wall of the orbit. As expected, branches of this nerve passed through the orbital roof to supply the supraorbital sensory canal.

The opening for the optic nerve and the optic artery is in the usual neoselachian position: just above the middle of the ventral orbital margin. Between the exit for the optic nerve and that for the efferent pseudobranchial artery there is another foramen (fig. 6) that is also present in "*Cladodus*" *wildungensis* Jaekel (fig. 25). This has been identified by Gross (1937) and by Stensiö (1937) as the canal for the ophthalmic artery. Assuming this identification to be correct, it means that the efferent pseudobranchial and the ophthalmic arteries separated within the orbital wall in "*C.*" *wildungensis* and *Xenacanthus* rather than outside of it as in neoselachians.

Behind the optic foramen there is a fairly deep ovoid fossa (fig. 6)—in part the trigemino-pituitary fossa of Allis (1923). The optic pedicel was presumably attached to the anterior end of the fossa, as in *Chlamydoselachus* (Allis, 1923), with the foramen for the pituitary vein close behind it. Unlike *Chlamydoselachus*, the trigemino-pituitary fossa in *Xenacanthus* continues posteriorly as a distinct groove that turns dorsolaterally to become confluent with the floor of the jugular canal. The foramen for the infraorbital

branches of the trigeminal and facial nerves (maxillary V and buccal VII) is situated on the medial wall of the fossa. The border of this foramen is not distinct in PU 22391 B (which is the only specimen in which the fossa is fully exposed) but its position is confirmed in grinding series D, sections 28–30.

The size, depth, and orientation of the trigemino-facialis recess in *Xenacanthus* suggest that it may have also served as a posterior myodome for the external rectus muscle. It should be noted that the orbit is relatively smaller and the foramina more closely spaced than in "*Cladodus*" (fig. 25; Gross, 1937; Stensiö, 1937), which is the only other Paleozoic shark that has provided morphologic detail in and around the orbit. The "eye stalk area" in "*C.*" *wildungensis* is separated from the pituitary and infraorbital foramina by a slight ridge and is more centrally located on the medial wall of the orbit than in *Xenacanthus*.

Identification of the foramina for the trochlear (IV) and abducens (VI) nerves, and of the interorbital canal (for the pituitary vein) remains uncertain. The locations in figure 6 are based mostly on PU 22391 and the wax plate reconstruction from grinding series C. As presently interpreted, the distribution of all the foramina in and around the orbit agrees closely with that in neoselachians.

The postorbital process (figs. 1–8) is massive, and has an ovoid, somewhat depressed articular area on its posterolateral surface for the otic process of the palatoquadrate. In overall aspect, including its concave orbital surface, large jugular canal and ventral extension to the basicranium, it resembles, at least superficially, the postorbital process of some paleonisciforms (Nielsen, 1942).

Although it has been agreed that the large canal in the postorbital process of "*Cladodus*" *wildungensis*, "*C.*" *hassaicus* and *Tamiodontis vetustus* served for the passage of the head (jugular) vein from the orbit (Gross, 1937; Stensiö, 1937; Romer, 1964), this determination has been questioned by Holmgren (1941, p. 18). Holmgren believed that the canal in *Chlamydoselachus* for the otic ramus of VII "corresponds" to the jugular canal of "*C.*" *wildungensis*. Although Allis

(1923) does not mention the foramen for the otic branch of the facial nerve in *Chlamydoselachus*, the course of this nerve is described and figured by El-Toubi (1949, figs. 13A, 15) for *Squalus*. Confusion between the two canals seem unlikely. Allis (1923, p. 154) notes that the jugular vein is ventral to the reduced postorbital process in *Chlamydoselachus*, which places it at about the same level as the large canal in "*C.*" *wildungensis*, *Tamiobatis*, and *Xenacanthus*. There is, in fact, no other obvious course for the head vein except through the canal in the postorbital process.

The general resemblance of the xenacanth postorbital process to the primitive teleostome one requires discussion, albeit mostly at the scenario level. As few neoselachians have a cartilaginous bridge lateral to the head (jugular) vein, we can only provide some calculated speculation about how this may have formed. It will be recalled that in actinopterygians the head vein and the orbital artery are covered laterally by the lateral commissure. This secondary structure, which also forms the side wall of the trigemino-facialis chamber, results from the junction of the prootic process of the auditory capsule and the postpalatine process of the basal plate (de Beer, 1937, p. 391). Beginning with Allis (1914) a number of embryologists and anatomists have attempted to provide a visceral arch origin for the actinopterygian lateral commissure. Most of this evidence has been reviewed by Bertmar (1959, 1963), who finally concludes that this structure in actinopterygians is entirely neurocranial. Bertmar insists, however, that in *Neoceratodus* the "lateral commissure" becomes detached from the top of the hyoid arch, and fused to the ventral side of the auditory cartilage (laterally) and the lateral margin of the basiotic lamina (medially). He further believes that this commissure in *Neoceratodus* represents the "infrasuprapharyngohyal." Jarvik (1954) favors a similar interpretation for the lateral commissure of *Eusthenopteron*, and this opinion is also supported by Bertmar (1959, 1963).

In regard to the neoselachians, Bertmar (1959, pp. 335–337) has found no evidence of

the suprapharyngomandibular in the side wall of the braincase but he believes that the infrapharyngomandibular is represented entirely or in part by the trabecula in all fishes, including the sharks. However, Jollie (1971) has discovered in a 35–37 mm. *Squalus* a tripartite blastemic connection between the dorsal extraotic cartilage (of El-Toubi, 1949) and, ventrally, the otic shelf. This blastemic tissue is lateral to the head vein and according to Jollie (1971, pp. 26, 37) has a connection with the palatoquadrate. He homologizes it with the selachian "lateral commissure" of Holmgren (1940, pp. 111–112; 1943, p. 63) and also agrees that it has a mandibular arch origin. But Jollie has also found evidence suggesting the incorporation of pharyngohyal tissue into the otic capsule around the articular area for the hyomandibula and the hypotic lamina. This tissue, in Jollie's opinion, is equivalent to the *Neoceratodus* lateral commissure.

As noted by Bertmar (1959), the presence of blastemic tissue between the palatoquadrate and/or the hyomandibula and adjacent parts of the chondrocranium has been reported numerous times and there is no reason to doubt its existence. The question is, of course, what does this "connection" mean both ontogenetically and phylogenetically. Although sometimes interpreted as demonstrating the inclusion of visceral arch tissue into the braincase, there is frequently enough reservation on the part of the investigator to make this entire matter equivocal. The consistent absence of a firm demonstration that a particular blastema is, in fact, the relic of a pharyngomandibula or a pharyngohyal speaks against this hypothesis. There is also no evidence from studies of neural crest cell migration that elements of the visceral skeleton were literally incorporated into the chondrocranium (e.g., Chibon, 1974; Schaeffer, 1975). Incidentally, Bertmar (1959, pp. 328, 338) attributes the apparent absence of visceral arch tissue in the side walls of the actinopterygian and neoselachian braincases to modifications in early phylogeny, which is perhaps another way of saying that ectomesenchyme and mesomesenchyme, under certain conditions, are equally competent to

form chondrocranial structures (see Le Lièvre, 1978, p. 31).

Returning to *Xenacanthus*, it seems most economical to assume that the complete postorbital process with a canal for the head vein was formed from neurocranial tissue only. The anlagen for the outer wall of the canal may be represented in the neoselachians by the connective tissue lamella that forms between postorbital process and the subocular shelf, as described by de Beer (1937), Holmgren (1940), and Jollie (1971). As the xenacanth postorbital process joins the braincase between the foramina for the trigeminal and hyomandibular VII, the primary cranial wall medial to the process was presumably formed by the prefacial commissure as in neoselachians and actinopterygians. De Beer (1937, p. 56) has noted that the head vein in adult *Squalus* may pass through a short canal, the medial wall of which is derived from the prefacial commissure and the lateral wall from a chondrified membrane that develops between the lateral surface of the auditory capsule and the edge of the subocular shelf. De Beer likens the lateral wall to the lateral commissure in actinopterygians. A "complete" postorbital process with a jugular canal has also been found in the squaloid *Scymnodon squamulosus* (Holmgren, 1941, pp. 30–31), and in *Squatina* (Compagno, 1973, p. 45).

On the ventral surface of the orbitotemporal region in *Xenacanthus* the hypophyseal fenestra (figs. 4–6, 8) is situated either in front of or just behind an imaginary line between the foramina for the efferent pseudobranchial arteries. The single median foramen (paired in one specimen, AMNH 7246) for the converging internal carotid arteries (figs. 4–6) is situated a short distance behind the hypophyseal fenestra. The course of the internal carotid arteries, between the anterior openings for the lateral aortae and the internal carotid foramen, is usually indicated by converging shallow grooves (fig. 4). The exposed course of the orbital artery is also marked by a shallow groove that branches off from the internal carotid groove (figs. 4, 6, 12A) and extends anteriorly to a short canal through which this artery

reached the rim of the subocular shelf. The anterior opening of this canal is a short distance behind the foramen for the efferent pseudobranchial artery, which is also on the edge of the subocular shelf.

Two additional foramina, one between the anterior and posterior openings of the orbital artery canal, and the other on the anteroventral border of the postorbital process, are identified with reservation as exits for branches of the palatine (VII) nerve. Both are labeled "fpal" in figures 4 and 6, and both occur in *Tamiobatis* (figs. 19, 21) and in "*Cladodus*" *wildungensis* (fig. 25). The foramen perforating the ventral wall of the orbital artery canal may have transmitted the mandibular branch of the orbital artery (Allis, 1923, pl. 19) along with (or instead of) a ramus of the palatine nerve. However, it has about the same position as the foramen for the palatine branch of the facial nerve in *Squalus*. Romer (1964) suggested that, in *Tamiobatis*, it may have been the opening for the efferent hyoidean artery, but it seems too far forward (fig. 12B). This matter is further considered in the section on the "*Cladodus*" neurocranium (p. 43). The foramen on the postorbital process of *Tamiobatis*, according to Romer (1964), may have been the exit for the pretrematic ramus of the same nerve. Presumably the same foramen is present, but not identified, in "*Cladodus*" *wildungensis* (Gross, 1937, fig. 2, ö). As shown by the *Xenacanthus* grinding series, the canal leading to this foramen begins in the jugular canal.

In addition to housing the foramen for a possible branch of palatine VII, the flared posterior portion of the jugular canal in *Xenacanthus* has a shallow but distinct pocket on its dorsal wall that opens widely into the back part of the canal. A similar pocket is present in "*C.*" *wildungensis* (Gross, 1937, fig. 3B, C), which Gross (1937, p. 93) believed, contained the ganglia of the trigeminal and facial nerves. However, if the position of the prefacial commissure has been correctly interpreted for *Xenacanthus* and for "*C.*" *wildungensis*, the trigeminal (and buccal VII) foramen should be close to the foramen for the pituitary vein, and in the tri-

gemino-facialis recess (see also de Beer, 1937, p. 56). It is probable that the foramen labeled "R VIII" in Gross, 1937, figure 3B, is the exit for the trigeminal; the one labeled "V + XII" could have served for the otic branch of VII. The latter foramen is apparently not present in *Xenacanthus*.

OTICO-OCCIPITAL REGION

This section, like the preceding ones, is devoted to aspects of the neurocranium that are not particularly reflected in, or demonstrated by, the contours of the endocast. As noted above, the otico-occipital region is noteworthy for its relative length, complicated topography, slotlike endolymphatic fossa bordered by prominent dorsal otic ridges, well-developed lateral otic processes and persistent otico-occipital fissure. In these respects *Xenacanthus* closely resembles *Tamiodontis* and to some extent "*Cladodus*" *wildungensis*, hence the description of these features in *Xenacanthus* will form a base for subsequent comparative discussion.

The dorsal otic ridges (figs. 5, 6, 9) are continuations of paired crests that rise behind the postorbital processes and above the posterior border of the jugular canals. These ridges become more accentuated and elevated as they extend posteriorly. In the region of the endolymphatic fossa, they are recurved laterally to form the dorsolateral otic fossae, which are delimited ventrally by the flangelike lateral otic ridges. Posteriorly the dorsal otic ridges overhang elevations formed by the posterior semicircular canals. The endolymphatic fossa is a narrow, elongated, relatively deep, V-shaped trench that extends posteriorly to the grooved anterior end of the median occipital crest on the occipital moiety. The anterior end of this crest, which may be nearly as high as the posterior ends of the dorsal otic ridges, is thickened and rounded to provide (presumably) an articular surface for the cephalic spine. The posterior elevations of the dorsal otic ridges may have served as muscle attachments for the cephalic spines. The lateral otic fossa, situated below the lateral otic ridge, housed the head

vein following its emergence from the jugular canal.

The foramen magnum is situated immediately posterior to the presumed cephalic spine articulation, and its ventral rim is some distance anterior to the posterior face of the occipital condyle. Although *Xenacanthus* neurocrania are usually crushed in this area, it is probable that the plane of the foramen magnum was no more than 60 degrees relative to the plane of the posterior basicranium. This angle was certainly no greater and it may have been smaller than in *Tamiodontis* (figs. 19, 21).

The endolymphatic (parietal) fossa is bordered laterally, as noted above, by the prominent dorsal otic ridges. The fossa narrows ventrally, where it joins the endocranial cavity through a slotlike opening which, in turn, is confluent posteriorly with the otico-occipital fissures (figs. 9, 14). There is no indication of endolymphatic or perilymphatic apertures in the walls of the fossa. However, the sections of grinding series B through the fossa and the saccular area (fig. 9) indicate what appears to be a significant resemblance to the neoselachian condition (figs. 10A, B, 11). In Recent sharks the endolymphatic fossa is filled with "fibrogelatinous" connective tissue (Norris, 1929). The shallow, usually ovoid fossa is floored, except where the endolymphatic ducts enter it and where the more posterior perilymphatic fenestrae are situated. The ventral or inner parts of the endolymphatic ducts extend to the upper part of the fossa where they become enlarged and turn horizontally to form the endolymphatic pouches. The ducts (or pouches) again decrease in diameter before reaching the surface of the head. As illustrated in figures 10 and 11, and as discussed on page 52, the perilymphatic fenestrae in the neoselachians have a unique developmental relationship with the posterior vertical and semicircular canals.

If we compare the transverse sections in figure 9I and J with those in figure 10A and B, it becomes apparent that the perilymphatic fenestrae in *Xenacanthus* must have opened into the bottom of the endolymphatic fossa in close proximity to the poste-

rior semicircular canal. Because of incomplete calcification, the exact relationships cannot be established, or is it possible to decide whether the endolymphatic and perilymphatic openings into the fossa were separate, or as in some neoselachians, confluent (Norris, 1929). In any case, I would expect the perilymphatic fenestrae to be close to the anterior border of the occipital segment, as in *Scyliorhinus* (fig. 11A-F).

Slips of epaxial musculature in living sharks extend forward on either side of the endolymphatic fossa (Marinelli and Strenger, 1959, fig. 141). According to Norris, extensions of this musculature also enter the fossa and attach to the endolymphatic pouches where they loop posteriorly toward their external openings. The dorsal otic ridges and the dorsolateral otic fossae on either side of the endolymphatic fossa in *Xenacanthus*, *Tamiobatis*, and "*Cladodus*" probably served for the attachment of cranial slips of the epaxial musculature. The epaxial muscles were presumably also attached to the lateral otic processes as well as to the dorsal surface of the otic segment.

In *Xenacanthus* and *Tamiobatis* the otic region is extended posteriorly and laterally to form the lateral otic processes (not to be confused with the otic processes of the palatoquadrate). The articulation for the hyomandibula, as demonstrated by the articulated specimen of *Xenacanthus* (fig. 1), is situated partly on the lateral otic process and partly on the lateral otic ridge. It is thus mostly lateral to the ventral otic notch, which possibly contained the exit for the glossopharyngeal nerve. In neoselachians, and apparently in *Cladoselache*, *Danaea* (Williams, MS) and *Cobelodus* (Zangerl and Case, 1976), the lateral otic process is much reduced, and the hyomandibula articulates with the auditory capsule immediately in front of the glossopharyngeal foramen. The lateral otic process in *Xenacanthus* and *Tamiobatis* apparently moved the hyomandibular articulation away from the foramen and more or less in line with the articulation between the otic process of the palatoquadrate and the postorbital process. In adult neoselachians, the posterior vertical semicir-

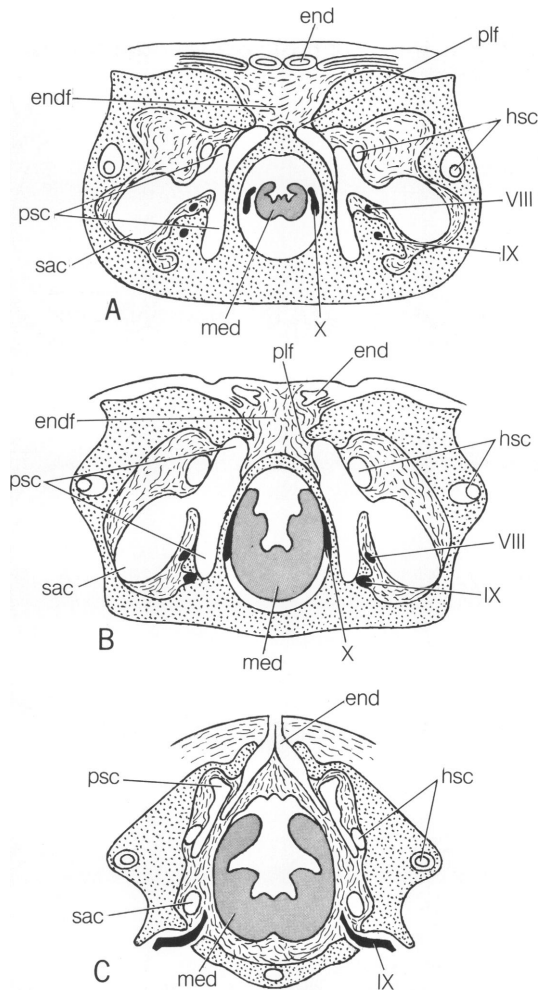


FIG. 10. Transverse sections through the endolymphatic pouches and labyrinth. A. *Notorynchus platycephalus*. B. *Squalus acanthias*. After Norris, 1929. C. *Callorhynchus* sp. After de Beer and Moy-Thomas, 1935. The endolymphatic pouches are parallel to the head surface in A and B.

cular canal frequently bulges into the posterior wall of the auditory capsule, which is not the case in *Xenacanthus* and *Tamiobatis* because of the large lateral otic process.

The occipital moiety is delimited dorsally and posteriorly by the otico-occipital fissure which extends from the endolymphatic fossa through the foramina for the vagus nerves

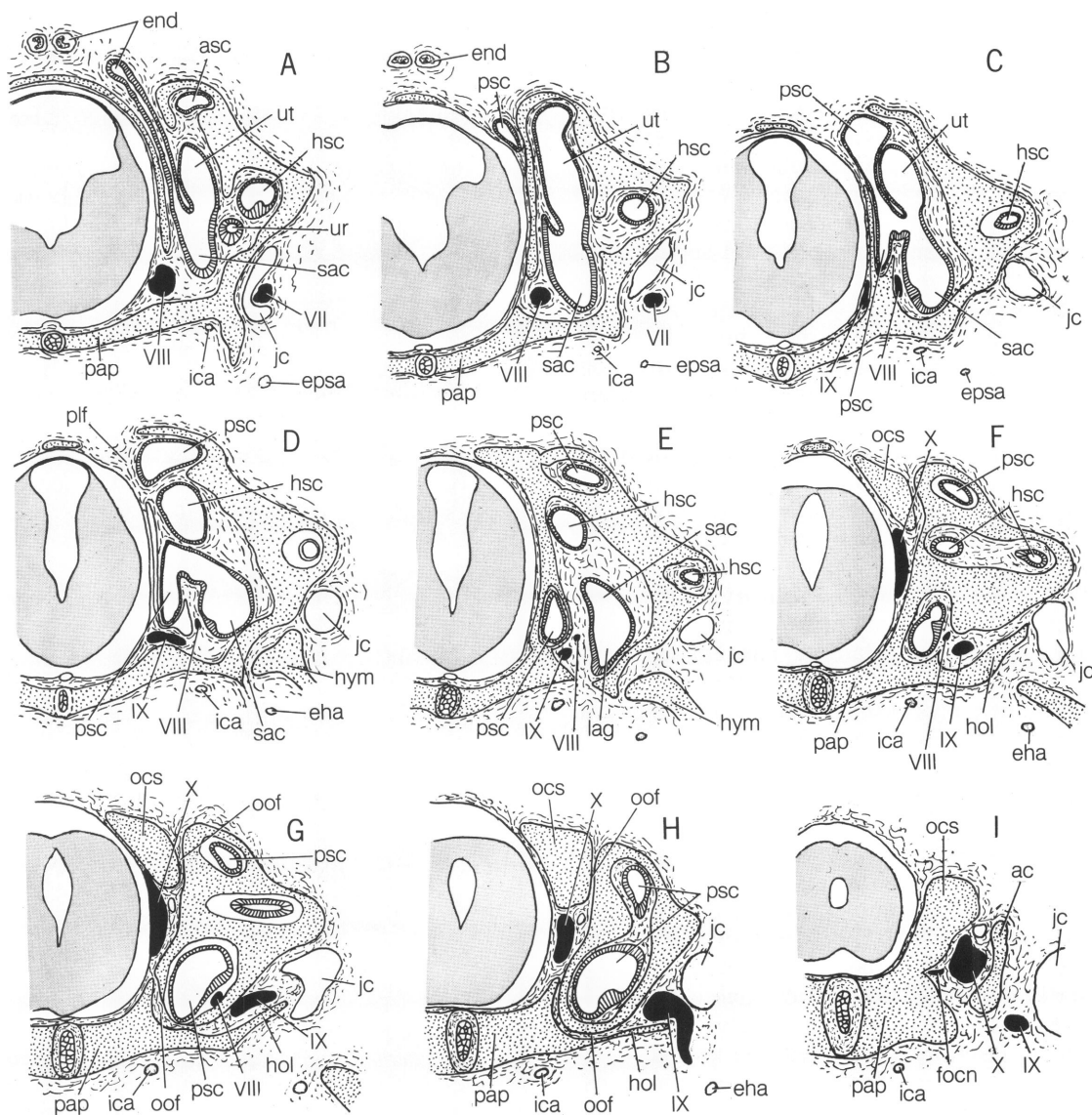


FIG. 11. *Scyliorhinus canicula*. Selected transverse sections through the endolymphatic fossa, labyrinth and hypotic lamina of embryonic neurocranium. After de Beer, 1931.

and terminates ventrally in the nearly horizontal, longitudinal slot here called the ventral otic notch (figs. 6, 9). It is evident from the orientation of the fissures that the auditory capsules overlap the occipital segment (fig. 9). This is also the situation in *Squalus* and *Scyliorhinus* (de Beer, 1937, p. 132 and

pls. 11, 13), in which the embryonic metotic fissure has a nearly anteroposterior orientation. A persistent metotic fissure in adult Recent sharks has not been reported (Compagno, personal commun.), but its position may be indicated by a slight ridge in the dried neurocranium. However, the cartilaginous

roof of the occipital segment in an 8 cm. braincase of *Scyliorhinus stellaris* in the departmental collection has remained uncalcified and is sharply distinguished from the calcified auditory capsule on either side.

Projection of the occipital segment well beyond the posterior borders of the auditory capsules is characteristic of both *Xenacanthus* and *Tamiodontis*. Both appear to have three pairs of occipito-spinal nerve canals (figs. 14, 24). The canal for the most anterior one may have joined the vagal canal but it seems more probable that all three canals had separate foramina behind the ventral otic notches. Following de Beer's (1937, pp. 15–20; 26–28) interpretation of head segmentation in neoselachians, *Xenacanthus* had at least three segments added behind the parachordals, and part of another to form the occipital condyle. However, as the occipital block extends behind the last occipito-spinal nerve canals evident in the serial sections, it is possible that additional segments were incorporated.

Although the otico-occipital fissures completely separate the auditory capsules from the occipital segment dorsally and laterally, there is no evidence of a fissure on the ventral surface (figs. 5, 6). There is a possibility that the dorsal and lateral portions of the fissures were partly filled with uncalcified cartilage in life, but their edges on the dorsal surface are slightly raised in a manner that suggests the borders of a cleft rather than simply the borders of an uncalcified zone.

The courses of the glossopharyngeal and vagus nerves in *Xenacanthus* cannot be surely determined from the serial sections, but the possibilities are clearly limited by the relationships of the otico-occipital fissure to the auditory capsule and the occipital segment. In neoselachians, the glossopharyngeal and vagus nerves are separated by the posterior semicircular canal (fig. 15). The metotic fissure in a 45 mm. *Scyliorhinus* embryo (de Beer, 1931, and fig. 11) passes ventrally between the auditory capsule and the occipital arch and then swings laterally under the ventral loop of the posterior semicircular canal where it opens below the capsule and just behind the hyomandibular articulation

(fig. 11, G–I). The vagus nerve enters the vertical part of the fissure from the cranial cavity about opposite the horizontal semicircular canal. The glossopharyngeal enters the fissure below the ventral loop of the posterior semicircular canal and immediately passes lateral to this canal until leaving the posterolateral corner of the neurocranium somewhat below the level of the vagal foramen.

Comparison of de Beer's (1931) sections through the otico-occipital region of a 36–45 mm. *Scyliorhinus* (fig. 11) with series B of *Xenacanthus* (fig. 9) shows the same topographic relationships between the otico-occipital fissure and the course of the vagus nerve. In *Xenacanthus*, as in the *Scyliorhinus* embryo, the vagus must have reached its foramen by way of the fissure, which is also posteromedial to the posterior semicircular canal (fig. 9 K–M). A clue regarding the course of the glossopharyngeal in *Xenacanthus* is provided by a shelf of calcified cartilage that extends laterally from the base of the occipital segment to form part of the slot-like ventral termination of the otico-occipital fissure (fig. 9L). This shelf is apparently the same as the lamina hypotica in the embryonic *Scyliorhinus* (de Beer, 1931 and fig. 11F–H), which extends laterally from the parachordal plate below the posterior part of the auditory capsule. In some neoselachians, such as *Scyliorhinus*, the posterior floor of the auditory capsule remains membranous and the glossopharyngeal nerve runs between the membrane and the lamina hypotica. In *Squalus*, the capsule floor is complete and fuses with the lamina to provide a canal for the glossopharyngeal (El-Toubi, 1949).

In *Xenacanthus* the floor of the auditory capsule is chondrified and calcified. The glossopharyngeal nerve was presumably situated between it and the hypotic lamina, and must have reached the surface of the neurocranium either through an opening in the ventral otic notch or, less probably, by curving around the posterior end of the capsule and sharing the same exit with the vagus nerve (fig. 9L, M).

BASICRANIAL CIRCULATION

The internal basicranial circulation, including that related to the hypophyseal area, has been reconstructed from grinding series A and D (fig. 12A). Although various details, such as the ramifications of the cerebral artery, have left no record, there is enough evidence to indicate a basic resemblance to the typical neoselachian basicranial pattern (Allis, 1923; Corrington, 1930; Meurling, 1967).

In living chondrichthyans, including the holocephalans, the dorsal aorta divides into paired lateral (radix) aortae at or behind the posterior limit of the neurocranium. The lateral aortae remain separated until just behind the hypophysis where they enter the basicranium to form the median cephalic sinus. In selachian embryos this sinus is ventral to the anterior tip of the notochord, which terminates just behind the hypophysis.

The lateral aortae together form the so-called aortic cephalic circle (Goodrich, 1930, p. 517). The elongated spindlelike configuration of this arterial loop in *Xenacanthus*, *Tamiobatis*, "*Cladodus*," *Cladoselache*, *Tristychius* (Dick, 1978), *Cobelodus* (figs. 12 and 13) and *Hybodus* (Maisey, personal commun.) as deduced from foramina, canals and grooves, contrasts with the bell- or mushroom-shaped pattern in neoselachians (fig. 13C). The neoselachian lateral aortae turn abruptly outward to form a sharply angled bifurcation with the internal carotid (as the anterior branch) and the efferent hyoidean artery (as the posterior one). There is no evidence of this bifurcation pattern in the fossil taxa, and it is probable that the efferent hyoidean artery separated from the lateral aorta anterior to the lateral aortic canal. *Tristychius* (Dick, 1978) and *Cobelodus* (Zangerl and Case, 1976) are of interest in this regard in that they lack lateral aortic canals (fig. 13B) in the basicranium. In consequence, the efferent hyoidean arteries may have branched off from the exposed lateral aortae closer to the hyoid arches, as in the neoselachians.

The internal carotid foramen in *Xenacan-*

thus opens into a triangular space below and somewhat behind the hypophyseal area. This space, which housed the median cephalic sinus plus the anterior continuations of the internal carotids and some veins, extends forward under the infundibulum as a pair of poorly defined canals, one on either side of the hypophyseal duct. The canals, which contained the internal carotids, can be followed in grinding series A as far forward as the level of the optic chiasma where each branches into three canals—for the optic plus cerebral, the ophthalmic, and efferent pseudobranchial arteries. The relationships of these arteries are shown in figure 12A. As noted earlier, the ophthalmic and efferent pseudobranchial arteries apparently have separate foramina in *Xenacanthus* and "*Cladodus*," but a single foramen in *Tamiobatis* (figs. 12B, C, 19, 21, 25). Stensiö (1937) also observed a single foramen on one side in "*C.*" *hassiacus*.

Although the foramen for the pituitary vein in "*C.*" *hassiacus* has also been identified in the orbital wall of *Xenacanthus* and "*Cladodus*" on the basis of foramen topography, there is no recognizable evidence of the interorbital canal in any of the *Xenacanthus* grinding series. There is little direct evidence of the cranial venous system in any fossil chondrichthyans except for the jugular canal and/or groove, and the pituitary foramen.

Except for a more anterior position for the efferent pseudobranchial artery foramen, the arrangement of the basicranial foramina is also similar in "*Cladodus*" *wildungensis* (fig. 25) and *Xenacanthus*. However, Gross (1937) identified the posterior opening of the orbital artery canal as the exit for the posterior ramus of the palatine nerve, and the anterior opening of that canal as the foramen for both the orbital artery (his external carotid) and the anterior ramus of the palatine. In "*C.*" *hassiacus* Stensiö (1937) the palatine foramen is somewhat dorsolateral to the orbital artery, as in *Heterodontus* Goodrich (1930, fig. 284).

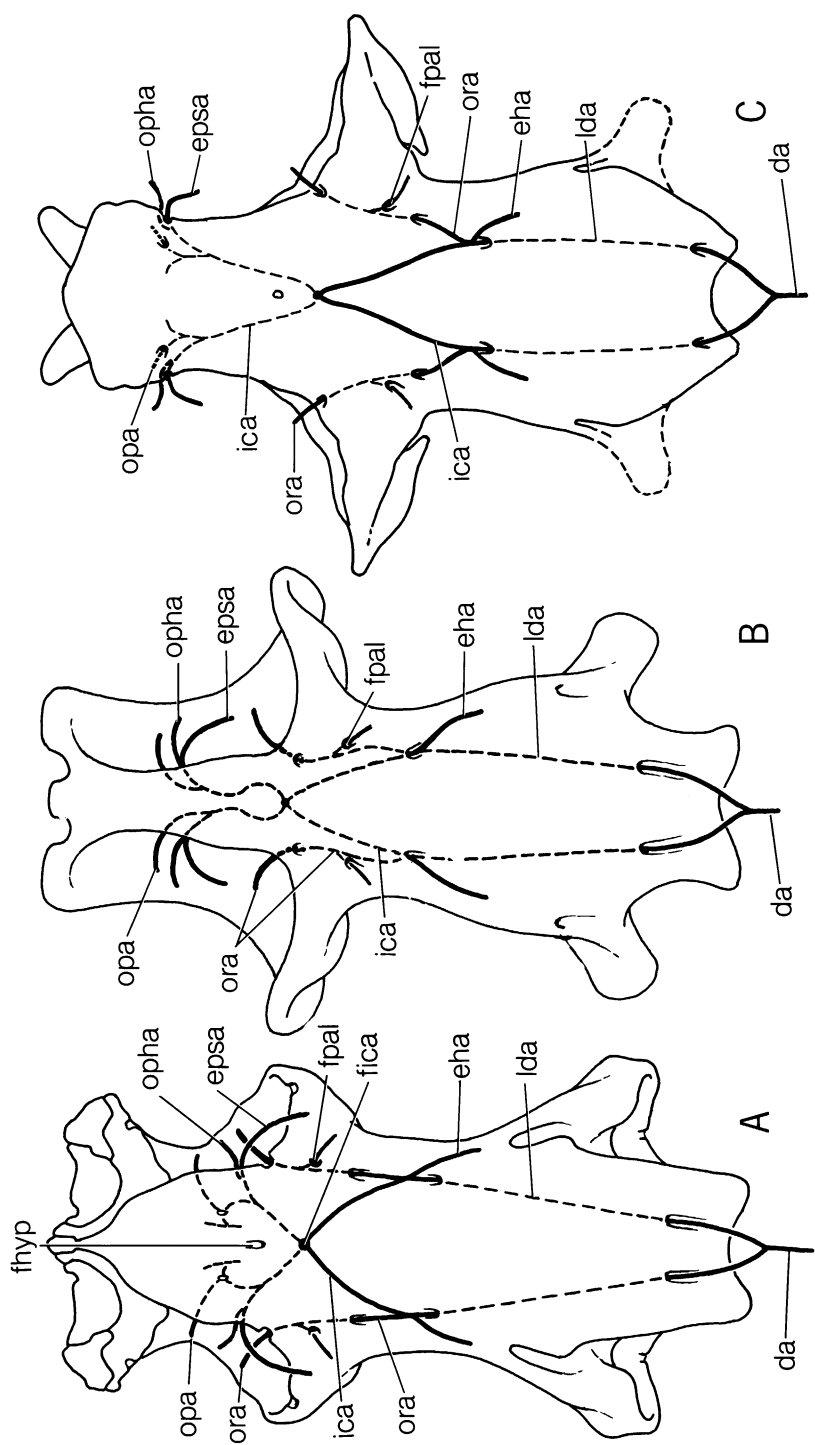


FIG. 12. Diagrams of basicranial circulation: A. *Xenacanthus* sp. B. *Tamiobatis vetustus*. Based on NMNH 1717. C. “*Cladodus*” *wildungensis*.

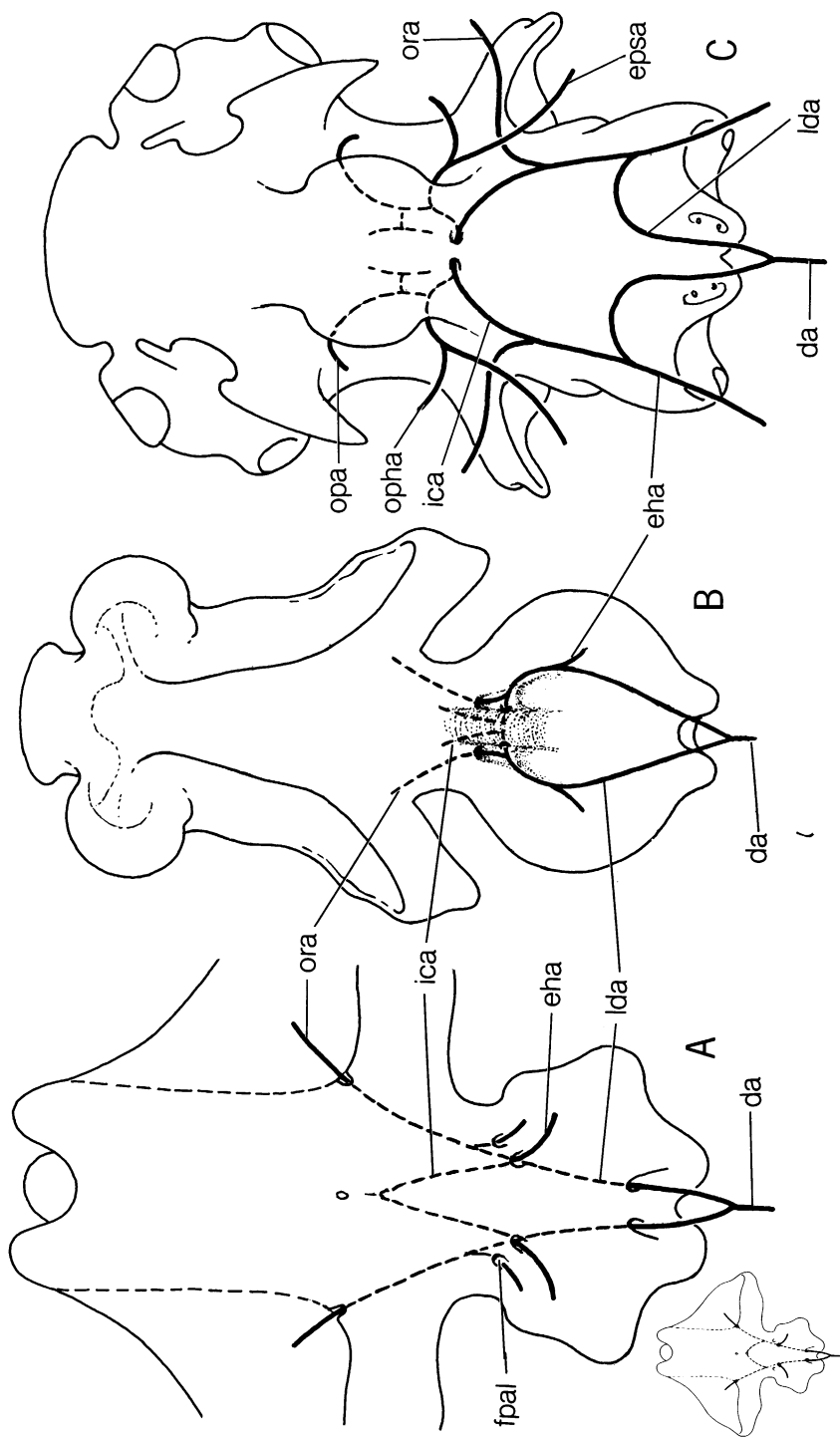


FIG. 13. Diagrams of basicranial circulation: A. *Cladoselache* sp. Based on CMNH 5769 and 6233. B. *Cobolodus aculeatus*. Based on FMNH 7472, 7475, 7832. C. *Chlamydoselachus anguineus*. After Allis, 1923.

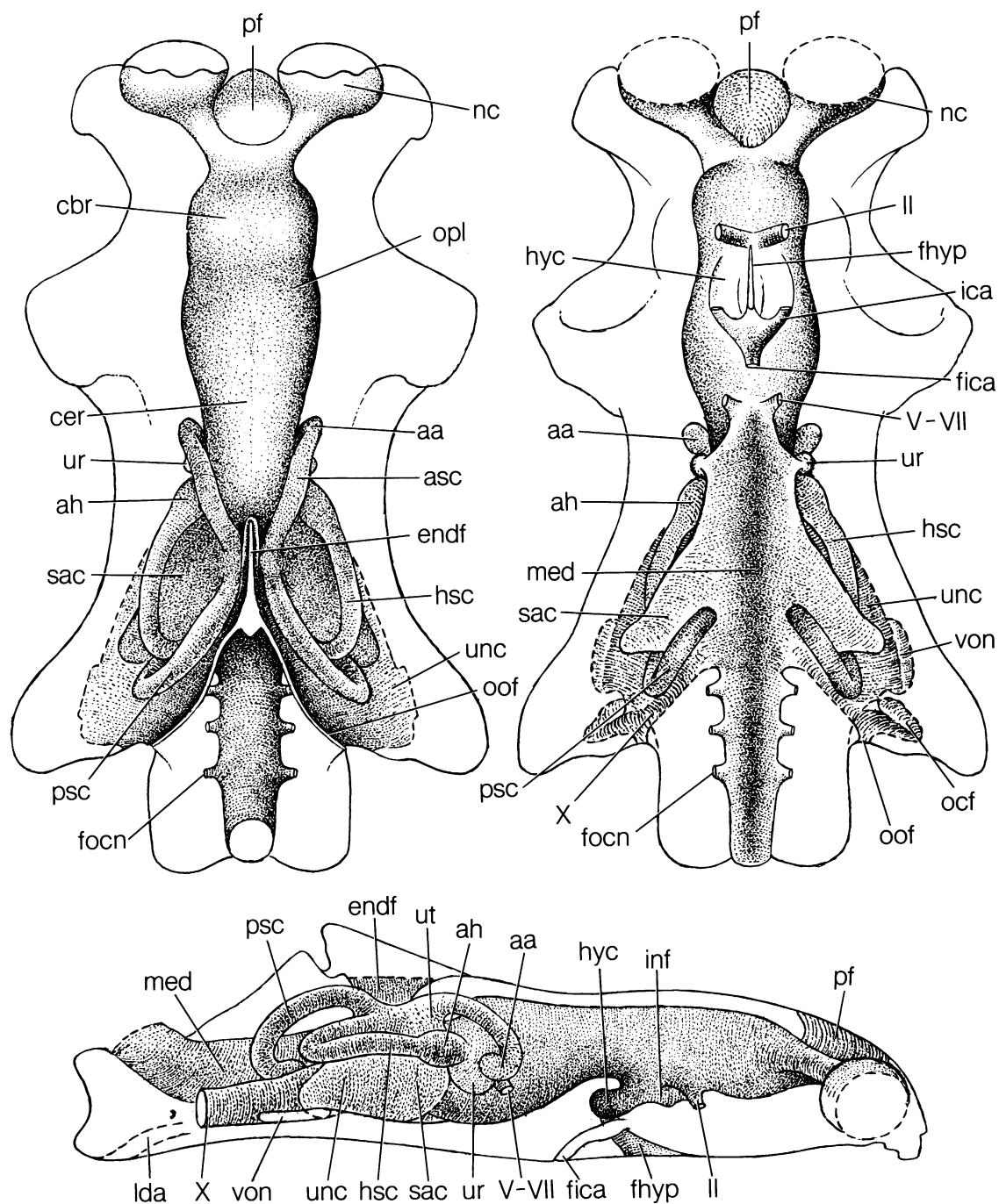


FIG. 14. *Xenacanthus* sp. Endocast reconstruction based mostly on grinding series D in dorsal, ventral and lateral aspects.

ENDOCAST

The restoration of the *Xenacanthus* endocast (fig. 14) is based mostly on grinding series D with some additions from A and B. For reasons of identification and comparison, an endocast of *Squalus* (fig. 25) was prepared by vacuum filling and embedding a well-cleaned neurocranium in a block of "Silastic" (Dow-Corning). After setting, the silicone rubber was pared away to the surface of the neurocranium and the cartilage dissolved with "Clorox" (a chlorine bleach), leaving behind the complete endocast.

Comparison of the brain stem in various neoselachians (Garman, 1913; Northcutt, 1978) indicates that the major subdivisions have similar relative proportions, although in some the cerebral hemispheres are enlarged, and the cerebellum may be elaborated and convoluted. The braincase of most Paleozoic selachians, e.g., *Cladoseleche* (fig. 13A), *Danaea*, *Symmorium*, and *Cobelodus* (fig. 13B), as well as that of *Hybodus* has short, compact otic and occipital regions, suggesting brain stem proportions similar to those of neoselachians. By contrast, the braincases of *Xenacanthus*, *Tamiodontis*, and "*Cladodus*" obviously have different relative dimensions (see figs. 12 and 13).

In order to analyze the proportional differences between the braincase and brain stem of *Xenacanthus* and *Squalus*, outlines of these structures have been superimposed with the distance between the internal carotid foramen and the optic chiasma approximately equalized, as illustrated in figure 16. From this diagram, it is evident that the proportions of the braincase and endocast between the nasal capsules and the postorbital processes are nearly the same in both taxa. Although the brain probably did not fill the endocranial cavity (which is the case in neoselachians generally), it is also evident from the low relief of the *Xenacanthus* endocast that the cerebral hemispheres, the optic lobes and the cerebellum were developed about as in *Squalus*.

If we define the medulla oblongata and that part of the brain stem with central connections for the fifth through the tenth cranial

nerves (labeled in figs. 14 and 15), the superposition diagram further shows that the *Xenacanthus* medulla was relatively longer than that of *Squalus*. Also the *Xenacanthus* occipital segment with its included portion of the spinal cord extends farther beyond the vagal foramen, as in *Tamiodontis*, and probably in "*Cladodus*."

Although the superposition diagram indicates that the semicircular canals of *Xenacanthus* are relatively larger than those of *Squalus*, the anteroposterior distance spanned by the two vertical semicircular canals in each taxon is about one-third of the total neurocranial length (anterior border of olfactory capsule to occipital condyle). In other words, the proportion of canal size to braincase size is about the same in both taxa. In *Squalus* and presumably other neoselachians the anterior and posterior semicircular canals, in dorsal aspect, are oriented at about 100 degrees to each other (fig. 15). In *Xenacanthus* this angle is close to 130 degrees—as reflected in the narrowness of the otic region above the level of the sacculus (fig. 5). The same wide angle is evident in *Tamiodontis* (figs. 18–21 and 24A) and in "*Cladodus*" (fig. 25).

The endocast of the *Xenacanthus* labyrinth unfortunately does not clarify some interesting and significant details. De Beer (1931, 1937) has noted that the posterior semicircular canal in neoselachians forms a nearly complete ring, except where it joins the posteromedial part of the sacculus. Also, the neoselachian anterior vertical and horizontal semicircular canals join each other to form a crus (Retzius, 1881; Jollie, 1962), whereas in chimaeroids and other gnathostomes the crus is formed by the anterior and posterior canals. This difference is not mentioned by de Beer (1937, p. 456), who states that the semicircular canals have a similar arrangement. The *Squalus* endocast (fig. 15) shows the ring-shaped posterior canal but not a convincing indication of the crus between the anterior and horizontal canals. The *Xenacanthus* endocast (fig. 14) indicates that the posterior canal was circular, but also does not demonstrate the presence of a crus. Nevertheless, as these

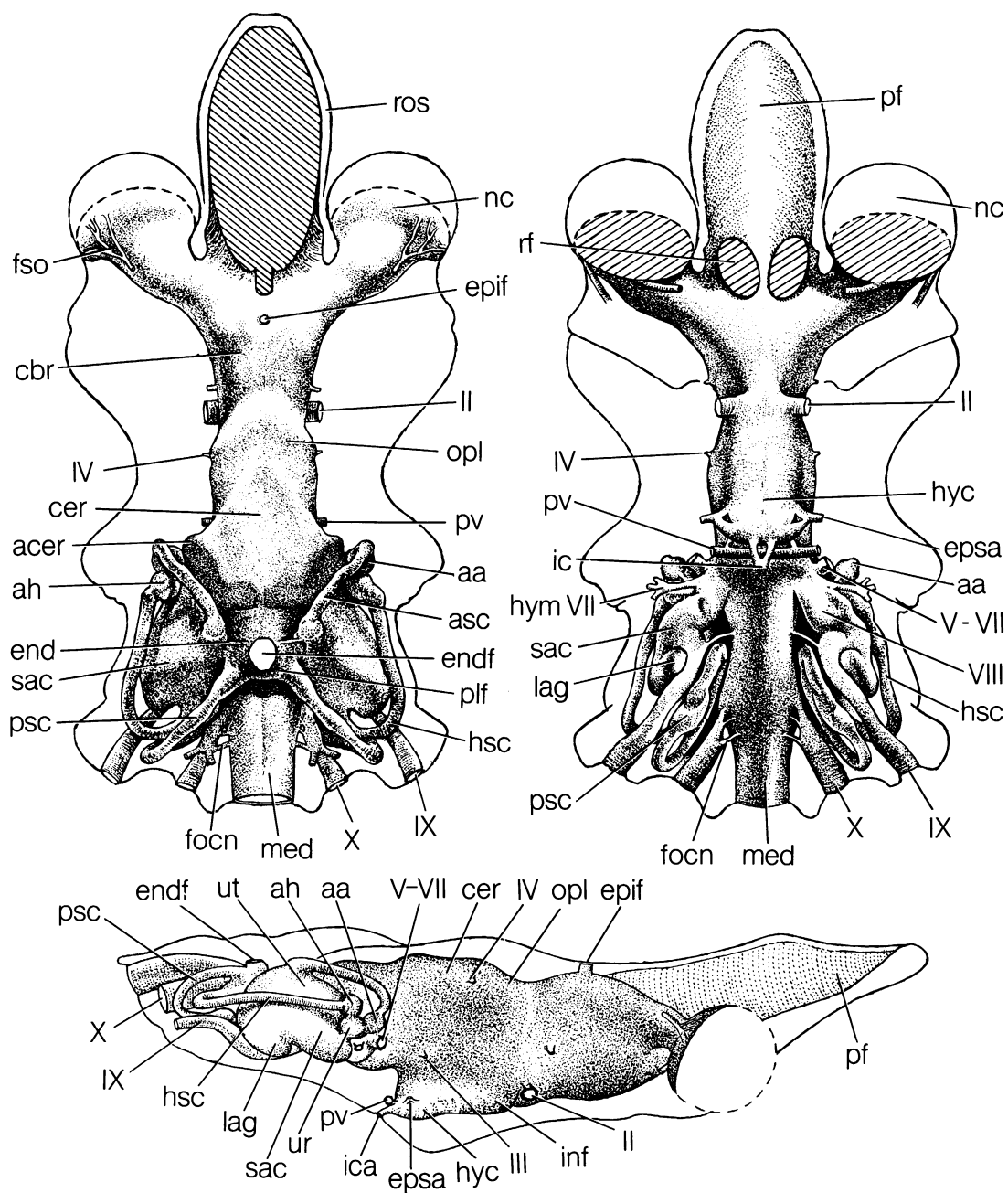


FIG. 15. *Squalus acanthias*. Endocast drawn from Silastic original in dorsal, ventral and lateral aspects.

two conditions in neoselachians are related, it is reasonable to assume that *Xenacanthus*

also had a crus between the anterior and horizontal semicircular canals.

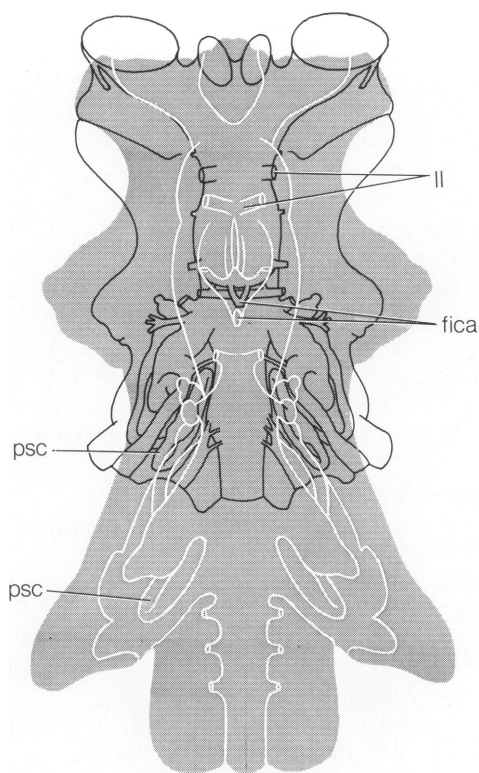


FIG. 16. Comparison of neurocranial and endocast proportions in *Xenacanthus* sp. and *Squalus acanthias*. Distance between optic chiasma and carotid foramen approximately equal.

The neoselachians and chimaeroids have a prominent utricular recess (Retzius, 1881), which is an evagination of the utriculus situated below the ampullae for the horizontal and anterior vertical semicircular canals (fig. 15, ur). This recess can also be identified in the *Xenacanthus* endocast (fig. 14), where it is about the same size as the ampullae.

Extending posteriorly from the area of the poorly defined *Xenacanthus* lagena, there is a more or less tubular, uncalcified space through which the vagus nerve passed to the outside of the braincase. As noted above, it is probable that the exit for the glossopharyngeal was through the notch above the hypotic lamina (fig. 9L)—in which case it must have been separated from the vagal foramen. In grinding series D there is an opening in

the partition between the vestibular and cranial cavities (at least in terms of a calcified wall) that extends from behind the trigemino-facialis canal to the vagal canal (fig. 9I, J, K). A small isolated bit of calcified cartilage below the endolymphatic fossa (fig. 9I, J) may represent the top of the otherwise uncalcified wall around the medulla, as in figure 10A, B.

The endocast of the hypophyseal region indicates that the inferior lobes of the infundibulum and the hypophysis had about the same form and relative proportions as in *Squalus* (Meurling, 1967). Unlike any living neoselachian, however, *Xenacanthus* has a well-developed hypophyseal duct (also present in *Cladoselache*, *Tamiobatis* and “*Cladodus*”) that arose from the median lobe of the hypophysis. The duct is narrowed laterally and opens on the ventral surface of the basicranium in a slotlike depression a short distance in front of the carotid foramen.

GROWTH AND HISTOLOGY

Growth of the chondrichthyan chondrocranium prior to and after fusion of the embryonic components is interstitial, involving cell multiplication and/or accretion through the modulation of perichondral cells into chondrocytes. The outer walls and the partitions of the braincase maintain about the same relative thickness during this increase in size, which is a further indication that growth is mostly interstitial.

According to Benzer (1944), the earliest centers of calcification in the *Squalus* chondrocranium develop in the basicranium anterior to the foramen magnum and extend forward to the level of the internal carotid foramen. Three pairs of centers then form on the ventral surface of the interorbital region and a medial, crescent-shaped center between the basal angles. Other paired centers appear on the ventral surface of the preorbital process, on the ventral border of the orbits and on the ventral surface of the postorbital process. Multiple centers develop on the auditory capsule and three centers form on the roof in a triangular configuration. All of these primary centers appear before the

dogfish is free-swimming (between 15 and 21 to 23 cm.). Following loss of the yolk sack, at about 25 cm., fusion of the individual centers is initiated and is completed at about 30 cm. As an adult, *Squalus* may reach a total length of over 90 cm. It is evident therefore that the neurocranium continues to enlarge long after the calcification centers are united. In the largest specimen Benzer studied (90 cm.) only the rostrum and the lateral surfaces of the palatobasal articular processes remained uncalcified.

Benzer (1944, p. 223) further notes that the primary centers are constant in location, at least in his study sample, and the subsequent fusion of the centers occurs in a fairly constant sequence. This specificity in the calcification pattern is also indicated in a 9 cm. long neurocranium of *Scyliorhinus*, which is completely calcified except for the rostrum, most of the nasal capsules, the outer edge of the suborbital shelf and, most interestingly, the roof of the occipital arch. This last non-calcified area is separated from the adjacent edges of the calcified otic capsules and, posteriorly, from the calcified first intercalary (interdorsal) arch.

From Benzer's data it is evident that the *Squalus* neurocranium grows considerably (roughly 25% of the adult length) before coalescence of the primary calcification centers. Although the individual prisms are tied together in all directions by collagen bundles (Bargmann, 1939), it is also evident that they enlarge after the primary centers are united.

Except for the vertebrae, calcification of the neoselachian endoskeleton occurs beneath the perichondrium as a single layer of prisms between the perichondrium and the unaltered cartilage. Both the inner and outer surfaces of the neurocranium are usually calcified, and prisms may form a layer around the semicircular canals and the larger blood vessels, as also in *Xenacanthus* and *Tamiodontis* (fig. 17).

The body of an individual prism is composed of globular calcified cartilage with typical basophilic contour lines ("Liesegang waves"). This microstructure is quite evident in the prisms of *Xenacanthus* as well as in those of neoselachians. However, Kemp

and Westrin (1979) have discovered that the outer zone of an individual prism consists of a calcified tissue layer that may be produced directly by perichondral fibroblasts without the intervention of chondroblasts. They suggest that the fibroblasts (or scleroblasts) may be osteoblasts, and that the outer zone may be a thin layer of perichondral bone. This hypothesis has particularly interesting phylogenetic implications in regard to the origin of the chondrichthyan skeleton, but in a sense it complicates a problem that has not received much attention—namely, how the chondrichthyan skeleton grows following calcification and the union of the primary calcification centers.

A further complication is evident in *Xenacanthus* and *Tamiodontis*. Unlike the condition in the neoselachians and *Hybodus* (Maisey, personal commun.), these taxa have multiple layers of prisms in the outer walls of the neurocranium (fig. 17) (but not always in the internal partitions or walls of canals) and in various elements of the visceral skeleton. The number of layers cannot be explained by postmortem compression of single inner and outer layers, or by the infolding of such layers. Comparison of a partial neurocranium of *Xenacanthus* about 9 cm. long (fig. 17, upper) and one approximately 28 cm. long (fig. 17, lower) does not show a definite increase in the number of prism layers with increase in size. As noted by N. E. Kemp (personal commun.), this condition suggests successive waves of sub-perichondral calcification interrupted by intervals of primary cartilage deposition. The taxonomic distribution of this multilayered condition remains to be worked out; the elucidation of the mechanism involved will require its presence in a living chondrichthyan.

In regard to the growth mode, Kemp (personal commun.) has noted that the *Squalus* prisms do, in fact, enlarge. There is also some evidence of this in figure 17, if the size of the prisms in the horizontal braincase peel (upper photograph) is compared with that in the vertical section of the much larger specimen. Nevertheless, the size range of the prisms in each varies considerably; so simple increase in size even related to periodic

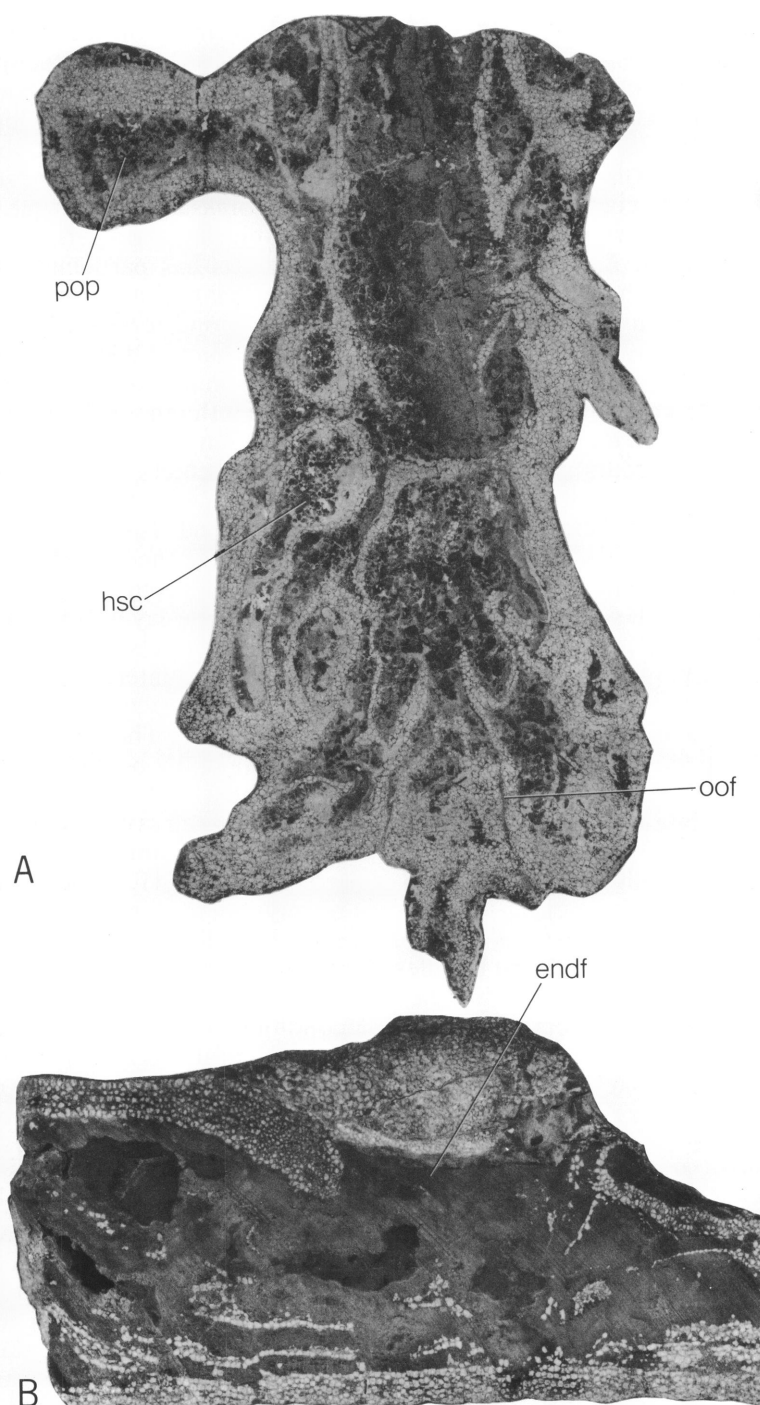


FIG. 17. *Xenacanthus* sp. Structure of neurocranial wall. A. Horizontal section from grinding series D at level of horizontal semi-circular canal. $\times 1.63$. B. AMNH 7254. Midsagittal section through the endolymphatic fossa. $\times .90$.

prism formation, cannot be the entire explanation. In a sectioned xenacanth branchial element, it is evident that the primary carti-

lage was almost entirely replaced by layers of prisms. The prismatic wall is also very thick in a sectioned mandible.

TAMIOBATIS NEUROCRANIUM

The original description of *Tamiobatis vetustus* Eastman 1897, was based on a somewhat compressed neurocranium (NMNH 1717) derived from Lower Mississippian limestones in eastern Powell County, Kentucky (Romer, 1964). This specimen (figs. 18, 19) was subsequently prepared and described by Romer (1964), who made some comparisons between it and the braincases of *Xenacanthus* and "*Cladodus*." A second, much larger, uncrushed neurocranium (AMNH 2140) here referred to as *Tamiobatis* sp., was collected about 1962 from the Salem Limestone, Lower Mississippian, Bedford, Indiana. This specimen was slabbed horizontally prior to its submission for identification thus revealing much of the internal morphology (figs. 22–24). In addition, the slabs have been reassembled (allowing for the width of the rock saw) to provide a reconstruction of the entire neurocranium (figs. 20, 21).

The relative proportions of the *Tamiobatis* braincases are nearly identical with those of *Xenacanthus*. The postorbital processes are less robust but more attenuated and recurved, and the lateral otic processes have a more pronounced lateral projection. The otico-occipital fissure differs from that of *Xenacanthus* mainly in having no apparent relationship with the endolymphatic fossa. It extends transversely behind the fossa from which it is separated in both specimens by a bridge of calcified cartilage. This bridge, presumably the posterior tectum (figs. 18–23), and the related portion of the fissure, also form the anterior border of a triangular uncalcified area, the apex of which is in front of the occipital crest. The occipital crest in both *Tamiobatis* specimens is less pronounced than in *Xenacanthus*, and there is no apparent articular surface for a cephalic spine. The occipital fossa, which enlarges

below the relatively long lateral otic process, houses the vagal foramen, which is actually a local enlargement of the otico-occipital fissure, as in *Xenacanthus*. Canals for three occipital nerves are evident in the Indiana neurocranium (fig. 24E, F), indicating the incorporation of three occipital arches into the occipital segment.

Unlike the basicranial circulation of *Xenacanthus*, that of *Tamiobatis* was apparently entirely confined within the basicranium (fig. 12). This is evident in both the Indiana specimen and in the braincase of *T. vetustus*. In the latter, the lumen of the canals for the internal carotids and the orbital arteries is exposed on the weathered ventral surface. Laterally directed foramina at the anterior terminations of the lateral aortic canals were presumably exits for the efferent hyoidean arteries (figs. 18, 19, 21, and 24). The palatine nerve foramina (fig. 19, 21) are recessed in shallow grooves that have a nearly posterior orientation. The relationship between the palatine nerve and the orbital artery is not entirely clear, but the relevant canals and foramina in both *Xenacanthus* and *Tamiobatis* suggest that the nerve reached the basicranium from the trigemino-facialis recess through an opening between the orbit and the dorsal wall of the orbital artery canal. As noted in the section on the basicranial circulation of *Xenacanthus*, this opening probably also transmitted a branch of the orbital artery directly into the orbit (as the opening is nearly opposite the palatine nerve foramen, its position is not indicated in the figures of the basicranium).

This interpretation of the basicranial foramina implies that the palatine and hyomandibular branches of the facial nerve had separate exits as in Goodrich's (1930, fig. 283) diagram of the situation in *Squalus*. This illustration and one of the embryonic selachi-

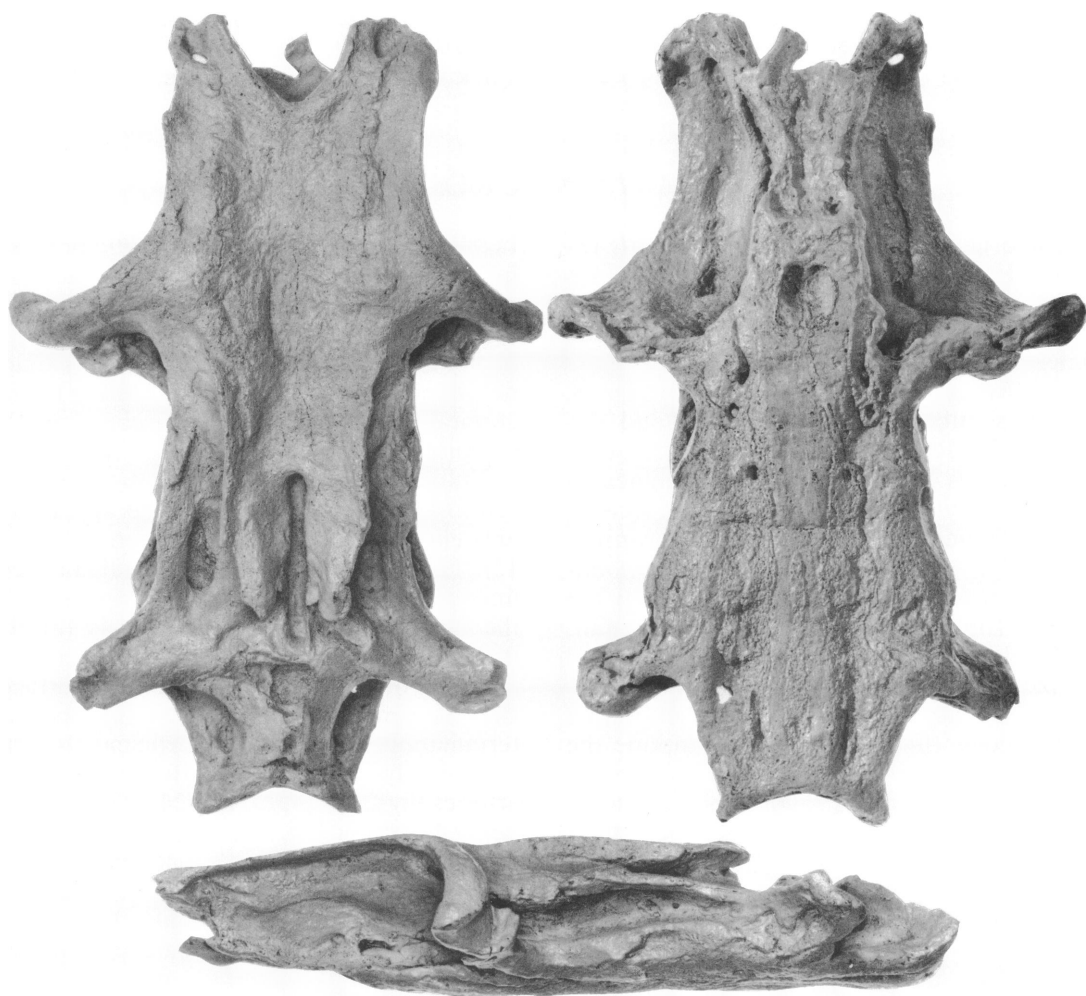


FIG. 18. *Tamiobatis vetustus*. NMNH 1717. Neurocranium in dorsal, ventral and lateral aspects. $\times .67$.

an chondrocranium (*ibid.*, 1930, fig. 246) show the relationships of the palatine nerve to the orbital artery. The major differences from the neoselachian condition is that the artery in the Paleozoic forms was directed forward and was partly or entirely enclosed in a canal. The identification of the palatine foramen is based on its closeness to the opening between the canal and the orbit in both *Tamiobatis* and *Xenacanthus*, as discussed above. Although these taxa plus

"*Cladodus*" have four foramina related to the anterior part of the lateral aorta and the orbital artery, it seems evident that the posterior two in *Xenacanthus* are not the same as the posterior two in *Tamiobatis* (compare A, B, and C in fig. 12). If we assume that the palatine foramen is correctly identified and that the sequence of the basicranial foramina is the same in *Cladodus* as in *Xenacanthus*, there appears to be an extra foramen in *Tamiobatis* between the palatine foramen and the

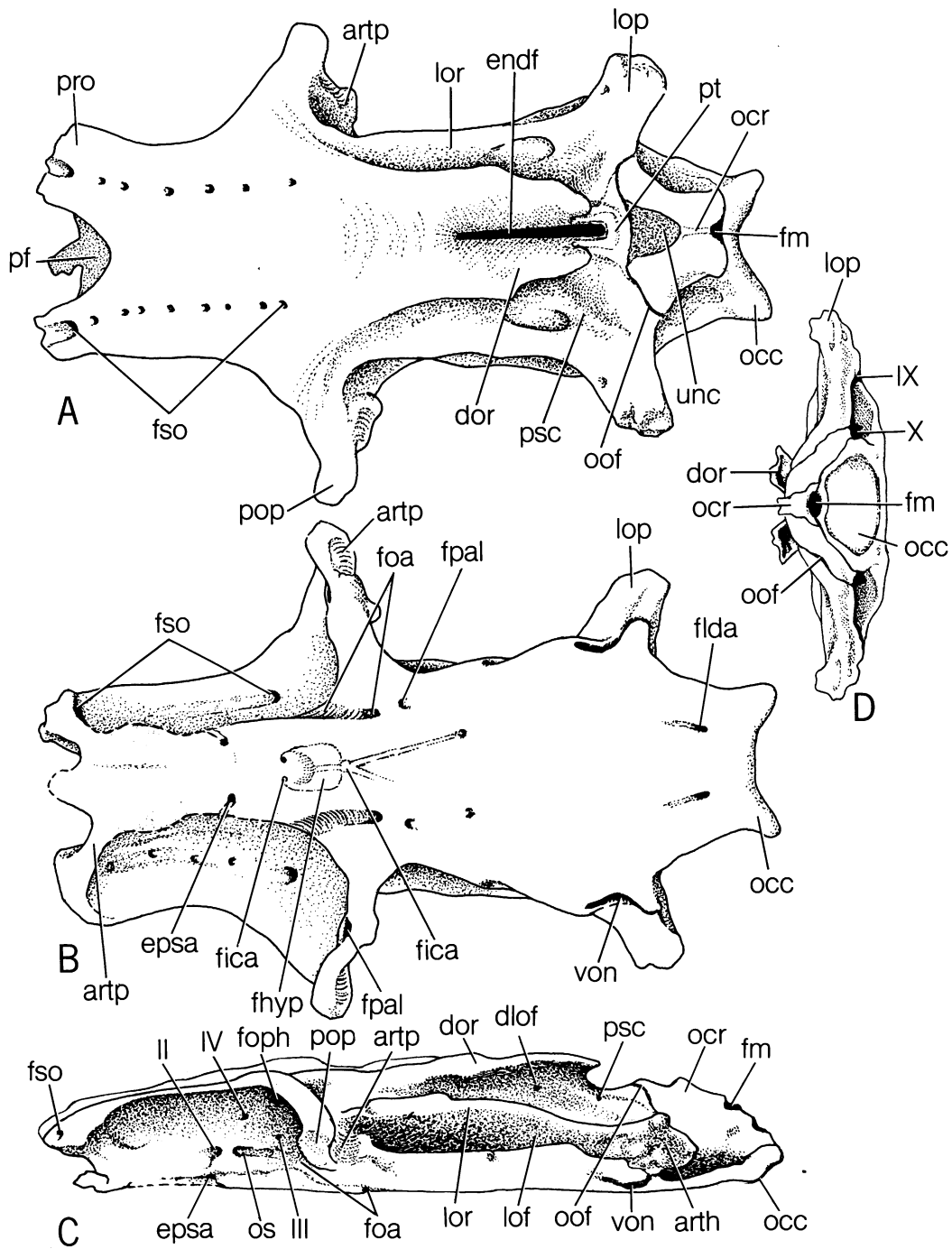


FIG. 19. *Tamiobatis vetustus*. Key diagrams for figure 18.



FIG. 20. *Tamiobatis* sp. AMNH 2140. Neurocranium reconstructed from slabbed original illustrated in figure 22. In dorsal and lateral aspects. $\times .37$.

one for the orbital artery on the rim of the suborbital shelf. This may have been the opening for the mandibular branch of the orbital artery, which had its exit here instead of through the orbit.

Aside from the several unique aspects of the basicranial circulation discussed above, the *Tamiobatis* neurocranium differs from

that of *Xenacanthus* in having less robust but longer postorbital and lateral otic processes and in having the endolymphatic fossa separated from the uncalcified area on the dorsal surface of the occipital segment by the posterior tectum. As revealed by the horizontal sections of the Indiana specimen (figs. 22, 23, 24), the internal structures of the

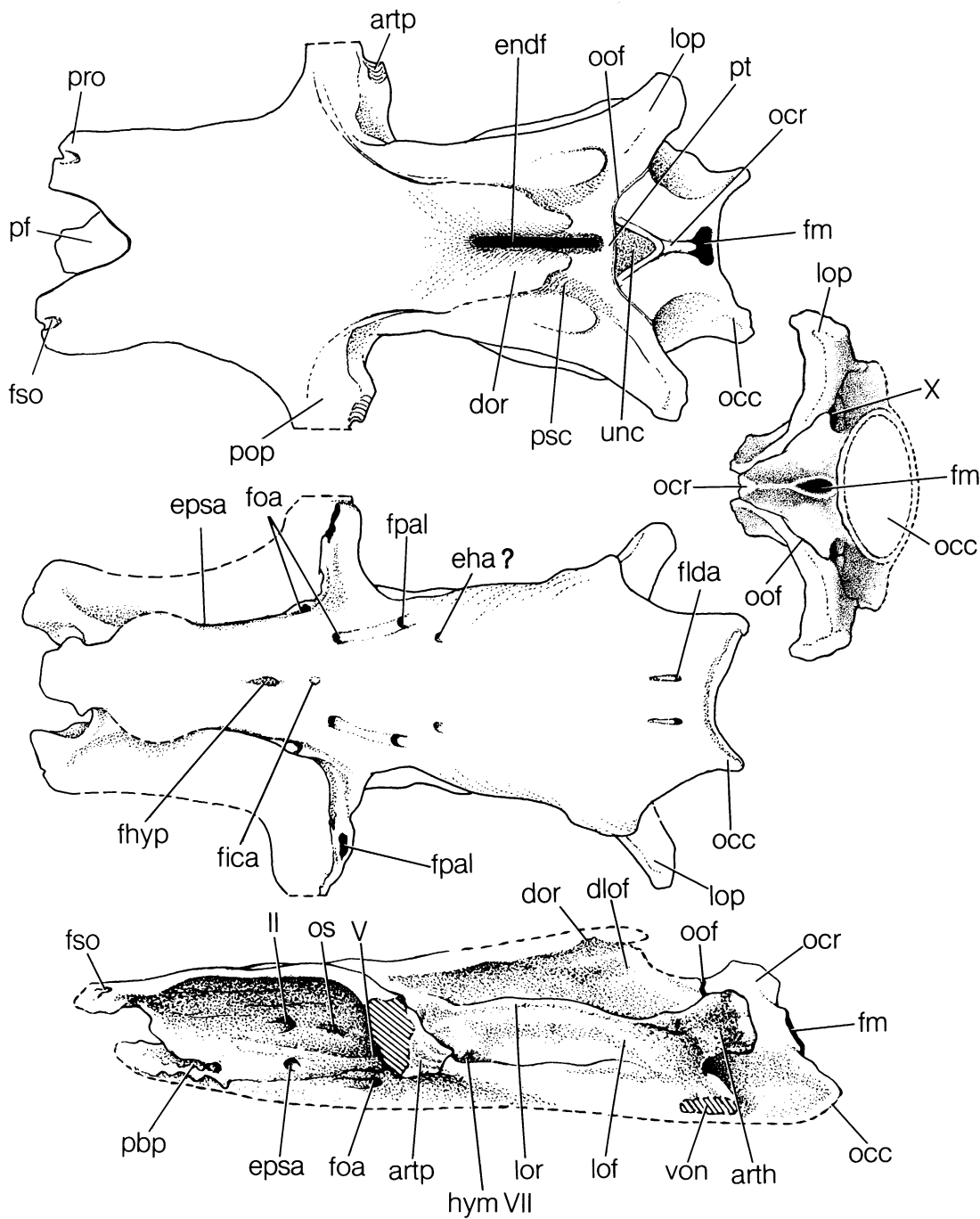


FIG. 21. *Tamiobatis* sp. Key diagrams for figure 20.

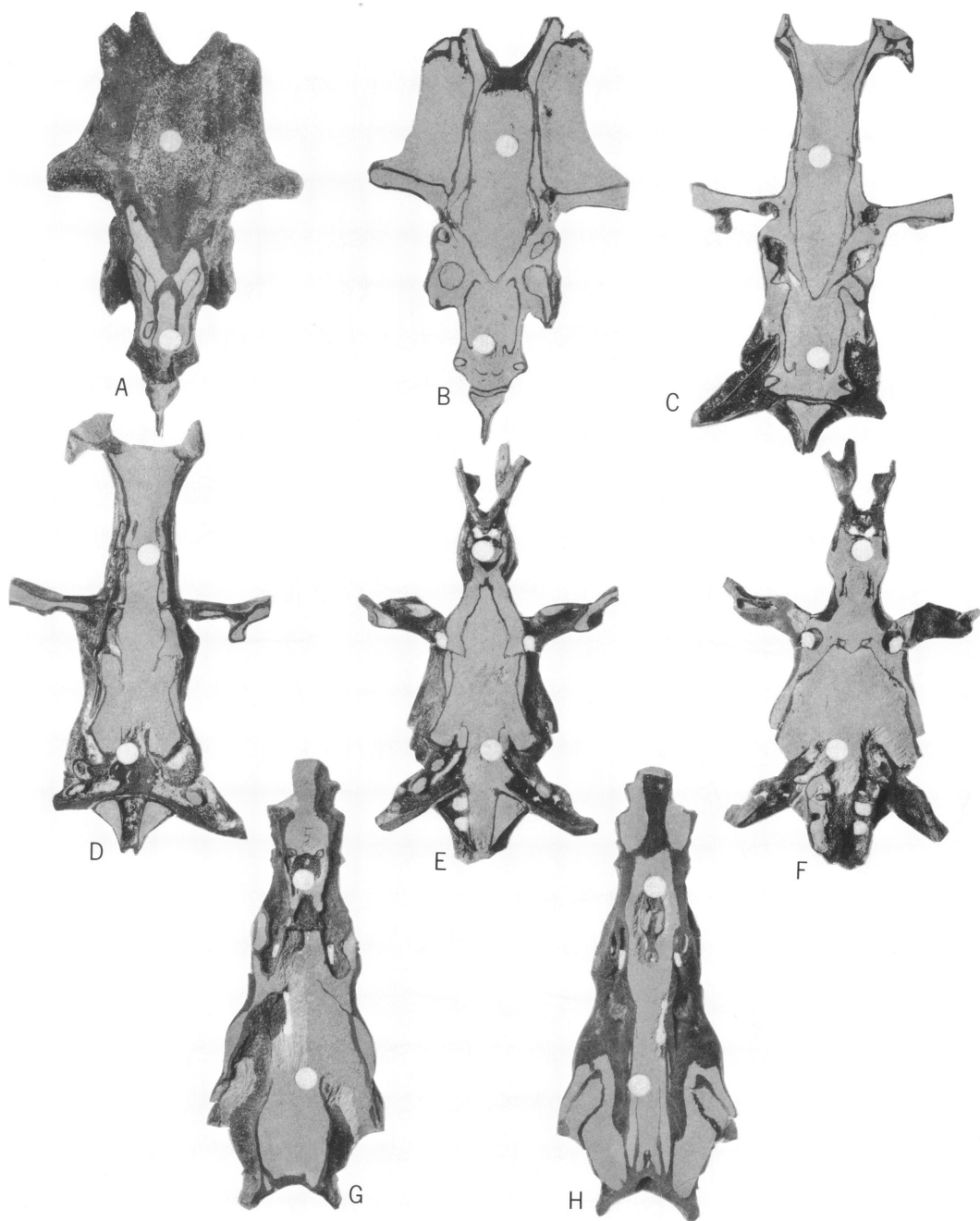


FIG. 22. *Tamiobatis* sp. AMNH 2140. Successive levels of horizontally slabbed neurocranium. A and B, C and D, E and F, G and H are opposite sides of successive slabs. $\times 26$.

braincase are readily comparable to those of *Xenacanthus*. The relative positions of the

posterior semicircular canal and of the vagal passageway behind this semicircular canal

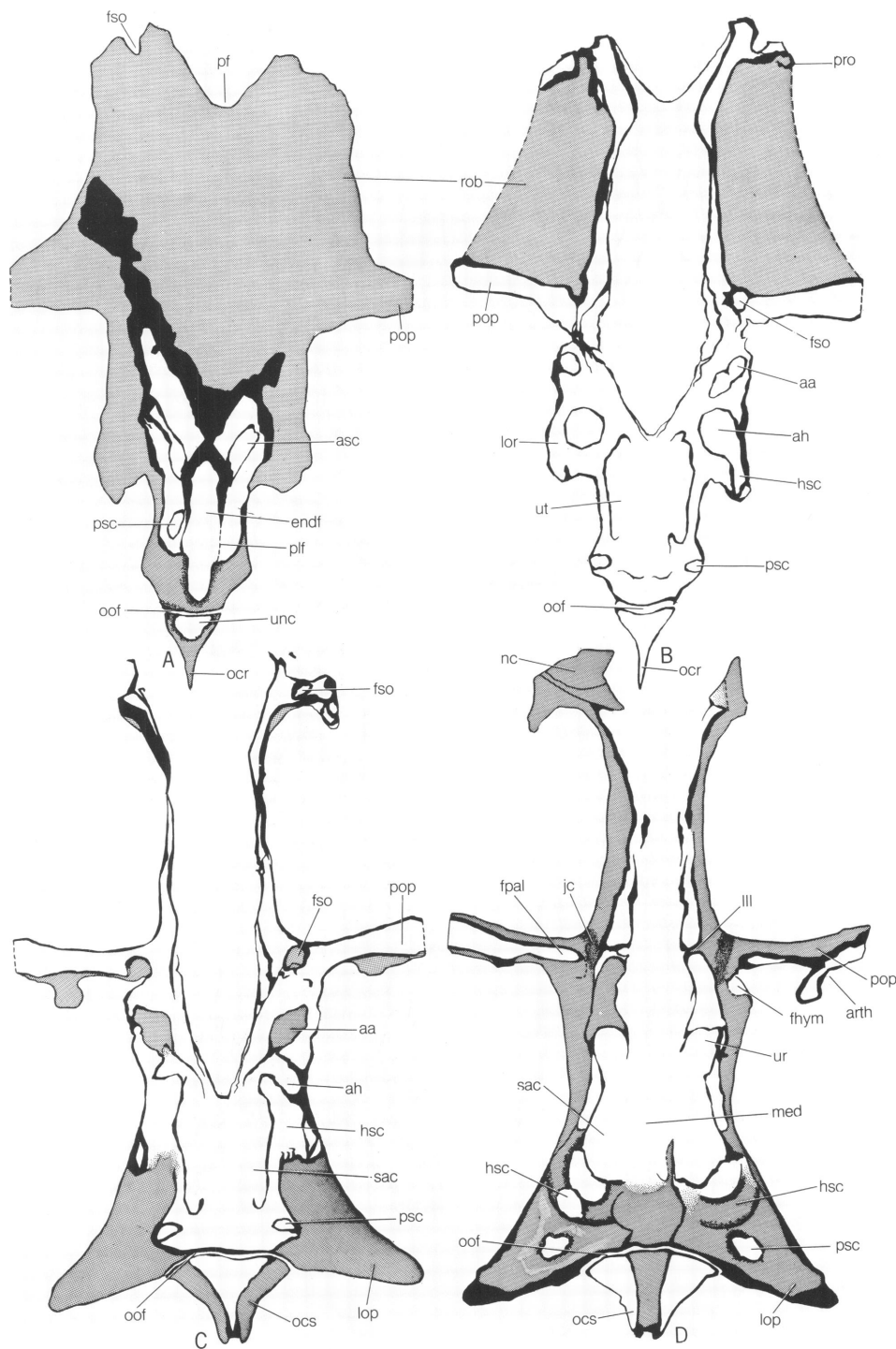


FIG. 23. *Tamiobatis* sp. Key diagrams for figure 22A-D.

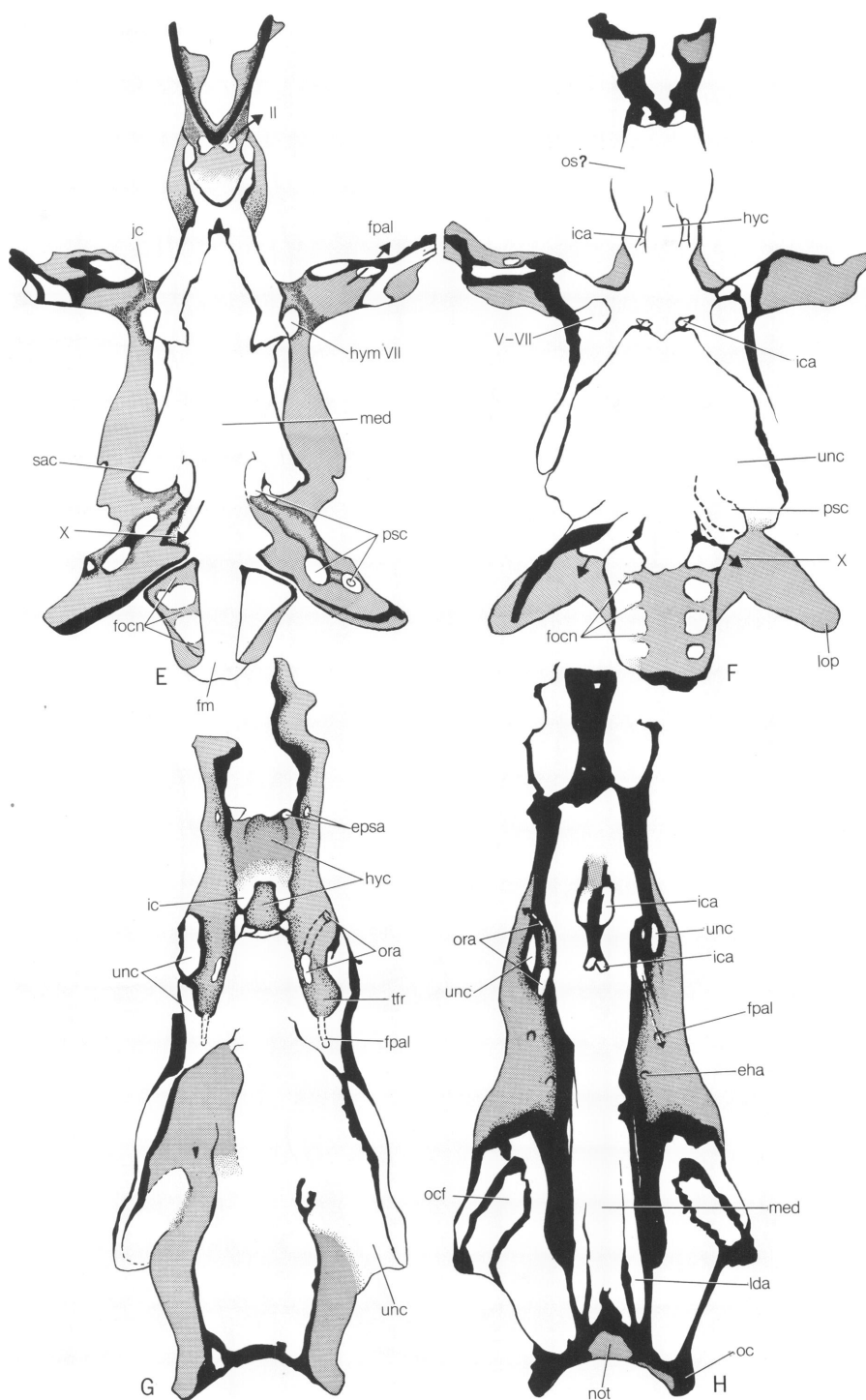


FIG. 24. *Tamiobatis* sp. Key diagrams for figure 22E-H.

(fig. 24E, F) are more easily compared with the situation in the neoselachians (fig. 15) than is possible with the *Xenacanthus* endocast (fig. 14). A detailed description of the Indiana braincase sections seems unneces-

sary in view of the remarks about the internal structure of the *Xenacanthus* neurocranium. However, the drawings of the former are labeled as fully as possible (figs. 23, 24).

“CLADODUS” NEUROCRANIUM

The type species of *Cladodus*, *C. mirabilis* Agassiz 1843, is based on detached teeth, as described by Woodward (1889, pp. 16–17). Although teeth of this general form are fairly common in late Paleozoic sediments, few specimens have been found with the skeleton and dentition associated. The fairly numerous specimens of *Cladoselache* and of the various Pennsylvanian forms under study by Zangerl and Case (1976) and by Williams (MS) are exceptions. These support the opinion that *Cladodus* is a form genus sustained only by our continuing ignorance of skeletal remains unequivocally related to the rather diverse tooth form called “cladodont.”

In 1921 Jaekel (1921, p. 228, fig. 8) published a restoration (without accompanying description) of the associated upper and lower jaws of a selachian from the Upper Devonian Wildungen deposits, which is now in Humboldt University. On the basis of the associated dentition plus the locality, he assigned these jaws to a new species of *Cladodus*, *C. wildungensis*. In 1937, Stensiö described an isolated, partial neurocranium also now in Humboldt University, and from the Wildungen deposits, which he referred to *Cladodus wildungensis*. Later in that same year, Gross described a second and more complete “*Cladodus*” braincase from Wildungen in the Senckenberg Museum. Although similar, these two neurocrania differ from each other in various respects (see below) as noted by Gross (1937, p. 101). Also according to Gross (1937), the jaws of *Cladodus wildungensis* figured by Jaekel and the neurocranium in the Senckenberg Museum were found at the same locality (Ense bei Wildungen), whereas the Humboldt University neurocranium with a different matrix and color must have been collected else-

where. For these reasons Gross (1937, p. 82) referred the Senckenberg neurocranium to *Cladodus wildungensis* and the one discussed by Stensiö (1937) to a new species, *C. hassiacus*. The main purpose in recounting these taxonomic manipulations is to emphasize the fact that the “*Cladodus*” braincases, like the *Tamiodontis* ones, were not found in direct association with other skeletal remains. Opinions regarding their systematic significance must therefore be based on their own morphology.

The apparent differences between *C. wildungensis* and *C. hassiacus* (Gross, 1937, p. 101) are mostly trivial or difficult to evaluate. According to Stensiö (1937), *C. hassiacus* has two canals in the postorbital wall, the lower one for the hyomandibular branch of VII and the upper one for the head vein; *C. wildungensis* has the usual single jugular canal with the foramen for hyomandibular VII behind it. In *C. hassiacus*, the presumed foramen for the palatine nerve is lateral to, rather than in line with, the canal for the orbital artery. Also the postorbital processes of *C. hassiacus* are curved anteriorly, more so than in *Tamiodontis*. There are also some differences between them in the position of the basicranial foramina. But in the present context these divergences have little significance and will be mostly ignored.

The proportions of the “*Cladodus*” neurocrania differ from those of *Xenacanthus* and *Tamiodontis* in that the otico-occipital area is slightly shorter, and apparently broader and deeper (fig. 12). In cross section the Senckenberg specimen is nearly equilateral (Gross, 1937, fig. 4, C). Although the dorsal and lateral walls of the occipital region in the Senckenberg specimen are missing, the position and the contours of the posterior

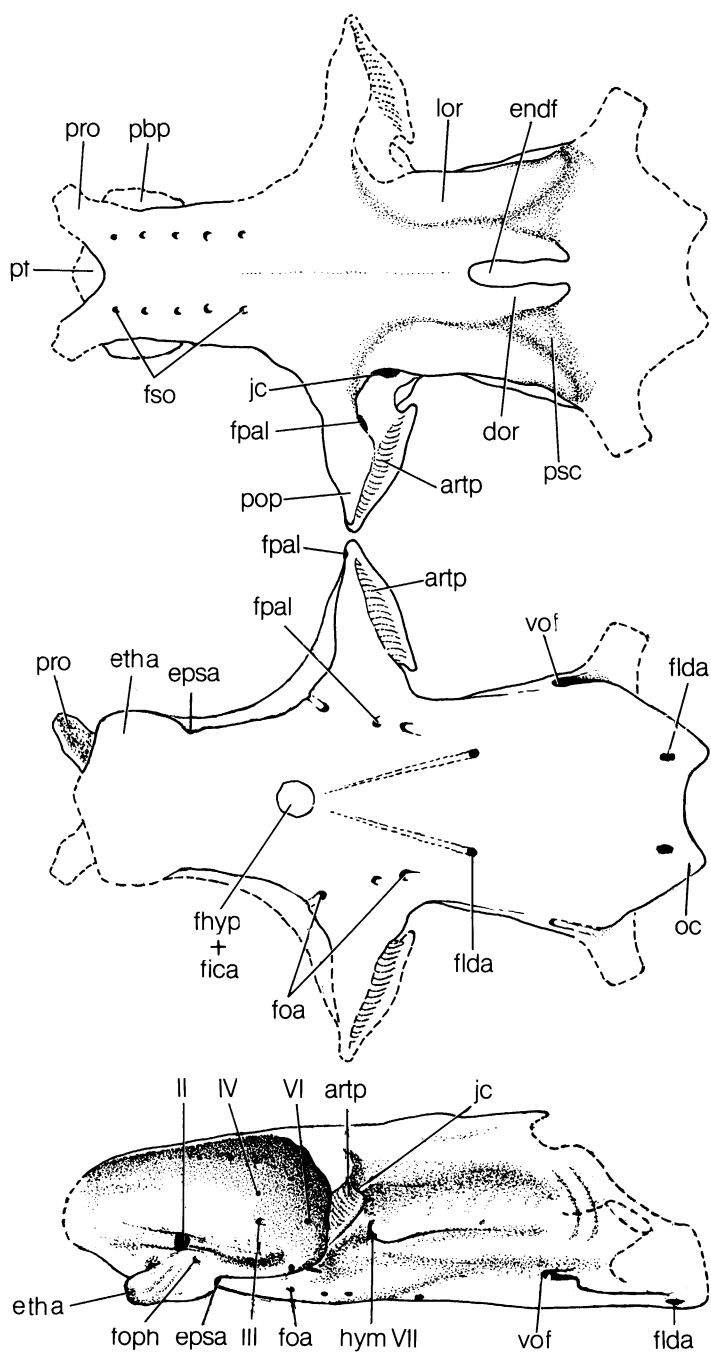


FIG. 25. "*Cladodus*" *wildungensis*. Reconstructed from cast of the original specimen and Gross, 1939. $\times 1.25$.

border of the otic region, as preserved on the right side, suggest that an otico-occipital fissure similar to that of *Xenacanthus* or *Tamiobatis* may have been present (fig. 25). The dorsal otic ridges are shorter and lower than in *Xenacanthus* and *Tamiobatis*. Also the dorsolateral and the ventrolateral otic fossae are much shallower.

The olfactory capsules are missing in the "*Cladodus*" specimens, but the remaining parts of the ethmoid region are as in *Xenacanthus* and *Tamiobatis*. The palatoquadrate articulation on the "*Cladodus*" postorbital process resembles that of *Tamiobatis* but is more elongated transversely. Gross (1937, fig. 2, ö, and p. 93) has noted the presence of a foramen on the outer edge of the postorbital process, that he suggests may have been the exit for a branch of buccal VII. This opening is in the same position as that for palatine VII in *Xenacanthus*.

Certain foramina associated with the orbit and the postorbital process have somewhat different positions, or identifications, in the "*Cladodus*" neurocrania than in *Xenacanthus* (figs. 6, 7, 21, 25). The trigeminal foramen in "*C.*" *hassiacus*, as identified by Stensiö (1937), is in about the same relative position as in *Squalus* (allowing for the reduced postorbital process), but in "*C.*" *wildungensis*, according to Gross (1937), the single foramen for the trigeminal and the buccal branch of the facial is situated behind and above the posterior opening of the jugular canal. In view of the foraminal pattern in the neoselachians, this is improbable; the foramen labeled "R VII" by Gross is more likely an exit for the main trunk of the trigeminal and buccal VII nerves. This is also the location of the trigemino-facialis recess in *Tamiobatis* and *Xenacanthus*.

NEUROCRANIA FROM THE CLEVELAND SHALE AND NEUROCRANIAL PROPORTIONS

Several dorsoventrally flattened neurocrania from the Upper Devonian Cleveland Shale in the Cleveland Museum of Natural History are associated with jaws and cladodont dentitions. In three of these (CMNH 5965, 6219, 7852), tentatively identified as "*Ctenacanthus*," the otico-occipital part of the braincase (as measured from the dorsal rim of the occipital condyle to a line drawn between the posterior borders of the postorbital processes) is nearly equal to the ethmo-orbital portion, as in "*Cladodus*" *wildungensis*. The proportions and outline of the fourth braincase (CMNH 9280) are similar to those of *Tamiobatis* (figs. 18–21). All of these specimens have well-developed postorbital and lateral otic processes. Although the surface details are partly obliterated, it is also evident that CMNH 5965 and 7852 have well-defined otic ridges on either side of the endolymphatic fossa that taper posteriorly much as in "*Cladodus*" (fig. 25).

In spite of their low information content compared with the three-dimensional neurocrania, the Cleveland Shale specimens provide, for the first time, positive evidence that braincases of *Xenacanthus*-*Tamiobatis*-"*Cladodus*" type may be associated with cladodont teeth.

The difference between the braincase proportions of the above taxa and of *Cladoseleache* (CMNH 5769, 6233) is indeed striking (figs. 12, 13A) as the length of the otico-occipital region is about one half that of the ethmo-orbital (fig. 13). Nevertheless, *Cladoseleache* (CMNH 9208) has a slitlike endolymphatic fossa and a basicranial circulation pattern that is nearly identical with the "*Cladodus*" one. Various Mississippian and Pennsylvanian genera are also known to have neoselachianlike neurocranial proportions: *Tristychius*, *Cobelodus*, *Symmorium*, *Danaea*, *Agassizodus*, and *Ornithoprion*, but few details can be deciphered from the

compressed specimens (R. Zangerl and M. E. Williams, personal commun.). However, the ventral surface of the otico-occipital area is fairly well preserved in several examples of *Cobelodus* (FMNH 7472, 7475, 7832). There are no posterior foramina for the lateral dorsal aortae, and it is probable that these arteries were not enclosed in canals. A possible interpretation of the circulatory pattern based on two pairs of more anterior foramina along with their surrounding ridges and grooves is represented in figure 13B. To complete the list of selachian taxa with interpretable neurocrania, it should be noted that *Hybodus* has a very short otico-occipital region and a *Xenacanthus*-like basicranial circulation pattern, but with partly exposed lateral dorsal aortae (J. G. Maisey, personal commun.). Elongation of the medulla, as discussed in the endocast section, is here regarded as secondary.

Differences in the relative size of the adult otic and occipital regions may have some functional significance related to the jaws, to the size of the semicircular canals, and to elongation of the medulla, but in terms of development, neoteny may very well be involved. During the early stages of neoselachian chondrocranial development that portion of the braincase including the parachordal plate, the otic capsules and the occipital arch is generally longer than, or about equal to, the length of the ethmo-or-

bital portion (trabeculae, orbital cartilages, and rudimentary nasal capsules). Although I have not found any studies on the relative growth of the neoselachian braincase, the illustrations in Harrison (1931), de Beer (1937), and Holmgren (1941) indicate that the otic (including the labyrinth) and occipital portions become relatively shorter as growth proceeds. It therefore seems reasonable to regard the proportional differences in the braincase of fossil and Recent selachians as a consequence of a variably retained embryonic condition. This supposition is enhanced for *Xenacanthus* and *Tamiodontis* by the presence of the otico-occipital fissures and the posterior extension of the occipital segment in the mature braincase. Goodrich's (1930, fig. 246) figure of an embryonic neoselachian chondrocranium, although diagrammatic and representing no particular taxon, is very suggestive of the proportions in both these genera.

If we assume that the various fossil taxa mentioned above are elasmobranchs along with the hybodonts and the neoselachians, it becomes evident that an otico-occipital region which is about the same length as, or shorter than, the ethmo-orbital represents the prevalent condition for this entire group of fishes. As this is also the condition in the holocephalans (see figures in Patterson, 1965), it may be regarded as primitive for the chondrichthyans.

ANALYSIS OF NEUROCRANIAL CHARACTERS

In order to deal with the problems of relationship raised by the foregoing descriptions and comparisons (see also discussion on pp. 60–62), this section is devoted to an outgroup analysis of 20 neurocranial characters as listed in table 1. In some combination or other most of these have been used to define or diagnose the living elasmobranchs with occasional reference to various extinct taxa for which some braincase characters have been available. The selection has also been influenced by the actual or presumed sharing of certain characters with other major groups, including the hol-

ocephalans, which are generally regarded as the sister group of the elasmobranchs.

The characters are arranged on the basis of developmental or positional criteria to the extent that this is meaningful or feasible. Several of them are known to be related ontogenetically, but are treated here more or less separately as they must be in dealing with the adult stages of living and fossil taxa. For practical reasons various Paleozoic forms are sometimes referred to as selachians, although the argument that they are in fact elasmobranchs is not set forth until the concluding section. Repetition of descriptive

information discussed in the previous parts on *Xenacanthus* et al. is unavoidable as it is essential for the outgroup comparisons.

1. PRISMATIC CALCIFICATION: Prismatic calcification is a chondrichthyan synapomorphy and is only mentioned here because *Xenacanthus* and *Tamiodontis* are known to have multiple layers of prisms in the neurocranial walls and the visceral skeleton (fig. 17) instead of a single layer of prisms on the outer and inner surfaces of the primary cartilage as in the neoselachians and the holocephalans (see p. 33). However, the distribution of the multilayered condition requires further examination before its systematic value can be ascertained.

2. CHONDROCRANIAL FUSION: The adult neoselachian neurocranium, which is actually the final stage of chondrocranial ontogeny, is a single unit as in the holocephalans. The embryonic components are indistinguishably fused together, which is also the condition in *Cladoseleache*, *Cobelodus* (Zangerl and Case, 1976), probably other anacanthous forms, and in *Hybodus*. The otico-occipital fissure in *Xenacanthus* and *Tamiodontis* thus may represent a unique condition among known chondrichthyans. But retention of cranial fissures in the mature braincase, as in the primitive actinopterygians, is a growth-related phenomenon, and their presence in two Paleozoic selachians does not therefore weaken the argument that the chondrichthyans primitively had a single-unit braincase. The placoderm endocranium is also a single unit (Denison, 1978; Young, 1980) although in some groups the nasal capsules are separate. With no meaningful input from the fossil or living agnathans, resolution is difficult at the gnathostome level, but the occurrence of fissures in some Paleozoic selachians as well as in acanthodians and primitive osteichthyans is compatible with the hypothesis that the otico-occipital fissure, at least in *Xenacanthus* and *Tamiodontis*, persisted into the adult stage.

3. NASAL CAPSULE FLOOR: De Beer (1937, p. 395) states that the gnathostome nasal capsule primitively lacked a floor, although the trabecular horns suggest that a solum nasi was once present. The floor is absent in neo-

selachians, in the one specimen of *Xenacanthus* that has the capsule preserved (MCZ 12872), and in the chimaeroids. The situation in placoderms is ambiguous, as discussed by Miles (1971, pp. 184–187). The nasal capsule is unknown in the acanthodians. According to Jarvik (1942), the capsule floor is complete in coelacanth and actinopterygians and open in rhipidistians and dipnoans (also Miles, 1977, p. 143). In any case, the absence of the solum nasi in chondrichthyans, including *Xenacanthus*, and the related ventral position of the nares cannot be proposed as a chondrichthyan or an elasmobranch synapomorphy. It may be a synapomorphous condition for gnathostomes as de Beer has suggested, but the significance of the trabecular horns requires further consideration. The floorless condition is tentatively regarded as a primitive gnathostome character.

4. ROSTRUM: The neoselachian rostrum develops either as an extension of the trabeculae or, in part, from a separate rostral cartilage that fuses with the trabeculae (de Beer, 1937). It is absent in the living agnathans, which lack trabeculae, although an exoskeletal rostrum is present in some heterostracans and osteostracans. In some form or other a trabecular rostrum is present in the Paleozoic selachians, hybodonts, neoselachians, holocephalans, some placoderms (Denison, 1978), and in various osteichthyans such as *Polyodon* and *Acipenser*. The design and relative size of the rostrum varies considerably even within the neoselachians. Its exact size and shape in the fossil sharks is poorly known, and this is true for both *Xenacanthus* and *Hybodus*, which have a rostral articulation with the palatoquadrate. In the sense that the rostrum is a forward extension of the trabecular plate, it may be regarded as a gnathostome synapomorphy.

5. PRECEREBRAL FONTANELLE: A prece-rebral (prefrontal epiphysial) fontanelle is present in the neoselachians, *Hybodus* and in the Paleozoic selachians in which this area is preserved. It represents the unchondrified anterior wall of the cranial cavity (de Beer, 1937, p. 55) and is situated just in front of the epiphysial foramen, which may form a notch on the posterior rim of the fontanelle.

De Beer and Moy-Thomas (1935, p. 300) have proposed that the pineal foramen in the embryonic *Callorhynchus* chondrocranium represents a remnant of the precerebral fontanelle in the chimaeroids. If we assume the validity of this conclusion, it follows that the precerebral fontanelle is a derived character for the chondrichthyans rather than only for the elasmobranchs. An important bit of corroborating evidence is that the elasmobranch precerebral cavity and the holocephalan ethmoidal canal are both extracranial, and have similar relationships to the dura mater, to the epiphysis, and to the ophthalmic nerves. The precerebral fontanelle does not occur in other gnathostome groups. The so-called precerebral fontanelle in an early stage of the *Acipenser* chondrocranium (de Beer, 1937, p. 92, pl. 30) is a transitory space between the medial walls of the nasal capsules.

6. ECTETHMOID (ANTORBITAL) PROCESS: This ventral, recurved extension of the orbitonasal lamina is well developed in the hexanchoids, *Chlamydoselachus*, in some galeoids, in the squaloids and in *Hybodus* (J. Maisey, personal commun.). It is absent in the Paleozoic selachian taxa, and in the holocephalans. The so-called ectethmoid process in arthrodires (Stensiö, 1963b; Goujet, 1975; Young, 1980) is probably also derived from the orbitonasal lamina but it projects laterally in the same manner as the ethmoid articulation in *Xenacanthus* (fig. 6), and it articulates with the autopalatine at its posterolateral corner. Ventrally the process is covered by the anterior supragnathal. In view of these relationships, there is no apparent reason for regarding this process as the homologue of the neoselachian ectethmoid process. There is also no indication of a neoselachianlike ectethmoid process in the acanthodians or in the osteichthyans. It thus appears to be a synapomorphy for *Hybodus* plus the neoselachians.

7. OPTIC PEDICLE: In adult neoselachians the optic pedicle is attached to the inner orbital wall behind and below the oculomotor foramen. The site of attachment is within the trigemino-facialis fossa as in *Chlamydoselachus*, or simply on the inner wall of the orbit,

which is the more common condition. Examination of dried neurocrania representing squaloids, galeoids, batoids, squatinoids and hexanchoids shows no positive indication of an attachment site. Yet it is evident that the optic pedicle is a shared derived character of neoselachians (according to Holmgren, 1941, it is absent only in *Oxynotus* and *Scyliorhinus*). In regard to extinct forms, there is no evidence of a pedicle in *Hybodus* (Maisey, personal commun.); in *Xenacanthus*, *Tamiodontis* and *Cladodus* the trigemino-facialis fossa presumably contained the base of the optic pedicle. The hypothesis that the optic pedicle is therefore an elasmobranch synapomorphy is difficult to test by direct evidence.

The optic pedicle is absent in the holocephalans, acanthodians and osteichthyans. According to Ørvig (1975) and Young (1978, 1980) a presumed eye-stalk attachment area has been found in certain euarthrodires. This discovery presents the same sort of problem in regard to placoderm-elasmobranch relationships as the apparent occurrence of claspers in the ptyctodont placoderms (Miles, 1977). But in view of homology uncertainties and unexplained distribution patterns, it seems most prudent to side-step these problems in assessing relationship, at least until more hard evidence is available. I tentatively regard the eye-stalk as a neoselachian synapomorphy.

8. POSTORBITAL PROCESS: The prominent postorbital process in the Paleozoic selachians is obviously related to a major articulation site for the palatoquadrate. This aspect is discussed later; the main consideration here is the ontogeny of this process, and its possible homology with the postorbital process in other groups.

In the Paleozoic selachians the postorbital process is bounded anteriorly by the trigeminal foramen and posteriorly by the opening for the hyomandibular nerve. The process is pierced by a large jugular canal, and another canal that presumably carried a branch of the palatine nerve to an exit on its anteroventral rim. According to de Beer (1937, p. 56), the medial wall of the jugular canal in *Squalus*, which is also the inner part of the postorbital

TABLE 1
List of Characters Included in Analysis^a

1. Prismatic calcification
 - a. single layered
 - b. multilayered
2. Chondrocranial fusion
 - a. complete
 - b. otico-occipital fissure present
3. Nasal capsule floor absent or rudimentary
4. Rostrum
5. Precerebral fontanelle and fossa
6. Ectethmoid process
7. Optic pedicle
8. Postorbital process
9. Basal angle
 - a. embryonic only
 - b. retained in adult
10. Utricular recess
11. Semicircular canals
 - a. crus between anterior and posterior canals
 - b. crus between anterior and horizontal canals
12. Endolymphatic fossa and circular posterior semicircular canal
13. Hypotic lamina and related glossopharyngeal canal
14. Lateral otic process
 - a. weakly developed or absent
 - b. pronounced
15. Cephalic circle
 - a. lenticular
 - b. bell-shaped
16. Efferent pseudobranchial artery over trabecula
17. Palatoquadrate attachments
 - a. rostral
 - b. ethmoid
 - c. postorbital
18. Hyomandibular articulation near glossopharyngeal foramen
19. Occipital arch between auditory capsules
 - a. Projecting behind capsule with separate foramina for occipitospinal nerves
 - b. Not projecting behind capsules and with most of occipitospinal nerves leaving braincase through vagus canal
20. Otic-occipital proportions
 - a. Less than ethmo-orbital portion
 - b. Equal to or greater than length of ethmo-orbital portion

^a For hypotheses regarding the polarity of the above characters refer to the proper number in the section on character analysis.

process, is derived from the embryonic pre-facial commissure. The lateral wall of the

canal, and thus the main body of the process, results from the subsequent chondrification of a connective tissue bridge that extends between the subocular shelf and the lateral wall of the auditory capsule directly above the shelf. In nearly all respects, the *Squalus* jugular canal develops as it does in the actinopterygians including its relationships to the trigeminal foramen and the hyomandibular nerve (which in the osteichthyans usually arises within the canal). As de Beer has also noted, the lateral wall of the *Squalus* jugular canal "corresponds" to the lateral commissure of the osteichthyans, and this has been confirmed by Holmgren (1940, pp. 111, 167).

The anterior postorbital process of the placoderms has about the same morphological relationship (Miles, 1971; Goujet, 1975; Young, 1978, 1980) as the postorbital process in primitive selachians and palaeoniscoids, with the hyomandibular foramen behind it instead of on its outer end as thought by Stensiö (1963b). Miles (1973) has identified an incomplete lateral commissure in *Acanthodes*, which may have projected laterally beyond the jugular vein, but there is no evidence of a jugular canal. Jarvik (1977) has interpreted the lateral wall of the *Acanthodes* dorsal ossification rather differently, but he also agrees that there is no jugular canal. In any case, the postorbital process of *Acanthodes*, and presumably of other acanthodians, is prominent and in its gross aspects resembles that of Paleozoic selachians and palaeoniscoids. Also it has about the same relationships to the basitrabecular process as it does in the primitive actinopterygians.

In view of this evidence it seems most economical to regard the postorbital process as homologous throughout the gnathostomes and as a gnathostome synapomorphy. The reduction of this process in the neoselachians, the rhipidistians and the dipnoans is therefore regarded as secondary.

9. BASAL ANGLE: According to El-Toubi (1949) the development of the basal angle in *Squalus* is associated with the orientation of the polar cartilages, which remain at a nearly

A detectable basal angle is present only in the hexanchoids and squaloids among the fossil and living chondrichthyans (Holmgren, 1942). Its absence in the other neoselachian taxa presumably means that the trabeculae and the parachordals become alined during ontogeny to form a nearly flat basicranium. The occurrence of a basal angle "in certain Coccoosteomorphs and Pachyosteomorphs" among the placoderms (Stensiö, 1963b, p.

407) has not been confirmed, and there is no indication of this condition in the acanthodians or the osteichthyans. This evidence indicates that the basal angle is a synapomorphy for the hexanchoids plus the squaloids. There is, however, a good possibility of independent acquisition because of the marked angle between the trabeculae and the parachordals in the early developmental stages of the chondrocranium in all neoselachians. This embryonic angle might, in fact, be regarded as a neoselachian or even an elasmobranch synapomorphy—depending in part on the condition in the early embryonic stages of the chimaeroid chondrocranium, as yet unknown.

10. **UTRICULAR RECESS:** The presence of a prominent utricular recess has been noted in the chondrichthyans (Retzius, 1881), dipnoans (Retzius, 1881; Miles, 1977, p. 99) and placoderms (Stensiö, 1950, 1963a,b). It is a well defined evagination of the utriculus situated below the ampullae for the horizontal and anterior semicircular canals (fig. 14) with a partly separate innervation by branches of the auditory nerve. Retzius (1881, p. 222) was so impressed by the resemblance between the chondrichthyan and dipnoan utricular recess that he considered these fishes as sister groups in his phylogenetic diagram. But examination of Retzius's illustrations of the actinopterygian labyrinth (*ibid.*, 1881, pp. 103, 112, 118, 120, 131, 139) indicates that an evagination resembling the utricular recess may be present in the ray-finned fishes in the same position and with the same innervation pattern. This suggests that we are concerned with the relative size of the evagination rather than with its presence or absence. In view of this possibility, with its implication for independent enlargement the distribution of the utricular recess becomes suspect as a test for relationship (see also Miles, 1977, pp. 99–100).

11. **SEMICIRCULAR CANALS:** The partial fusion of the anterior and the horizontal semicircular canals in the neoselachians is correlated with the relative detachment of the posterior semicircular canal which, in turn, has only a restricted connection to the median wall of the sacculus via the posterior

utriculus (Retzius, 1881; de Beer, 1931, 1937; fig. 10A, B). As discussed earlier (p. 30), the ringlike form of the posterior canal can be confirmed in *Xenacanthus*, but not, with certainty, a crus between the anterior and horizontal canals.

In the holocephalans (Retzius, 1881), acanthodians (Miles, 1973, fig. 6) and osteichthyans (Retzius, 1881; Stensiö, 1963a; Millot and Anthony, 1965) the anterior and horizontal canals are separated, but the anterior and posterior vertical canals meet to form a crus commune. This striking difference between the neoselachians and other living gnathostomes was first emphasized by de Beer (1931, p. 617) and has been also noted by Jollie, 1962. The condition in the placoderms is difficult to evaluate. On the basis of the reconstructed endocasts for *Jagorina* (Stensiö, 1950, fig. 3), *Kujdanowiaspis* (Stensiö, 1963b, fig. 34) and *Tapinosteus* (Stensiö, 1963b, fig. 66), Stensiö has stressed the apparent resemblance of the placoderm labyrinth pattern to the neoselachian one. The posterior vertical semicircular canal may have formed a nearly complete ring, but, as suggested by the *Squalus* endocast (fig. 15), the other canal relationships in placoderms remain obscure. The systematic value of these semicircular canal characters in terms of defining the elasmobranchs might appear to be compromised by the situation in the placoderms. However, the general distribution of the crus between the anterior and posterior canals, which includes the holocephalans, points to this condition as the primitive gnathostome one, an opinion also supported by the labyrinth studies of Hagelin (1974). I therefore propose the hypothesis that the crus between the anterior and horizontal canals and the relative independence of the nearly circular posterior semicircular canal represent a synapomorphic complex for the neoselachians plus *Xenacanthus*, and that any resemblance in these regards between the elasmobranchs and the placoderms is the result of parallelism.

12. **ENDOLYMPHATIC FOSSA:** The medial wall of the auditory capsule is chondrified in neoselachians (figs. 10A, B, 11) but not in holocephalans (fig. 10C; Stahl, 1967, p. 170),

actinopterygians or dipnoans. De Beer (1937, p. 456) regards this difference as an important one separating the neoselachians from the osteichthyans, and he would presumably add the holocephalans. The absence of a medial chondrified wall, on the basis of this evidence, may be primitive for the gnathostomes.

In *Scyliorhinus*, as discussed earlier, the posterior semicircular canal protrudes into a vacuity in the medial capsular wall (de Beer, 1931, 1937, p. 62; Holmgren, 1940, p. 168). This vacuity, which becomes the perilymphatic fenestra, brings the perilymphatic space into direct communication with the endolymphatic fossa (fig. 11C). According to de Beer (1931, p. 619), the formation of the vacuity early in the development of the auditory capsule prevents the opposite capsules from contributing to the formation of the intercapsular chondrocranial roof. The resulting hiatus becomes the endolymphatic fossa, which is bordered anteriorly by the synotic tectum (a bridge between the auditory capsules) and posteriorly by the posterior tectum, which connects the occipital arches (Holmgren, 1940, p. 142). The endolymphatic duct typically opens into the fossa in front of the perilymphatic fenestra but it is not directly involved in the formation of the fossa. The recorded exceptions to this developmental sequence (Norris, 1929) are found in *Heterodontus* (*Cestracion*), *Gymnura* (*Pteroplatea*) and *Sphyrna* (*Syrrhina*) where the perilymphatic fenestra becomes confluent with the endolymphatic foramen. This is simply a variant of the condition described above and it may be regarded as secondary.

There is evidence in *Xenacanthus* (figs. 9, 14), *Tamiobatis* (fig. 23), *Tristychius* (Dick, 1978, fig. 7) and *Hybodus* (J. G. Maisey, personal commun.) of a close association between the posterior semicircular canal and the endolymphatic fossa. There are also uncalcified areas in the braincases of both *Xenacanthus* (fig. 9) and *Tamiobatis* (fig. 23) that may have included the perilymphatic fenestra and the endolymphatic foramen. Both have been identified in *Tristychius* (Dick,

1978) and in *Hybodus* (J. G. Maisey, personal commun.). In regard to outgroup comparison, an endolymphatic fossa, as well as the modifications in the labyrinth related to its development, are absent in the holocephalans (fig. 10C), placoderms (Stensiö, 1963b; Young, 1980), acanthodians, (Miles, 1973) and osteichthyans (de Beer, 1937; Patterson, 1975). The endolymphatic ducts in these groups, when present, reach the surface of the neurocranium directly. The space occupied by the endolymphatic sacs of *Protopterus* (Goodrich, 1909, fig. 214) is sometimes called the supraotic cavity. This cavity is extradural, but beneath the cranial roof and between opposite anterior and posterior semicircular canals (Miles, 1977, pp. 100–103). A supraotic cavity may be present in some actinopterygians, dipnoans and *Eusthenopteron*, but I can find no reason to homologize it with the endolymphatic fossa of the neoselachians. Although both house endolymphatic sacs, their origin and location are quite different.

It thus appears that *Xenacanthus*, *Tamiobatis*, "*Cladodus*," *Tristychius*, *Cladoselache*, and specimens in the Cleveland Museum labeled "*Ctenacanthus*" share an endolymphatic fossa with *Hybodus* and the neoselachians.

13. HYPOTIC LAMINA AND GLOSSOPHARYNGEAL CANAL: In *Scyliorhinus* according to de Beer (1931, 1937) the hypotic lamina extends laterally from the parachordal plate beneath the posterior part of the auditory capsule. Although the selachian capsule may be attached to the parachordal by anterior and posterior basicapsular commissures (de Beer, 1937, p. 399), the latter is "obscured" by the development of the hypotic lamina. At an earlier stage of *Scyliorhinus* development (de Beer, 1931, p. 597) the posterior basicapsular commissure has not differentiated, and the basicapsular fenestra is therefore confluent with the metotic fissure. The glossopharyngeal nerve leaves the cranial cavity by way of the basicapsular part of the fissure and runs between the floor of the capsule above, and the hypotic lamina below. These fuse in *Squalus* (El-Toubi, 1947, pp.

273–275) to form the actual glossopharyngeal canal. In *Scyliorhinus* (de Beer, 1931, p. 620), which has only a membranous capsular floor, the hypotic lamina forms a partial secondary floor and the glossopharyngeal then seems to pass through the auditory capsule—from which it is actually separated “only by some remnants of membrane” (*ibid.*, p. 620). If, in fact, neoselachians have a posterior basicapsular commissure, this may be represented in *Squalus* by the fused area between the hypotic lamina and the medial wall of the auditory capsule.

Most of de Beer’s observations, as summarized above, have been questioned by Holmgren (1943, pp. 140–148). He claims that the hypotic lamina is actually the basicapsular commissure (or lamina), which extends posteriorly below the glossopharyngeal nerve, that the glossopharyngeal nerve actually passes through the auditory capsule, and that the basicapsular fenestra and the metotic fissure can never combine because of their different locations. These conclusions are based on embryos of *Scyliorhinus*, *Etmopterus* and *Raja*.

Aside from El-Toubi (1947), I have found no discussion of these problems except for some brief remarks by Jollie (1971). Omitting his conviction regarding the incorporation of certain visceral elements into the neurocranium (see p. 20), it appears that Jollie’s observations on the chondrocranium of a 35–37 mm. *Squalus* support the existence of the hypotic lamina (his lateral pharyngohyal plate). Also, he agrees that the formation of the neoselachian glossopharyngeal canal is unique among vertebrates in that it is formed by the fusion of the hypotic lamina with the otic capsule. Finally, one of Jollie’s sections (1971, fig. 9) is similar to one of de Beer’s for the *Scyliorhinus* chondrocranium (fig. 11G) in showing a clear indication of continuity between the metotic fissure and the basicapsular fenestra containing the glossopharyngeal nerve.

Turning to the fossil taxa, only *Xenacanthus* and *Tamiodontis* supply information that can be compared with *Scyliorhinus* and *Squalus*. In the former, the canal for the va-

gus nerve parallels, and is close to, the posterior semicircular canal (figs. 9, 14, 24). Although the exact course of the glossopharyngeal remains unknown, it was surely lateral to the posterior canal, and, as discussed earlier, probably reached the surface of the neurocranium through the ventral otic notch. The strong lateral flange projecting from the base of the otic segment in the area of the otico-occipital fissure in *Xenacanthus* (fig. 9K, L) can be compared favorably with the hypotic flange in *Scyliorhinus* (fig. 11F, G, H) and has been so identified. In fact, no other interpretation seems to be compatible with the known evidence. Thus, I propose that the canal for the glossopharyngeal nerve in *Xenacanthus* and *Tamiodontis* was formed in the same way as the canal in *Squalus*, *Scyliorhinus* and presumably other neoselachians. There is, of course, one important difference. The situation in these extinct taxa must be compared with the embryonic condition in the neoselachians rather than with the adult one.

There is no indication of the hypotic lamina in *Callorhynchus* (fig. 10C) or in other holocephalans. The glossopharyngeal nerve reaches the surface of the neurocranium through a short canal just in front of the vagus. In regard to the placoderms, the details of the otic region are known in relatively few taxa. In the rhenanid *Brindabellaspis* (Young, 1980) and in the euarthroires *Kujdanowiaspis* and *Tapinosteus* (Stensiö, 1963b, figs. 31B, C, 32A, and 64A) the otic basicranium is very broad. This surely represents the parachordal plate, which must have extended laterally to the saccular area. As in the sharks, there is no firm evidence that the glossopharyngeal nerve passed through the labyrinth cavity, but the general morphology of the area in these placoderms does not resemble in any other significant detail that of the elasmobranchs (see particularly Young, 1980). In osteichthyans, the glossopharyngeal crosses the cavity of the auditory capsule, which also contrasts with the situation in the elasmobranchs.

These data as assembled and interpreted lead to the hypothesis that the glossophary-

ryngeal nerve in elasmobranchs passes through a canal formed jointly by the floor of the auditory capsule and the hypotic lamina. The lamina and the mode of canal formation are regarded as related elasmobranch synapomorphies, including the condition in *Xenacanthus* and *Tamiobatis*.

14. LATERAL OTIC PROCESS: *Xenacanthus* (fig. 6) and *Tamiobatis* (figs. 19, 21) are noteworthy for their relatively large, robust lateral otic processes. Several specimens in the Cleveland Museum collection, including a *Tamiobatis*-like braincase (CMNH 9280) and another neurocranium labeled "*Ctenacanthus*" (CMNH 6219) have similarly developed lateral otic processes. As both of the Cleveland specimens possess cladodont teeth, it is evident that these processes are not peculiar to the xenacanth. The xenacanth neurocrania figured by Fritsch (1895) apparently have lateral otic processes similar to those of the Texas braincases, which are not flared laterally to the same extent as in *Tamiobatis*. The size and shape of the processes in "*Cladodus*" remain unknown but there is evidence of their presence. The nature of the lateral otic processes in *Cladoseleache* remains equivocal; they appear to be less developed than in *Xenacanthus*. In *Tristychius* (Dick, 1978), the processes are very short and located on the widest part of the otic region. Lateral otic processes are absent in the anacanthous Paleozoic forms described by Zangerl (1973) and Williams (1979). In regard to the neoselachians, they are also absent in the galeoids, pristiphorids, batoids, and most squaloids. There are, however, strong posterolateral otic projections in *Notorhynchus* (Holmgren, 1941, fig. 5) and in *Squatina* (Holmgren, 1941, fig. 33). *Squalus* has small otic extensions called postotic processes by Holmgren (1941, fig. 22).

The lateral otic process represents a projection of the lateral otic wall immediately anterior to the metotic fissure and to the vagal foramen. In *Xenacanthus*, *Tamiobatis*, and *Tristychius* it is above the exit for the glossopharyngeal nerve. In *Squalus* this foramen is behind the process, which, along

with the occipital surface has attachment areas for the epaxial musculature. It is accordingly reasonable to conclude that the enlarged processes in *Xenacanthus* and *Tamiobatis* provided extensive insertion areas for these muscles, which also reached into the dorsolateral otic fossae. Lateral expansion of the otic region in relation to the attachment of the epaxial musculature has apparently occurred in varying degrees among the neoselachians, but is pronounced in only a few taxa. In regard to the Paleozoic selachians, *Xenacanthus*, *Tamiobatis*, and the Cleveland Shale "*Ctenacanthus*" are the only known forms with greatly expanded lateral otic processes. This shared condition, presumably derived, is an additional reason for postulating a common ancestry for these taxa.

There is no evidence of a lateral otic process in the holocephalans, although the epaxial muscles are attached to the posterior surface of the relatively inflated otic capsules in the chimaeroids.

The arthrodire posterior postorbital and supravagal processes have nearly the same relationships to the cranial and occipito-spinal nerves as the lateral otic process in selachians, but quite different relationships with the visceral skeleton and its musculature (Miles, 1969; Young, 1980, fig. 18). In the placoderms it is probable that the parietal division of the epaxial musculature was attached to the neurocranium above the supravagal process and in the subparanuchal fossa (see Stensiö, 1963b, fig. 26), in which case it would have no contact with the posterior postorbital process. This evidence points to an independent origin for the selachian lateral otic process and the placoderm posterior postorbital process in spite of certain morphological similarities.

Lateral expansion of the otic rather than the occipital region in relation to the parietal epaxial musculature does not occur in either the acanthodians or the actinopterygians, but it is present in the rhipidistians among the sarcopterygians.

15. CEPHALIC CIRCLE: In gnathostomes generally the lateral dorsal aortae differen-

tiate on either side of the front part of the notochord. Subsequent fusion of these vessels below and anterior to the notochord forms a loop frequently called the cephalic circle (see Bertin, 1958, pp. 1418–1420). In the early embryonic stages of the neoselachian head, the cephalic circle may extend posteriorly as far as the third or fourth epibranchial artery. At about the stage when the parachordals fuse to form the parachordal plate, the “circle” becomes relatively smaller and expands laterally in front of the efferent hyoidean arteries (Goodrich, 1930; El-Toubi, 1949) to form a characteristic bell-shaped pattern. The widest part of the “bell” is at the junction of the efferent hyoideans and the lateral dorsal aortae. Behind this junction, the lateral aortae abruptly converge and may run parallel to each other before joining the dorsal aorta. The course and persistence of the lateral aortae vary considerably in different groups of neoselachians.

The cephalic circle in *Xenacanthus*, *Tamiodontis*, “*Cladodus*,” *Cladoselache*, probably *Cobelodus* (figs. 12, 13A, B) and *Hybodus* (J. G. Maisey, personal commun.) resembles the embryonic one in that the lateral dorsal aortae formed a more or less lenticular pattern. But unlike the neoselachian embryonic pattern, the epibranchial arteries joined the dorsal aorta or possibly the rear of the cephalic circle behind the braincase, as in adult neoselachians. As discussed earlier, the lateral dorsal aortae were contained in basicranial canals in all the above taxa except *Cobelodus* and, in part, *Hybodus*.

The adult chimaeroid dorsal aorta divides into lateral aortae below the vagal foramen and the elliptical cephalic circle receives all the epibranchial arteries (de Beer and Moy-Thomas, 1935)—a condition that is surely related to the subcranial position of the branchial arches. Interestingly enough, the branchial arches are always postcranial in embryonic neoselachians even though some of the epibranchial arteries join the cephalic circle.

According to Stensiö (1963b and Young, 1980) all the branchial arteries in the arthrodires also joined the cephalic circle—and the

branchial arches were under the basicranium. The basicranial circulation in the acanthodians is essentially unknown but there is evidence of one efferent branchial artery branching off the dorsal aorta (Miles, 1973). The shape of the cephalic circle is highly variable in the actinopterygians both in extent and in the number of related epibranchial arteries (Goodrich, 1930; Poplin, 1967; Bertmar, 1962). The dipnoan cephalic circle is joined by bunched epibranchial arteries (Bertmar, 1966) making a pattern that is rather distinctive among the osteichthyans. The cephalic circle in *Latimeria* receives all epibranchial arteries (Anthony and Robineau, 1967).

Taken together, this evidence is consistent with the hypotheses that the bell-shaped cephalic circle, although somewhat variable in form, is a neoselachian synapomorphy and that the exclusion of the epibranchial arteries from the arterial circle is an adult elasmobranch synapomorphy. The fact that the cephalic circle receives all or most of the epibranchial arteries in early embryonic neoselachians as well as in adult chimaeroids, placoderms, many actinopterygians, dipnoans, and *Latimeria* is also consistent with the hypothesis that this condition is primitive for the gnathostomes.

16. EFFERENT PSEUDOBANCHIAL ARTERY: The position of the foramen for the efferent pseudobranchial artery on the suborbital shelf in *Xenacanthus*, *Tamiodontis*, and “*Cladodus*” and the union of this vessel with the internal carotid within the neurocranium (fig. 12A) in *Xenacanthus* (according to the serial sections) suggest that the efferent pseudobranchial artery in these taxa ran dorsal to the trabecula to enter the cranial cavity. As de Beer (1924, p. 330; 1937, p. 377) has emphasized, this is the condition in the neoselachians, which differs from that in the osteichthyans where the efferent pseudobranchial runs ventral to the trabecula to meet the internal carotid.

Although the chimaeroids (e.g., *Callorhynchus*) lack a pseudobranch, and both the internal carotid and ophthalmic arteries degenerate, the efferent pseudobranchial artery

persists and functions as the only blood supply to the brain. According to de Beer and Moy-Thomas (1935, pp. 292–293, fig. 8), its main branch passes through the trabecular plate on its way to the cranial cavity, which indicates that its relationship to the trabecula is the same as in the neoselachians.

In regard to the placoderms, Stensiö (1963b, pp. 57, 174) believes that the efferent pseudobranchial artery in *Kujdanowiaspis*, *Tapinoosteus* and *Pholidosteus* also passed over the trabecula. The canal for the efferent pseudobranchial, as identified by him, is on the so-called subnasal shelf below the orbital foramen (*ibid.*, figs. 13 and 16). According to the endocast of *Kujdanowiaspis* (*ibid.*, figs. 28 and 30), this canal is a branch of the internal carotid that terminates in an anterior myodome and its identification, in my opinion, remains uncertain. In a new Australian placoderm, Young (1979; 1980, p. 40) has found evidence that the efferent pseudobranchial artery joined the internal carotid before the latter entered the braincase, and that the canal presumed by Stensiö to transmit the efferent pseudobranchial probably carried the ophthalmic artery.

On the basis of this recent opinion regarding the course of the efferent pseudobranchial artery in the placoderms, it is reasonable to propose the hypothesis that the course of this artery as described by de Beer for the neoselachians is in reality a synapomorphy for the chondrichthyans.

17. PALATOQUADRATE ATTACHMENTS: Along with the general connective tissue attachments between the neurocranium and the palatoquadrate, there are specific attachment sites or articulations that are usually designated as rostral, ethmoidal, orbital, and postorbital. All are not known to be present in a single chondrichthyan taxon, but except in the batoids, there is always at least one of these connections with the basicranium in addition to the indirect attachment through the hyomandibular.

A rostral attachment has been found only in *Xenacanthus* and in *Hybodus* (J. G. Maisey, personal commun.). This disjunct character distribution suggests a much wider oc-

currence among some Paleozoic selachians and the hybodonts, but at present the systematic significance of this attachment remains obscure.

An ethmoid connection, either in the form of a direct ligamentous attachment as in *Carcharhinus* (Moss, 1972) or as a sliding articulation as in *Chlamydoselachus* (Allis, 1923), is present in *Xenacanthus*, *Tamiobatis*, "*Cladodus*," *Hybodus*, and in neoselachians in which the palatoquadrate reaches the ethmoid region. According to Holmgren (1943, p. 57), the ethmoid attachment cannot always be distinguished from the orbital articulation (as in *Squalus* and *Etmopterus*) as this connection, in his opinion, shifts posteriorly during development in relation to the relative growth of the trabecula. The observations of El-Toubi (1949), however, do not support this opinion. His reconstructions of the developing *Squalus* skull show that the orbital process of the palatoquadrate maintains a constant relationship with the rear of the trabecula from the 39 mm. to the adult stage. Furthermore, *Chlamydoselachus* has both attachments—an ethmoid one that is medial to the nasal capsule and the ectethmoid process, and an orbital attachment that is within the orbit behind the optic foramen.

The orbital articulation is confined to certain groups of neoselachians (hexanchoids, *Chlamydoselachus*, squaloids, *Squatina*, and *Pristiophorus*). It always involves the development of a palatoquadrate orbital process that moves against an articular area on the medial wall of the orbit between the foramina for the optic nerve and the efferent pseudobranchial artery. As Holmgren (1942) and others have pointed out, the position of the attachment varies somewhat within the orbit—far anterior in *Chlamydoselachus*, more posterior in *Squalus*. As this attachment does not occur in the Paleozoic selachians, further consideration is not necessary (see Maisey, 1980), but one additional matter related to it does deserve some attention here. In the hexanchoids and the squaloids there is an elevated area just posterior to the orbital attachment that is usually called the palatobasal process.

During elevation of the palatoquadrate, the orbital process may skirt the palatobasal process, but the main ramus of the palatoquadrate must move over it when the mouth is completely closed. The palatobasal process is sometimes referred to as an articular surface, but it is more frequently asserted that the orbital articulation is not a palatobasal (basitrabecular) one (Holmgren, 1940, 1942, 1943; El-Toubi, 1949; Miles, 1964). These confusing remarks stem from the conviction (see de Beer, 1937, pp. 391–392) that the basitrabecular process is a lateral extension of the polar cartilage area of the basicranium, and that the basitrabecular process of the osteichthyans is represented in the selachians by a part of the suborbital shelf. Holmgren (1942, pp. 138–140) confirmed these observations in *Etmopterus* (see Holmgren, 1940, fig. 87), but claimed that the embryonic basitrabecular process in the squaloids disappears during development in favor of a more anterior orbital articulation. It has been stated repeatedly that the selachians have no basitrabecular process or articulation (El-Toubi, 1949, p. 262; Miles, 1965, p. 238; Jollie, 1971, p. 32), but there is firm evidence that the squaloid palatobasal process, which is at the apex of the basal angle, is formed at the site of the polar cartilage (de Beer, 1931; Jollie, 1971, p. 21). The fact that this articulation is not present in known Paleozoic selachians, in *Hybodus* (J. G. Maisey, personal commun.), or in the galeoids may mean that its development is suppressed for functional reasons, or that it was independently acquired by one or more monophyletic groups within the neoselachians. The evidence is not satisfactory to test either of these hypotheses.

The postorbital articulation requires only brief comment in regard to its distribution. It is present in the Paleozoic selachians, in the acanthodians, primitive actinopterygians, and perhaps in much modified form in the coelacanth and rhipidistians, all of which have it associated with the cleaver-shaped palatoquadrate (Schaeffer, 1975). It is therefore a synapomorphy for the chon-

drichthyans plus the acanthodians and the osteichthyans. The present evidence regarding the placoderm palatoquadrate and its connections does not favor the hypothesis that the placoderm ancestors had a postorbital-palatal articulation. On the other hand, these fishes have a postorbital process which served in part as an anchor for the hyomandibular.

In chimaeroids (de Beer and Moy-Thomas, 1935) the palatoquadrate is fused anteriorly to the ethmoid area below the orbitonasal canal. Posteriorly it is joined to the basicranium below the foramina for the efferent pseudobranchial artery and the oculomotor nerve and somewhat anterior to the openings for the palatine nerve and the orbital artery. The fusion is presumably in the area of the polar cartilage.

The placoderms had an ethmoid-orbital and apparently a suborbital attachment, but no orbital connection of squaloid design. Although the palatoquadrate of most placoderms seems to be quite unlike that of the elasmobranchs, acanthodians, and osteichthyans (see Miles, 1971 and Schaeffer, 1975), this element in the euarthrodire *Buchanosteus* (Young, 1979) has features that suggest the "cleaver" type, including a fossa between it and the dermal cheek for the adductor jaw musculature. Although a reevaluation of the placoderm palatoquadrate is perhaps premature, there is the possibility that the cleaver-shaped primary upper jaw with certain neurocranial attachments and muscle arrangements may be a synapomorphy for the gnathostomes. The so-called basitrabecular process in the euarthrodires *Tapinosteus* and *Pholidosteus* (Stensiö, 1963b) is considered to be homologous with the anterior postorbital process in other euarthrodires (Miles, 1971; Goujet, 1975; Young, 1979, 1980) as it has an articulation for the hyomandibular.

On the basis of this limited outgroup comparison, several hypotheses may be offered regarding the significance of the palatoquadrate attachments: (1) The ethmoid attachment, although variable in detail, may be regarded as a primitive gnathostome character

distinct from the rostral and the orbital attachments. (2) A connective tissue attachment between the suborbital shelf and the dorsal rim of the palatoquadrate is another primitive gnathostome character. An orbital process articulation with the basicranium may be a synapomorphy for one group of neoselachians, but not for all of them. The palatobasal-basitrabecular problem requires further investigation before a meaningful hypothesis regarding its history can be proposed. (3) The postorbital articulation presently appears to be a unique derived character for the chondrichthyans, acanthodians, and actinopterygians. The sarcopterygian condition may be secondary, but this is nearly impossible to corroborate.

18. **HYOMANDIBULAR ARTICULATION:** In neoselachians, regardless of the relative length of the otico-occipital region, the hyomandibular articulates with the braincase below the ridge for the horizontal semicircular canal and just anterior to, or lateral to, the foramen for the glossopharyngeal nerve (see figures in Holmgren, 1941; Jollie, 1971, fig. 9; this paper, fig. 11). This articular position is also present in *Xenacanthus*, probably in *Cladoselache* (CMNH 9280), *Tamiobatis*, *Cobelodus* (Zangerl, 1976, fig. 4), and *Hybodus* (Maisey, personal commun.). One possible and as yet unexplained exception has been figured by Dick (1978) for the Carboniferous selachian *Tristychius*, in which the hyomandibula is shown in contact with the braincase just behind the postorbital process and well in front of the glossopharyngeal foramen.

In marked contrast with the condition in the neoselachians, the chimaeroids have a complete hyoid arch including a separate dorsal element frequently identified as the pharyngohyal. As no other vertebrate group, living or extinct, has a pharyngohyal, and no evidence of its existence has been found during the development of the visceral skeleton, the presence of this element in the chimaeroids might well be regarded as an autapomorphy. The problem is complicated, however, by the close similarity of the chimaeroid hyoid arch to the branchial arches particularly in regard to the presence of a pharyngeal seg-

ment. Accordingly, de Beer and Moy-Thomas (1935) have proposed that the chimaeroid hyoid arch represents a retention of the primitive gnathostome condition (recall that no agnathans have segmented visceral arches). This argument has been favorably discussed by Nelson (1969), Miles (1971), Schaeffer (1975), and Schaeffer and Williams (1977).

Aside from the problem of determining polarity, there is an apparent anatomical difficulty with this hypothesis as first pointed out by Watson (1937, p. 141). As concisely stated by Patterson (1965, p. 103, footnote), it involves the position of the efferent hyoidean artery in relation to the chimaeroid pharyngohyal. In a lateral reconstruction of the head skeleton of a 96 mm. *Callorhynchus* by de Beer and Moy-Thomas (1935) the efferent hyoidean runs medial to the tip of the pharyngohyal, which is anatomically incorrect if this element is in fact a pharyngohyal. However, in a labeled transverse section (*ibid.*, fig. 9) this vessel appears to be lateral to both the pharyngohyal and the adjacent first epibranchial. If these relationships prove to be correct, it means that the course of the efferent hyoidean artery has the same position in respect to its arch as the efferent branchial arteries have to their arches. Even so, the case for the primitiveness of the chimaeroid hyoid arch is otherwise untested, and will probably remain in limbo. But the main purpose of this section is to note the several different positions for the articulation between the hyomandibula with the braincase, and to offer some economical explanation for this situation. In this regard, the chimaeroid hyoid arch is in an anterior position, roughly below the foramen for the hyomandibular nerve (see Jollie's 1962 illustrations of the head skeleton in *Callorhynchus* and *Hydrolagus*), where it presumably has a connective tissue connection with the basicranium.

The placoderm hyomandibula and its relationship to the neurocranium are best known in *Jagorina* (Stensiö, 1963b, 1969). This evidence has been carefully reviewed by Miles (1971, pp. 196–204), along with some information from other placoderms including *Holonema*. In summary, the hyomandibular in

these fishes articulates with the braincase in front of the foramen for the hyomandibular nerve instead of above or more commonly behind this foramen. Goujet (1975) has found this to be the case in *Dicksonosteus* and also Young (1979) in *Buchanosteus*. As Miles has noted, this is a unique situation in fishes (compare Miles, 1975, fig. 112, and Young, 1980, figs. 14, 25 with Goodrich, 1930, fig. 284), and it has led him to conclude that the hyomandibula, and, by implication, its articulation with the braincase, arose independently in the placoderms.

In acanthodians, according to Miles (1973, p. 72 and fig. 15), the hyomandibula articulated with braincase behind the otic condyle (which articulated with the otic process of the palatoquadrate), above the jugular vein, posterior to the lateral commissure, and well anterior to the glossopharyngeal foramen. Jarvik (1977) has challenged this interpretation by concluding that the hyomandibula articulated with the braincase below the head vein. An important point in favor of Miles's interpretation is the orientation of the hyomandibular groove on the medial surface of the palatoquadrate, which directs the head of the hyomandibula above the jugular groove rather than below it. But regardless of whether the articulation was above or below the jugular vein, there is no convincing evidence that it was related to the lateral commissure as in the osteichthyans, or that it was located near the glossopharyngeal foramen as in the elasmobranchs.

In the palaeonisciforms, rhipidistians and coelacanth, the hyomandibula articulates with the posterior border of the lateral commissure. This articulation is dorsal to the head vein in the primitive actinopterygians and about lateral to it in the other osteichthyan groups. The presence of a lateral commissure has not been demonstrated in dipnans (Miles, 1977, pp. 90–94), but it would be necessarily situated in the anterior part of the otic region medial to the hyomandibular facet.

There is thus evidence for three of four different hyomandibular articulation sites in the gnathostome fishes. Aside from some sort of hyomandibular articular "migration,"

which presumably did occur during the rise of the neopterygians, the most economical way to explain this situation is with de Beer's (1937, pp. 411, 423) thesis that the hyomandibular-neurocranial attachment developed independently at least three times. This means that the pharyngohyal, which presumably existed in the earliest gnathostomes on the basis of serial homology (and according to some on the basis of the condition in the chimaeroids), was lost perhaps three times. I can see no way of testing this proposal, but it does provide an explanation, not only for the different articulation locations, but also for the different relationships of the hyomandibula with the head vein and with the hyomandibular branch of the facial nerve in the placoderms, elasmobranchs, osteichthyans, and perhaps the acanthodians. As the neoselachian hyomandibular-neurocranial relationship is different from that in the other major groups of gnathostome fishes, it may be regarded as an elasmobranch synapomorphy.

19. OCCIPITAL ARCH: During the later stages of chondrocranial development in the neoselachians the fused occipital arches become wedged between the posterior parts of the auditory capsules (e.g., de Beer, 1937, pl. 13, fig. 8). As a result, the metotic fissures acquire an oblique orientation similar to that of the otico-occipital fissures in *Xenacanthus*. The relatively forward position of the occipital segment in the neoselachians accounts for the fact that the occipitospinal nerves leave the braincase through the vagal canal or behind the condyles (Norris and Hughes, 1920; fig. 44) rather than separately along the sides of the occipital segment.

In regard to the fossil selachians, it is evident that the occipital segment is partly situated between the capsules in *Xenacanthus* and to a lesser extent in *Tamiodontis*. It is probable, but not yet demonstrable, that a similar condition exists in the other taxa, but there is reason to believe that the degree of overlap between the occiput and the capsules is somewhat variable. Separate occipitospinal nerve foramina have not been found in *Cladoselache*, *Cobelodus*, or "*Cladodus*," but the occipital segment in each pro-

jects beyond the posterior limit of the capsules (figs. 12, 13). The truncated posterior border of the *Danaea* braincase (Schaeffer and Williams, 1977) suggests a situation similar to that of the neoselachians, *Hybodus* probably has at least one pair of occipitospinal nerve foramina even though the occipital segment must be very short (J. G. Maisey, personal commun.). The considerable projection of the occipital segment behind the capsules in *Xenacanthus*, *Tamiodontis*, and *Tristychius* (Dick, 1978) is correlated with several pairs of well spaced occipitospinal nerve foramina.

In chimaeroids (Jollie, 1962, figs. 5–18 and 5–19), placoderms (Stensiö, 1963; Young, 1979), acanthodians (Miles, 1973) and osteichthyans generally I can find no evidence that the occipital segment is ever situated between the otic capsules except for the condition in *Clupea* (de Beer, 1937, p. 132), presumably other clupeoids, and to some extent in the pholidophorids and mormyroids (Patterson, 1975, p. 429). In any case, this character is restricted within the actinopterygians, and is unrelated to the condition in sharks. It is of interest that the occipitospinal nerves in *Latimeria* are entirely behind the

neurocranium (Millot and Anthony, 1965, fig. 34).

The evidence cited above is consistent with the hypothesis that the position of the occipital arch between the auditory capsules is a synapomorphy shared by *Xenacanthus*, *Tamiodontis*, presumably the other extinct selachian taxa mentioned above including *Hybodus*, and the neoselachians. The strong projection of the occipital segment behind the auditory capsules in *Xenacanthus* and *Tamiodontis*, perhaps to provide an expanded attachment area for the epaxial muscles, is proposed as a derived condition that relates these taxa.

20. OTICO-OCCIPITAL PROPORTIONS: For reasons possibly related to neoteny, the otico-occipital region in *Xenacanthus*, *Tamiodontis* and “*Cladodus*” is equal to or longer than the ethmo-orbital. As discussed on page 45, this condition is unknown in other Paleozoic or later selachians, and may therefore be regarded a unique derived character for these taxa. It also involves a corresponding increase in the size of the semicircular canals and an obvious projection of the occipital segment behind the lateral otic processes with separate external foramina for most or all the occipitospinal nerves.

NEUROCRANIAL CHARACTERS AND LEVELS OF MONOPHYLY

A principal purpose of the preceding character analysis is to provide a base for testing the hypothesis that *Xenacanthus*, as well as *Tamiodontis*, *Cladodus*, and certain other Paleozoic taxa are elasmobranchs rather than representatives of an unresolved paraphyletic condition within the Chondrichthyes. In other words, can we ascertain which, if any, neurocranial characters point to a common ancestry for these taxa *plus* the hybodonts and neoselachians that are not shared with the holocephalans?

As noted in the analysis section, and as shown in the cladograms (fig. 26), certain of the selected characters may actually be syn-

apomorphic for higher monophyletic groups that include the Elasmobranchii. The rostrum (4) in its various manifestations is proposed as a ganthostome synapomorphy along with the postorbital process traversed by the jugular canal (8). The degree of chondrocranial fusion (2) remains ambiguous as does the development of the nasal capsule floor (3). The postorbital articulation with the otic process of the palatoquadrate (17c) is present in the primitive chondrichthyans, osteichthyans, and acanthodians, but presumably not in the placoderms.

Although the presence of prismatic calcified cartilage (1) is consistent with the hy-

pothesis that the elasmobranchs and holocephalans are sister groups (Schaeffer and Williams, 1977), the meaning of the multiple prismatic layers (1b) in the neurocranium and visceral skeleton of *Xenacanthus* and in the braincase of *Tamiodontis* remains enigmatic. Other characters indicating a sister relationship (or the monophyly of the Chondrichthyes) are the precerebral fontanelle (5) and the course of the efferent pseudobranchial artery (16). The utricular recess (10), which occurs in both groups, may also be present in placoderms and some actinopterygians so its significance is ambiguous. There are few holocephalan neurocranial characters not shared with the elasmobranchs that might be regarded as primitive chondrichthyan or gnathostome characters. One of these is the crus between the anterior and posterior canals, which also occurs in *Acanthodes*, osteichthyan and tetrapods (see character 11a), but not in the elasmobranchs, which have 11b.

The neurocranial characters that are regarded as synapomorphic for the Elasmobranchii, including the Paleozoic taxa cited above, are: the semicircular canal relationships (11b), the presence of an endolymphatic fossa (12), the hypotic lamina and the formation of the glossopharyngeal canal (13), and the location of the hyomandibular articulation on the neurocranium (18). In regard to characters (11) and (12) it is important to recall that both are related developmentally to the separate, circular posterior semicircular canal. The optic pedicle (7), which is present in neoselachians and absent in holocephalans, may occur in some arthrodires. Its distribution is presently ambiguous. The articulation between the rostrum and the palatoquadrate (17a), known only in *Xenacanthus* and *Hybodus*, is also ambiguous. In summary, the present of characters (11b), (12), (13), and (18) is consistent with the hypothesis that *Xenacanthus*, *Tamiodontis*, "*Cladodus*," *Cladoselache*, *Cobelodus*, *Tristychius*, and the Cleveland "*Ctenacanthus*" are elasmobranchs along with *Hybodus* and the neoselachians.

Within the Elasmobranchii, as just defined, *Xenacanthus*, *Tamiodontis* and probably "*Cladodus*" have broad lateral otic pro-

cesses (14b), an otico-occipital fissure (2b), and a posteriorly projecting occipital segment (19a). The *Tamiodontis*-like neurocranium (CMNH 9280) is associated with cladodont teeth. The Cleveland "*Ctenacanthus*" braincase (CMNH 6219), which is also associated with cladodont teeth and a ctenacanth dorsal spine, has similarly enlarged lateral otic processes, and may have an otico-occipital fissure, but the otic region is shorter, with about the same relative proportions as that of *Cladoselache*. The neurocrania of *Xenacanthus* and *Tamiodontis* can be readily separated by the shape of the lateral otic processes and by several characters associated with the otico-occipital fissure, as discussed above. Although "*Cladodus*" is related to *Xenacanthus* and *Tamiodontis*, it is distinctive in having shallow lateral otic fossae and in having a relatively short endolymphatic fossa. Unfortunately, the significant portion of the occipital segment remains unknown.

Considered together, this evidence favors a sister relationship between *Xenacanthus* and *Tamiodontis*, with "*Cladodus*" as the closest known relative of these two. These taxa, in turn, seem to represent a sister group to the Cleveland "*Ctenacanthus*." There may also be a restricted relationship between the phalacanthus forms listed by Zangerl (1973) and the taxa discussed above with broad otic processes. In contrast, the anacanthous forms also listed by Zangerl (excluding *Cladoselache*, which is phalacanthous) have no or only weakly developed lateral otic processes, a relatively short otico-occipital region and an occipital segment that is between rather than partly behind the auditory capsules. Unfortunately, the braincases of the anacanthous forms described to date are poorly preserved and characters (11), (12), (13), and (18) are not discernible. *Cladoselache* apparently has an endolymphatic fossa (CMNH 9208). It agrees with the anacanthous forms in having weak lateral otic processes, a short otic region and an occipital segment situated entirely between the auditory capsules. But *Cladoselache* (*sensu lato*) also has dorsal fin spines that may be primitive in their histology and insertion (Maisey, 1977) for elasmobranchs and pos-

sibly for holocephalans. Although the systematic position of this taxon is still problematical, it could represent the most plesiomorphic of the Paleozoic elasmobranchs. In this case the short otic region, weak lateral otic processes, and non-protruding occipital moiety would represent primitive elasmobranch characters, as discussed on page 46. As the data base derived from fossil neurocrania is obviously limited, it will be necessary to follow up on these hypotheses of relationship by further consideration of the visceral and postcranial skeletons.

Of the remaining three characters included in the analysis, the ectethmoid process (6) is known only in *Hybodus* and some groups of neoselachians. It is not considered to be homologous with a process so named in certain placoderms. The basal angle (9) is absent in mature placoderms, and among adult elasmobranchs it persists only in hexanchoids and squaloids. The cephalic circle (15) is a neoselachian synapomorphy.

The cladogram presented in figure 26B differs in several respects from the one proposed by Schaeffer and Williams (1977, fig. 2). Reasons for the changed position of *Cladoseleache* include the braincase characters noted above and the recently confirmed absence of a posterior dorsal fin spine (compare Schaeffer and Williams, 1977, p. 297). In regard to the possible inclusion of the Cleveland ctenacanth in the same group as *Xenacanthus*, this is presently justified on the basis of neurocranial characters (including the multilayered prismatic condition) and on unpublished evidence which indicates that the cephalic spine in primitive xenacanth was either absent or transposed from the anterior border of the dorsal fin. There is also evidence that the primitive xenacanth pectoral fin was tribasal, as appears to be the case in most of the phalacanthous elasmobranchs. The distribution of the tribasal condition is indicated in figure 26B by an asterisk.

LITERATURE CITED

- Agassiz, Louis
1837. Recherches sur les poissons fossiles, vol. 2, VIII + 390 pp.
- Allis, E. P.
1914. The pituitary fossa and trigemino-facialis chamber in selachians. *Anat. Anz.*, vol. 46, pp. 225-253.
1923. The cranial anatomy of *Chlamydoselachus anguineus*. *Acta Zool.*, vol. 4, pp. 123-221.
- Anthony, Jean, and D. Ronineau
1967. Le cercle céphalique de *Latimeria* (Poisson coelacanthidé). *Compt. Rendu Acad. Sci. Paris*, ser. D, vol. 265, pp. 343-346.
- Bargmann, W.
1939. Zur Kenntnis der Knorpel-architekturen (Untersuchungen am Skeletsystem von Selachiern). *Zeitschr. Zellforsch. Mikroskop.* *Anat. Abt. A*, vol. 29, pp. 405-424.
- DeBeer, G. R.
1931. The development of the skull of *Scyliorhinus* (*Scyliorhinus*) *canicula* L. *Quatt. Jour. Micro. Sci.*, new ser., vol. 74, pp. 591-652.
1937. The development of the vertebrate skull. Oxford, Clarendon Press, XXIV + 552 pp.
- De Beer, G. R., and J. A. Moy-Thomas
1935. On the skull of holocephali. *Phil. Trans. Roy. Soc. London*, ser. B, vol. 224, pp. 287-312.
- Benzer, Paul
1944. Morphology of calcification in *Squalus acanthias*. *Copeia*, no. 4, pp. 217-224.
- Berman, David S.
1970. Vertebrate fossils from the Lueders Formation, Lower Permian of north-central Texas. *Univ. Calif. Publ. Geol. Sci.*, vol. 86, pp. 1-39.
- Bertin, Leon
1958. Appareil circulatoire [super-classe des poissons]. In Grassé, Pierre P. (ed.), *Traité de zoologie*. Paris, Masson et Cie, vol. 13, fasc. 2, pp. 1399-1458.
- Bertmar, Gunnar
1959. On the ontogeny of the chondral skull

- in Characidae, with a discussion on the chondrocranial base and the visceral chondrocranium in fishes. *Acta Zool.*, vol. 40, pp. 203–364.
1962. On the ontogeny and evolution of the arterial vascular system in the head of the African characidean fish *Hepsetus odoë*. *Ibid.*, vol. 43, pp. 255–295.
1963. The trigemino-facialis chamber, the cavum epiptericum and the cavum orbitonasale, three serially homologous extracranial spaces in fishes. *Ibid.*, vol. 44, pp. 329–344.
1966. The development of skeleton, bloodvessels and nerves in the dipnoan snout, with a discussion on the homology of the dipnoan posterior nostrils. *Ibid.*, vol. 47, pp. 81–150.
- Beyrih, E.
1848. Ueber *Xenacanthus decheni* und *Holacanthus gracilis*, zwei Fische aus der Formation des Rothliegenden in Nord-Deutschland. Bericht Verhandl. K. Preuss. Akad. Wissensch. Berlin, pp. 24–33.
- Broili, F.
1904. Ueber *Diacranodus texensis* Cope (= *Didymodus* ? compressus Cope). Neues Jahrb. für Min. Geol. und Palaeont., vol. 19, pp. 467–484.
- Chibon, P.
1967. Marquage nucléaire par la thymidine tritiée des dérivés de la crête neurale chez l'Amphibien *Pleurodeles waltlii* Michah. XX. Jour. Embryol. exp. Morph., vol. 18, pp. 343–358.
1974. Un système morphogénétique remarquable; la crête neurale des vertébrés. Ann. Biol., vol. 13, pp. 459–480.
- Compagno, Leonard J.
1973. Interrelationships of living elasmobranchs. In: Greenwood, P. H., R. S. Miles and C. Patterson (eds.), Interrelationships of fishes. Zool. Jour. Linnean Soc., vol. 53 (suppl. 1). London, Academic Press, pp. 15–61.
- [MS] Carcharinoid sharks: morphology, systematics, and phylogeny. Ph.D. dissertation, Stanford Univ., 1979, Univ. Microfilms Internat., no. 7917217, 932 pp.
- Cope, E. D.
1883. On some *Vertebrata* from the Permian of Illinois. Proc. Acad. Nat. Sci. Philadelphia, 1883, pp. 108–110.
1884. On the structure of the skull in the elasmobranch genus *Didymodus*. Proc. Amer. Phil. Soc., vol. 21, pp. 572–590.
1888. Systematic catalogue of the species of *Vertebrata* found in the beds of the Permian epoch in North America, with notes and descriptions. Trans. Amer. Phil. Soc., vol. 16, pp. 285–297.
- Corrington, Julian D.
1930. Morphology of the anterior arteries of sharks. *Acta Zool.*, vol. 11, pp. 185–261.
- Denison, Robert
1978. Placodermi. In: Schultze, H.-P. (ed.), Handbook of Paleichthyology. Stuttgart and New York, Gustav Fischer Verlag, vol. 2, 128 pp.
- Dick, John R. R.
1978. On the carboniferous shark *Tristychius arcuatus* Agassiz from Scotland. Trans. Roy. Soc. Edinburgh, vol. 70, pp. 63–109.
- Eastman, C. R.
1897. *Tamiobatis vetustus*: a new form of fossil skate. Amer. Jour. Sci., 4th ser., vol. 4, pp. 85–90.
- Egerton, P. G.
1857. On the unity of the genera *Pleuracanthus*, *Diplodus*, and *Xenacanthus*, and on the specific distinction of the Permian fossil *Xenacanthus decheni* (Beyrich.). Ann. Mag. Nat. Hist., ser. 2, vol. 20, pp. 423–424.
- El-Toubi, M. R.
1949. The development of the chondrocranium of the spiny dogfish, *Acanthias vulgaris* (*Squalus acanthias*). Part I. Neurocranium, mandibular and hyoid arches. Jour. Morph., vol. 84, pp. 227–279.
- Fritsch, A.
1895. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens, Sitzungsber. K. böhmischen Gesell. Wissensch., vol. III, pp. 1–132.
- Garman, Samuel
1884. An extraordinary shark. Bull. Essex Inst., vol. 16, pp. 47–52.
1885. *Chlamydoselachus anguineus* Garm., a living species of Cladodont shark. Bull. Mus. Comp. Zool., vol. 12, pp. 1–35.
1913. The Plagiostomia (sharks, skates and rays). Mem. Mus. Comp. Zool., vol. 36, pp. 1–528.
- Goodrich, E. S.
1909. *Vertebrata craniata* (First fasc: cyclo-

- stomes and fishes). A treatise on zoology (R. Lankester, ed.), London, A. and C. Black, xvi + 518 pp.
1930. Studies on the structure and development of vertebrates. London, Mac-Millan and Co. Ltd., 837 pp.
- Goujet, D.
1975. *Dicksonosteus*, un nouvel Arthrodire du Devonien du Spitsberg, remarques sur le séquelette viscéral Dolichothoraci. Colloq. Internat. C.N.R.S., no. 218, pp. 81–99.
- Gross, W.
1937. Das Kopfskelett von *Cladodus wildungensis* Jaekel. I. Teil. Endocranium und Palatoquadratum. Senckenbergiana, vol. 19, pp. 80–107.
1938. Das Kopfskelett von *Cladodus wildungensis* Jaekel, 2. Teil: Der Kieferbogen. *Ibid.*, vol. 20, pp. 123–145.
- Hagelin, L. O.
1974. Development of the membraneous labyrinth in lampreys. Acta Zool., suppl. 1974, pp. 1–215.
- Harrison, Bruce M.
1931. Developmental stages of the chondrocranium in some selachians. Jour. Morph., vol. 52, pp. 565–592.
- Holmgren, Nils
1940. Studies on the head in fishes. Pt. 1. Development of the skull in sharks and rays. Acta Zool., vol. 21, pp. 51–267.
1941. Studies on the head of fishes. Pt. 2: Comparative anatomy of the adult selachian skull, with remarks on the dorsal fins in the sharks. *Ibid.*, vol. 22, pp. 1–100.
1942. Studies on the head in fishes. Pt. 3: The phylogeny of Elasmobranch fishes. *Ibid.*, vol. 23, pp. 129–262.
1943. Studies on the head in fishes. Pt. 4: General morphology of the head in fish. *Ibid.*, vol. 24, pp. 1–188.
- Hotton, Nicholas
1952. Jaws and teeth of American xenacanth sharks. Jour. Paleont., vol. 26, pp. 489–500.
- Jaekel, O.
1906. Neue Rekonstruktionen von *Pleuranthus sessilis* und von *Polyacrodus* (*Hyobodus*) *Hauffianus*. Sitzber. Ber. Naturt. Fr. Berlin, pp. 155–159.
- Jarvik, Erik
1942. On the structure of the snout of crossopterygians and lower gnathostomes in general. Zool. Bidrag Uppsala, vol. 21, pp. 235–675.
1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid and palatoquadrate in fishes. Kungl. Svenska. Vetenskapsakad. Handl., vol. 5, pp. 1–104.
1977. The systematic position of acanthodian fishes. In Andrews, S. M. and others (eds.), Problems in vertebrate evolution. London, Academic Press, pp. 199–225.
- Jollie, Malcolm
1962. Chordate morphology. New York, Reinhold Publ. Co., 478 pp.
1971. Some developmental aspects of the head skeleton of the 35–37 *Squalus acanthias* foetus. Jour. Morph., vol. 133, pp. 17–40.
- Jordan, D. S.
1923. A classification of fishes including families and genera as far as known. Stanford Univ. Publ., Univ. ser., Biol. Sci., vol. 3, no. 2, pp. 79–243 + X.
- Kemp, Norman E., and Sandra K. Westrin
1979. Ultrastructure of calcified cartilage in the endoskeletal tesserae of sharks. Jour. Morph., vol. 160, pp. 75–87.
- Le Lièvre, Christiane S.
1978. Participation of neural crest-derived cells in the genesis of the skull in birds. Jour. Embryol. Exp. Morph., vol. 47, pp. 17–37.
- Lund, Richard
1969. Fossil fishes from southwestern Pennsylvania. Pt. 1: Fishes from the Duquesne limestones (Conemaugh, Pennsylvania). Ann. Carnegie Museum, vol. 41, pp. 231–261.
- Maisey, John G.
1975. The interrelationships of phalacanthous selachians. Neues Jahrb. Geol. Paläont., pt. 9, 1975, pp. 553–567.
1977. Structural notes on a cladoselachian dorsal spine. *Ibid.*, pt. 1, 1977, pp. 47–55.
1980. An evaluation of jaw suspension in sharks. Amer. Mus. Novitates, no. 2706, pp. 1–17.
- Marinelli, W., and A. Strenger
1959. Vergleichende Anatomie und Morphologie der Wirbeltiere. III. Lieferung, pt. 2, *Squalus acanthias*. Wien, Franz Deuticke, pp. 179–308.

Meurling, Patrick

1967. The vascularization of the pituitary in elasmobranchs. *Sarsia*, no. 28, pp. 1–104.

Miles, Roger S.

1964. A reinterpretation of the visceral skeleton of *Acanthodes*. *Nature*, no. 4957, pp. 457–459.
1965. Some features in the cranial morphology of acanthodians and the relationships of the Acanthodii. *Acta Zool.*, vol. 46, pp. 233–255.
1971. The Holonematidae (placoderm fishes), a review based on new specimens of *Holonema* from the Upper Devonian of western Australia. *Phil. Trans. Roy. Soc. London*, vol. 263, pp. 101–234.
1973. Relationships of acanthodians. In Greenwood, P. H., and others (eds.), *Interrelationships of fishes*. London and New York, Academic Press, pp. 63–103.
1977. Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *Zool. Jour. Linnean Soc.*, vol. 61, pp. 1–328.

Miles, Roger S., and G. C. Young

1977. Placoderm interrelationships reconsidered in the light of new ptyctodontids from Gogo, Western Australia. In Andrews, S. M., and others (eds.), *Problems in Vertebrate Evolution*. London, Academic Press, pp. 123–198.

Millot, J., et J. Anthony

1965. Anatomie de *Latimeria chalumnae*. II. Système nerveux et organes des sens. Paris, C.N.R.S., 131 pp.

Moss, Sanford A.

1972. The feeding mechanism of sharks of the family Carcharhinidae. *Jour. Zool. London*, vol. 167, pp. 423–436.

Moy-Thomas, J. A.

1939. The Early Evolution and Relationships of the Elasmobranchs. *Biol. Rev.*, vol. 14, pp. 1–26.

Moy-Thomas, J. A., and R. S. Miles

1971. *Palaeozoic fishes*, 2nd ed., Philadelphia and Toronto, W. B. Saunders Co., xi + 259 pp.

Nelson, Gareth, J.

1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bull. Amer. Mus. Nat. Hist.*, vol. 141, pp. 475–552.

Newberry, J. S.

1856. Description of several new genera and species of fossil fishes from the Carboniferous strata of Ohio. *Proc. Acad. Nat. Sci. Philadelphia*, vol. 8, pp. 96–100.

Nielsen, Eigil

1942. Studies on Triassic Fishes from East Greenland. 1. *Glaucolepis* and *Boreosomus*. *Medd. Grønland*, vol. 138, pp. 1–403.

Norris, H. W.

1929. The parietal fossa and related structures in the plagiostome fishes. *Jour. Morph.*, vol. 48, pp. 543–561.

Norris, H. W., and Sally P. Hughes

1920. The cranial, occipital and anterior spinal nerves of the dogfish, *Squalus acanthias*. *Jour. Comp. Neurol.*, vol. 31, pp. 293–402.

Northcutt, R. Glenn

1978. Brain organization in the cartilaginous fishes. In Hodgson, E. S., and R. F. Mathewson (eds.), *Sensory biology of sharks, skates and rays*. Arlington, Virginia, Office of Naval Research, Department of the Navy, XI + 666 pp.

Obruchev, D. V.

1967. Agnatha, Pisces. In Orlov, Y. A. (ed.), *Fundamentals of Paleontology*, vol. XI. Jerusalem, Israel, S. Monson. (Translated from the Russian). x + 825 pp.

Ørvig, Tor

1975. Description, with special reference to the dermal skeleton, of a new radotinid arthrodire from the Gedinian of Arctic Canada. *Colloq. Internatl. C.N.R.S.*, no. 218, pp. 41–71.

Olson, Everett C.

1965. New Permian vertebrates from the Chickasha formation Oklahoma. *Oklahoma Geol. Surv., Cir. 70*, Norman, Univ. Oklahoma, pp. 1–70.

Parker, W. K.

1879. On the structure and development of the skull in sharks and rays. *Trans. Zool. Soc. London*, vol. 10, pp. 189–234.

Patterson, Colin

1965. Phylogeny of the chimaeroids. *Phil. Trans. Roy. Soc. London*, vol. 249, pp. 101–219.

Poplin, Cecile

1975. Remarques sur le système artériel épi-branchial chez les actinopérygiens primitifs fossiles. *Colloq. Internatl. C.N.R.S.*, no. 218, pp. 265–271.

- Reis, O. M.
1897. Das Skelett der Pleuracanthiden und ihre systematischen Beziehungen. Abhandl. Senckenb. Naturforsch. Gesellsch., vol. 20, pp. 57–155.
- Retzius, Gustaf
1881. Das Gehörorgan der Wirbelthiere. 1. Das Gehörorgan der Fische und Amphibien, Stockholm: Sampson and Wallin, 222 pp.
- Romer, Alfred Sherwood
1964. The braincase of the Paleozoic elasmobranch *Tamiodontis*. Bull. Museum Comp. Zool., vol. 131, no. 4, pp. 89–106, 3 figs., 1 pl.
1966. Vertebrate Paleontology. Chicago, Univ. Chicago Press, 3rd ed., 468 pp.
- Schaeffer, Bobb
1967. Comments on elasmobranch evolution. In P. W. Gilbert, F. R. Mathewson, and D. P. Rall (eds.), Sharks, skates and rays. Baltimore, Maryland, Johns Hopkins Press, pp. 3–35.
1975. Comments on the origin and basic radiation of the gnathostome fishes with particular reference to the feeding mechanism. Colloq. Internatl. C.R.N.S., no. 218, pp. 101–109.
- Schaeffer, Bobb, and Michael Williams
1977. Relationships of fossil and living elasmobranchs. Amer. Zool., no. 17, pp. 293–302.
- Stahl, Barbara J.
1967. Morphology and relationships of the Holocephali with special reference to the venous system. Bull. Mus. Comp. Zool., vol. 135, pp. 141–213.
- Stensiö, Erik A.
1937. Notes on the endocranium of a Devonian *Cladodus*. Bull. Geol. Inst. Uppsala, vol. 27, pp. 128–144.
1950. La cavité labyrinthique, l'ossification sclérotique et l'orbite de *Jagorina*. In Paleontologie et transformisme. Sciences d'aujourd'hui. Coll. dir. André George. Paris, Albin Michél, pp. 9–43.
1963a. The brain and the cranial nerves in fossil, lower craniate vertebrates. Skrifter Norske Vidensk. Akad. Oslo, 1. Mat.-Naturv. Kl. Ny Ser., no. 13, pp. 1–120.
1963b. Anatomical studies on the arthrodiran head. Pt. 1. Preface, geological and geographical distribution, the organization of the arthrodirans, the anatomy of the head in the Dolichothoraci, Coccosteomorphi and Pachyosteomorphi. Taxonomic appendix. Kungl. Svensk Vetenskapsakademiens Handl. Fjärde Ser., vol. 9, pp. 1–419.
- Watson, D. M. S.
1937. The Acanthodian Fishes. Phil. Trans. Roy. Soc. London, ser. B, vol. 228, no. 549, pp. 49–146.
- Williams, Michael E.
[MS] The “cladodont level” sharks of the Pennsylvanian black shales of Central North America. Ph.D. dissertation, Univ. Kansas, 1979. Univ. Microfilms Internatl., no. 7925849, 203 pp.
- Woodward, A. S.
1889. Catalogue of the fossil fishes in the British Museum (Natural History), Pt. 1, The Elasmobranchii. British Museum (Nat. Hist.), London, 474 pp.
- Young, G. C.
1979. New information on the structure and relationships of *Buchanosteus* (Placodermi: Euarthrodira) from the Early Devonian of New South Wales. Zool. Jour. Linnean Soc., vol. 66, pp. 309–352.
1980. A new early Devonian placoderm from New South Wales, Australia, with a discussion of placoderm phylogeny. Palaeontographica, vol. 167, pp. 10–76.
- Zangerl, Rainer
1973. Interrelationships of early chondrichthyans. In Greenwood, P. H., and others (eds.), Interrelationships of fishes, London and New York, Academic Press, pp. 1–14.
- Zangerl, Rainer, and Gerard R. Case
1976. *Cobelodus aculeatus*, an Anacanthous shark from Pennsylvanian black shales of North America. Abt. A, vol. 154, pp. 107–157.
- Zidek, Jiri
1978. New chondrichthyan spines from the late Paleozoic of Oklahoma. Jour. Paleont., vol. 52, pp. 1070–1078.

