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A Palaeonisciform Braincase from the Permian of Texas, With Comments on Cranial Fissures and the Posterior Myodome

BOBB SCHAEFFER¹ AND WALTER W. DALQUEST²

ABSTRACT

A single, large palaeonisciform braincase from the Lower Permian Lueders Formation, Baylor County, Texas, is described as a new genus and species within the Palaeonisciformes, *incertae sedis*.

This specimen has also occasioned a review of the actinopterygian cranial fissures and the posterior myodome.

INTRODUCTION

The completely ossified, sutureless braincase characteristic of most paleopterygians (the Chondrostei of most classifications) and of a few neopterygians has been described in varying detail in about 15 genera. Although this braincase type is generally regarded as primitive for the Actinopterygii, there are frequently differences in general proportions and in the development of certain characters such as the basiptyergoid process, the fossa bridgei, the posterior myodome, the ventral otic and otico-occipital fissures and the vestibular fontanelle that give the braincase of a particular taxon a distinctive appearance.

In 1973 Ted Emsoff, a student at Midwestern University, discovered a large (150 mm. long), massively ossified neurocranium, apparently palaeoniscoid, and an associated median rostral element, in the Lower Permian Lueders Formation near the Lake Kemp Dam in Baylor County, Texas. This unique specimen

was presented by Emsoff and Walter Dalquest to the American Museum of Natural History. Preparation of the braincase, by Walter Sorensen, proved difficult and tedious. Various techniques were used to expose the specimen, which is complete and little damaged except for dorsoventral compression that has caved in the fossa bridgei and produced an up-warping of the ethmoid region. As acid preparation proved to be inadvisable, the braincase was cut midsagittally to reveal some of the internal structures.

In addition to describing the braincase and associated rostral bone (fig. 1), we have briefly discussed two problems involving the paleopterygian neurocranium that have recently received considerable attention. One relates to the position and significance of the ventral otic fissure and the other to the origin and history of the posterior myodome. The systematic position of the Lueders palaeoniscoid remains obscure,

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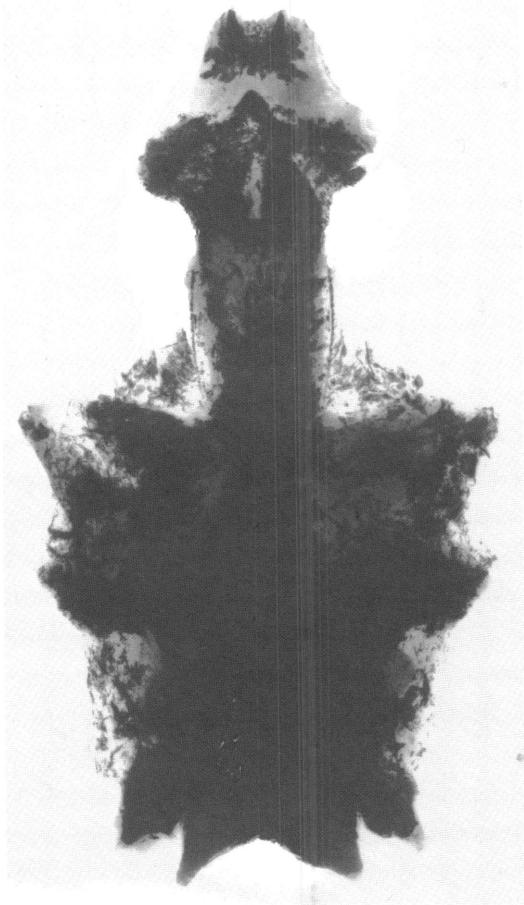


FIG. 1. *Luederia kempii*, new genus and species, AMNH 8998. Radiogram of neurocranium and associated rostral element in dorsal aspect prior to preparation. $\times 1$.

but on the basis of present evidence it has several unique derived characters in both the braincase and the rostral element that justify formal taxonomic treatment.

ABBREVIATIONS

ANATOMICAL

aort, aortic canal
aps, foramen for pseudobranchial artery
art ifbr, articular facet for 1st infrapharyngobranchial
art pq, articular facet for autopalatine

art sfbr, articular facet for 1st suprapharyngobranchial

asp, ascending process of parasphenoid

bhc, bucco-hypophysial canal

bls, bony lamina overhanging saccular recess

bocc, basioccipital ossification

bpt, basipterygoid process

bsph, basisphenoid ossification

cro, occipital crest (ridge)

crsp, cranio-spinal process

eff art, opening for efferent branchial arteries

erm, external rectus muscle

fhym, hyomandibular facet

fm, foramen magnum

font, dorsal fontanelle (covered by dermal bone)

fontv, vestibular fontanelle

fos, otico-sphenoid fissure

foto, otico-occipital fissure

foto, ventral otic fissure

goa, groove for orbital artery

hv, head vein

ic, foramen for internal carotid artery

ifv, inferior orbital vein

ios, interorbital septum

juc, jugular canal and groove

not, notochordal canal or pit

?np, ?nasal pit

occa, foramen for occipital artery

opa, ophthalmic artery groove

ora, foramen for orbital artery

pas, parasphenoid

pf, pituitary fossa

pmy, posterior myodome

prb, prootic bridge

popr, postorbital process

?ptr, ?postrostral

pv, pituitary vein

sef, sub-epiotic fossa

spic, opening for spiracular canal

sv, sacculus vasculosis

utr, utricular recess

I, canal for olfactory nerve

II, foramen for optic nerve

III, foramen for oculomotor nerve

IV, foramen for trochlear nerve

V and VII op sup, fossa with foramina for superficial ophthalmic nerves

VII hym, foramen for hyomandibular branch of facial nerve

IX, foramen for glossopharyngeal nerve

X, foramen for vagus nerve

INSTITUTION

AMNH, the American Museum of Natural History

ACKNOWLEDGMENTS

We are indebted to Dr. Cécile Poplin and Dr. Colin Patterson for helpful comments provided during the preparation of the present paper. The drawings were made by Ms. Lorraine Meeker and the photographs were taken by Mr. Chester S. Tarka.

DESCRIPTION

In its general topography and proportions, including the relative size of the basipterygoid processes and the size of the ascending processes of the parasphenoid, the Lueders braincase (figs. 2-7) resembles the neurocranium of *Pteronisculus* (*Glaucolepis*) as described and figured by Nielsen (1942), Lehman (1952), Beltan (1968), and Patterson (1975, p. 461). It differs from the *Pteronisculus* neurocranium in the complete ossification of the interorbital septum, in the near absence of a vestibular fontanelle, in the partial closure of the lateral otic fissure, and in the relations of the ventral otic fissure to certain neighboring structures and foramina (see p. 5).

The dorsal surface of the neurocranium is covered with thick, rugose or tuberculated dermal bones. Sutures are not visible in spite of careful cleaning, and it is possible that some of the dermal elements are co-ossified. The separate rostral bone is finely tuberculated and there is evidence of similar ornamentation above the orbits. A dorsal fontanelle in the neurocranium is indicated by an additional depression in the dermal roof between and behind the orbits (for comparison see Nielsen, 1942, fig. 21). The anterodorsal surface of the ethmoid area is partly exposed but the paired depressions identified by Nielsen (1942, fig. 7) as nasal pits (fossae) are not evident.

The ethmoid articular processes for the autopalatines are unusually well developed for a paleopterygian. Grooves situated anterior and dorsal to these processes presumably housed the maxillary branch of the trigeminal nerve and related structures (Nielsen, 1942, fig. 6). On the ventral surface of the ethmoid region paired grooves separated by an elevation of the nasal septum may have carried the palatine

branch of the facial nerve and associated blood vessels. The interorbital septum is complete from the ethmoid area to the basisphenoid pillar and the posterior orbital wall. The canal for the olfactory nerves thus passes through the entire length of the septum. The post-mortem compression has obscured and distorted much of the detail on the posterior face of the ethmoid and in the orbitotemporal region including the posterior wall of the orbit. There is no sure evidence of anterior myodomes or of canals for the ethmoid ramifications of the trigeminal and facial nerves, as identified by Nielsen (1942, fig. 65) in *Boreosomus* and by Poplin (1974, figs. 18, 19) in *Kansasiella*.

The basipterygoid process is relatively long and deep as in *Pteronisculus*, and has both dermal and endochondral components. The foramen for the efferent pseudobranchial artery is situated on the anterior face of the process laterally to the groove for the ophthalmic artery. As the interorbital septum is completely united to the basisphenoid pillar, the optic foramen (which is vaguely evident) is divided where it exits from the braincase. It is obvious from the midsagittal section that the posterior myodome is unpaired; its opening into the orbit is also well defined. The position of the jugular canal can be accurately located but the details of the trigeminofacialis chamber are obscure. A depression in the postorbital wall, dorsal and somewhat medial to the trigeminofacialis chamber, presumably includes the foramina for the superior ophthalmic and trochlear nerves. In a photograph of the postorbital wall in *Pteronisculus magnus* (Nielsen, 1942, pl. 6, fig. 2) there is an unidentified depression just behind the trochlear foramen that resembles the one in the Lueders braincase.

The anterior part of the optic region is dominated by the broad and high ascending process of the parasphenoid, which extends upward to the ventral exit of the spiracular canal. The last typically opens into the anterior part of the fossa bridgei, in this specimen almost eliminated by the post-mortem compression. The articular facet of the hyomandibular has a nearly vertical orientation, indicating that the suspensorium was oblique as in many other palaeo-

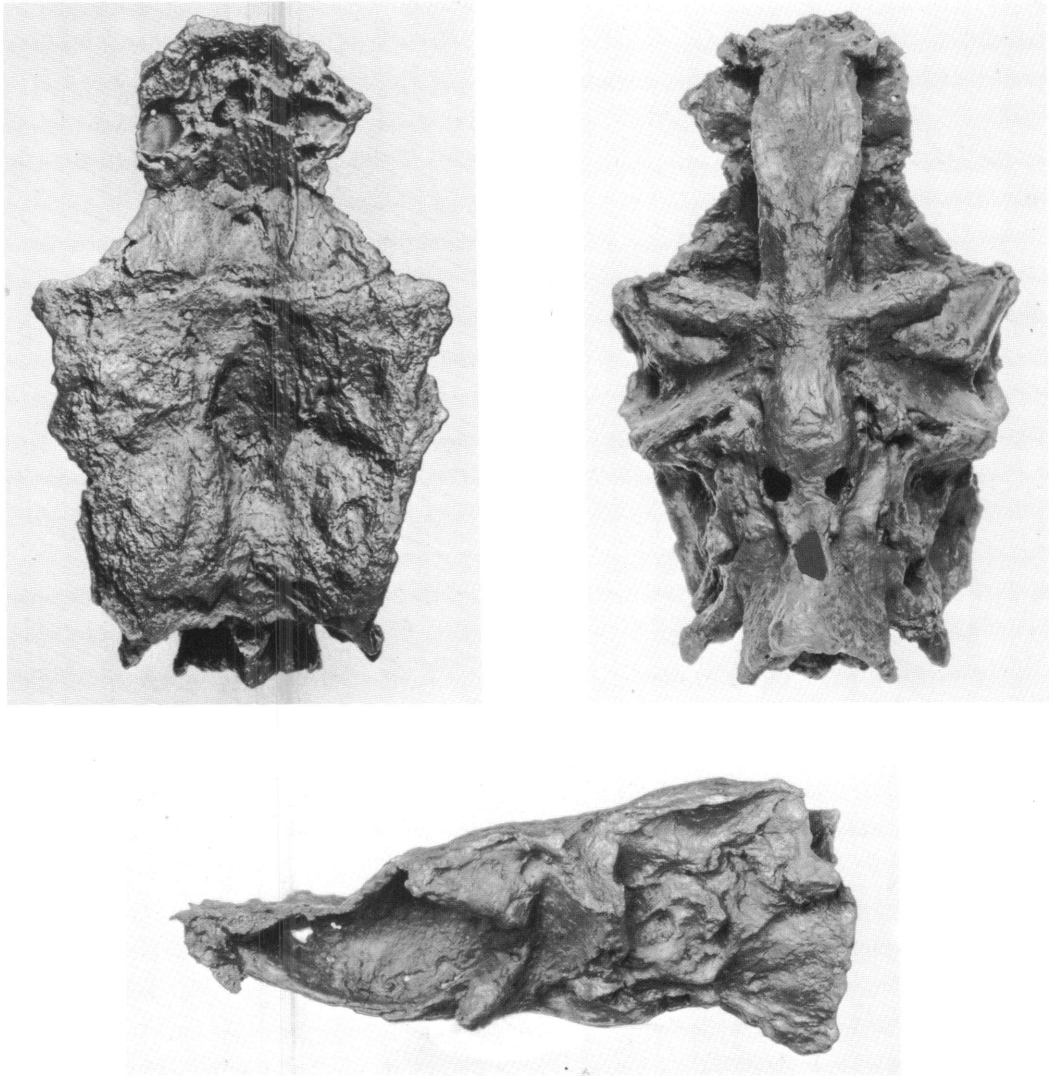


FIG. 2. *Luederia kemp*, new genus and species, AMNH 8998. Neurocranium in dorsal, ventral, and lateral views. $\times 1.25$.

niscoids. The posterior opening of the jugular canal and the jugular groove behind the lower part of the hyomandibular facet are also typically situated. Midway along the posterior border of the ascending process there is a foramen that presumably served as the entrance to the elongated orbital artery, which occupied the well-defined groove bordering the medial side

of the articular protuberance for the first infrapharyngobranchial (see Nielsen, 1942, fig. 6; Gardiner and Bartram, 1977, fig. 2), and which may have continued anteriorly as the internal carotid. The orbital artery (the external carotid of Nielsen, but see Poplin, 1974, p. 92) has a separate opening into the jugular canal from which it presumably passed into the trigemi-

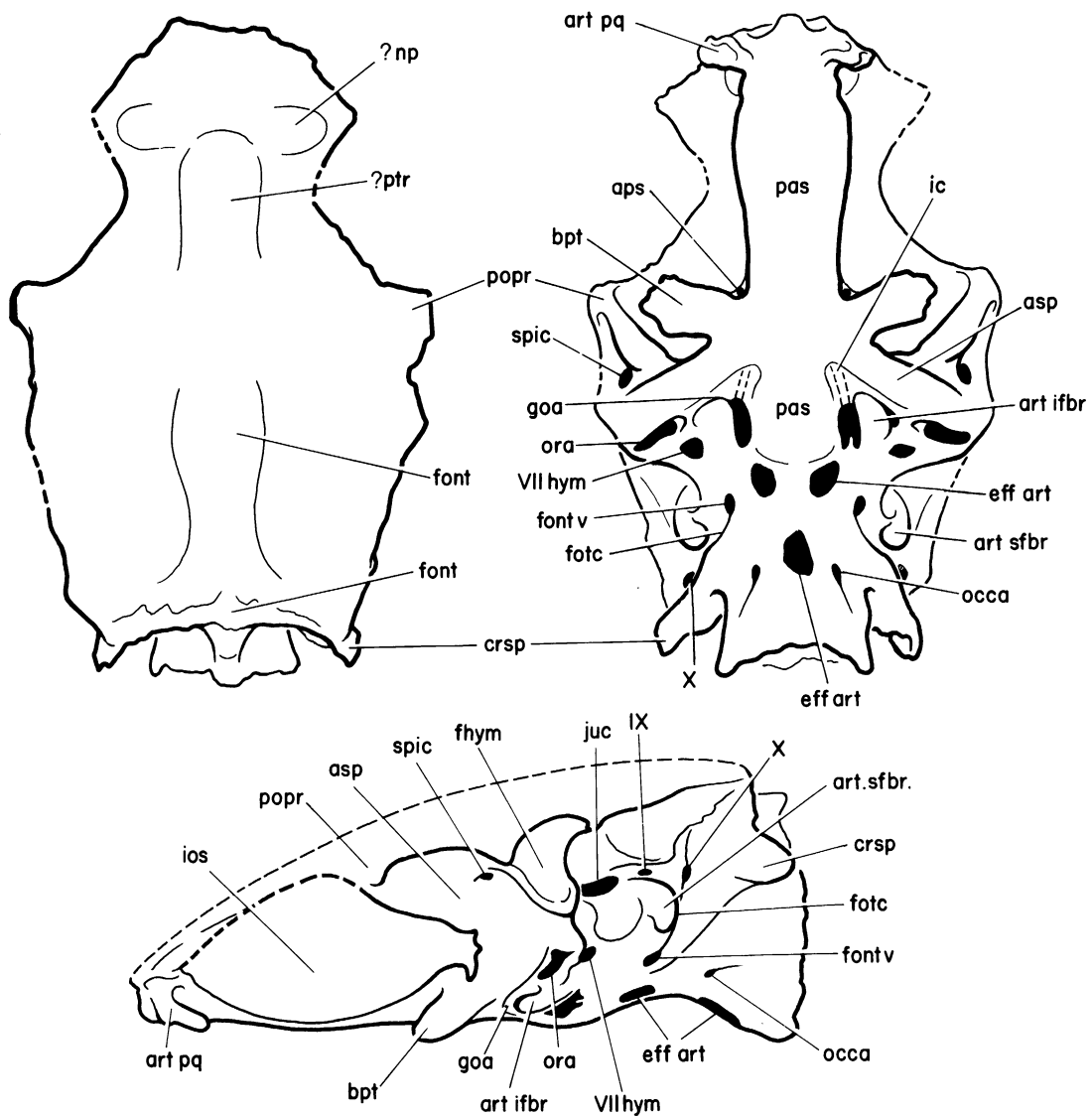


FIG. 3. *Luederia kempfi*, new genus and species, AMNH 8998. Key diagrams for figure 2.

nofacialis chamber and the orbit. A small foramen below and somewhat behind the orbital foramen may have been the exit for the hyomandibular branch of the facial nerve.

The parasphenoid slightly overlaps the ventral otic fissure and has a relatively greater extension behind the basiptyergoid processes than in, for instance, *Pteronisculus*. Although it

more or less covers the "triangular area" between the grooves for the lateral aortae, as in *Pteronisculus* (Patterson, 1975, p. 538), the ventral fissure (as revealed in sagittal section) is in the same relative position as in other palaeoniscoids. Because of this extension, however, the articulations for the first infrapharyngo-branchials are lateral to the parasphenoid rather

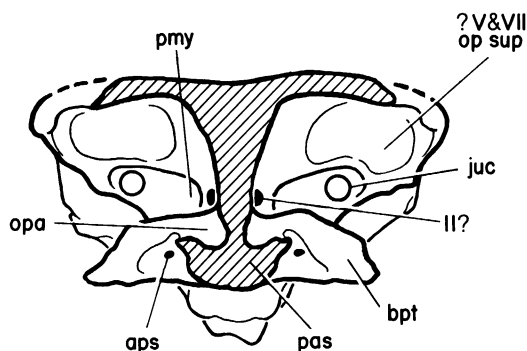


FIG. 4. *Luederia kempii*, new genus and species, AMNH 8998. Cross section of neurocranium at level of postorbital wall.

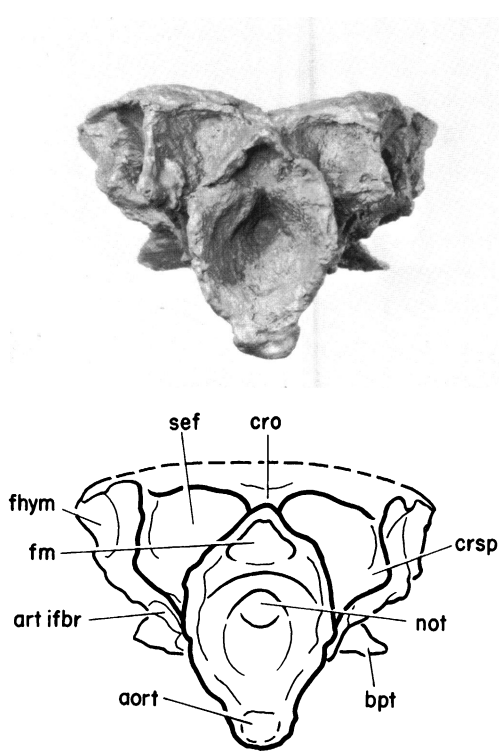


FIG. 5. *Luederia kempii*, new genus and species, AMNH 8998. Neurocranium in posterior view.

than behind it. Paired openings for efferent branchial arteries are situated near the posterior border of the parasphenoid, and behind them there is a median, slotlike aperture, also for

efferent branchial arteries, as in *Pteronisculus stensiöi* (Nielsen, 1942, fig. 6). Apparently there was considerable variation among the palaeoniscoids in the number and arrangement of the openings for the efferent branchials (Poplin, 1975).

In lateral aspect, the otic region has two prominent topographic features—the tuberosity that carries the articulation for the first supratharyngobranchial and the robust craniospinal process that includes the articulation for the second supratharyngobranchial. Below the tuberosity, on the right side, the infravagal portion of the otico-occipital fissure is open and lined with perichondral bone. It terminates ventrally in the much-reduced vestibular fontanelle. Above the tuberosity, and on the left side, the otico-occipital fissure appears to be closed, suggesting that this is an aging phenomenon. The location of the glossopharyngeal foramen is not evident, but it must be nearly in line with the jugular depression and the vagal foramen.

In midsagittal section (fig. 6), the posterior myodome, the prootic bridge and the basisphenoid ossification are well defined. The ventral otic fissure, which is typically situated behind the posterior myodome, is not lined with perichondral bone and, as preserved, is filled with cancellous bone. The significance of the filling is obscure; in any case, the fissure does not join the vestigial vestibular fontanelle. Various other features visible in the midsagittal plane have been distorted by the post-mortem compression.

In posterior aspect it is evident that the cranial roof has been forced downward to the thick, projecting rim of the foramen magnum. This rim is more or less confluent with that of the deep notochordal pit. On both lateral surfaces of the rim there is an oblique groove and related foramen for an occipital artery. The most unusual aspect of the posterior occipital surface is the presence of paired depressions on either side of the foramen magnum that may be regarded as sub-epiotic fossae.¹ They are bordered dorsally by the horizontal occipital pro-

¹According to Patterson (personal commun.) these depressions are the sub-epiotic fossae of Phillips (1942), not the post-temporal fossae, which lie anterior and lateral to the otico-occipital fissure.

tuberances (see Poplin, 1974, figs. 11 and 13) and ventrolaterally by strongly developed craniospinal processes. The occipital crest separating the two fossae above the foramen magnum has been mostly eliminated by the depression of the cranial roof. It is probable, however, that the distance from the dorsal rim of the foramen magnum to the posterior edge of the roof approached that in *Pteronisculus* (Nielsen, 1942, p. 32) and in *Boreosomus* (Nielsen, 1942, fig. 61).

The associated noncranial rostral element (fig. 7) is a tooth-bearing bone that was situ-

ated immediately in front of the ethmoid (fig. 1). Notches on both lateral borders lead into a transverse canal—presumably the ethmoid commissure. The outer, anterior surface is finely denticulated like the anterior part of the skull roof. The median (or inner) surface is divided by a strongly developed horizontal lamina. There is some indication that this shelf represents fused, paired elements, although there is no indication of such fusion elsewhere (see also Patterson, 1975, fig. 138). Above the shelf there is a shallow concavity that may have formed the anterior wall of the nasal capsules.

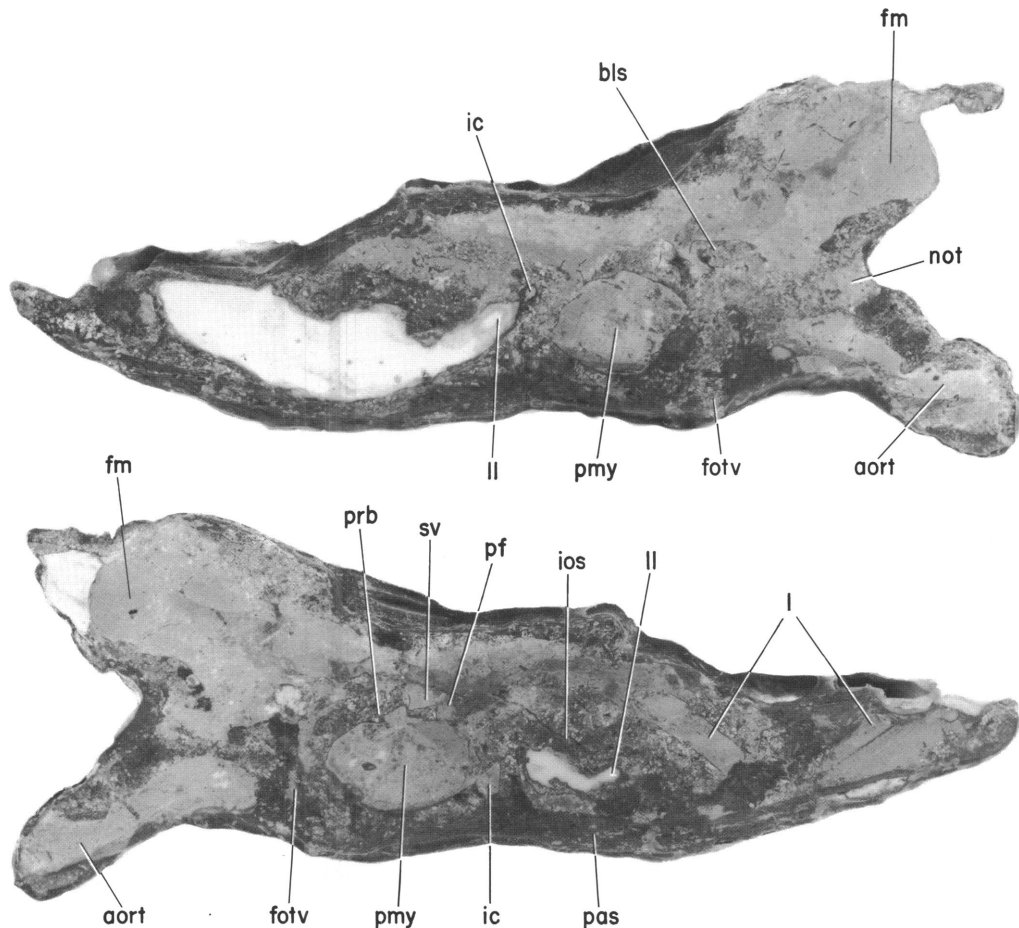


FIG. 6. *Luederia kempii*, new genus and species, AMNH 8998. Sagittal section of neurocranium. Most of the interorbital septum is included in the left half. $\times 2$.

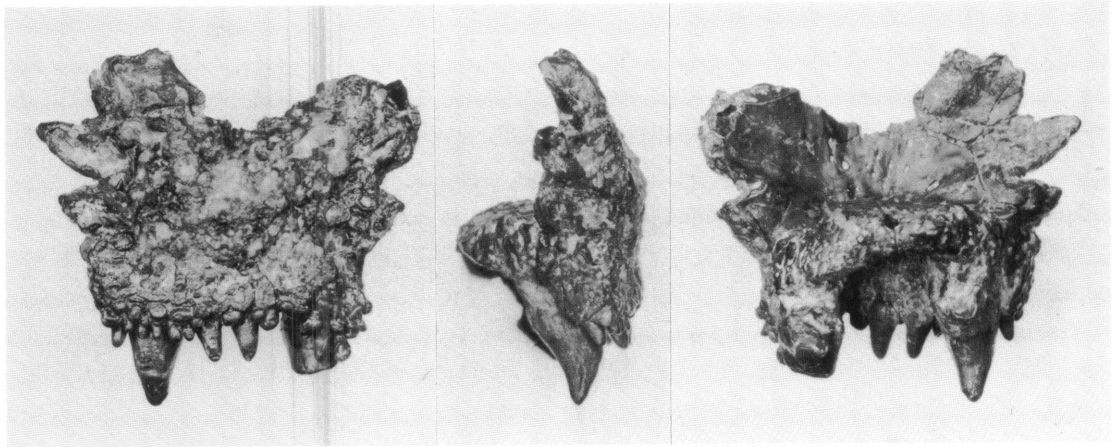


FIG. 7. *Luederia kempfi*, new genus and species, AMNH 8998. Rostral element in anterior, lateral and posterior (internal) views. $\times 3.4$.

Below the shelf, and fused to it, are a pair of robust, tusklike teeth that are separated from each other by a deep, dorsally directed concavity. The spacing of these enlarged teeth also favors the possibility that the shelf, at least, represents a fusion of paired elements. The smaller teeth along the ventral margin of the denticulated outer surface are entirely anterior to the much larger paired tusks. Because of crushing on the upper part of the ethmoid region, the exact relationships of the rostral bone to other dermal elements or to the neurocranium cannot be determined.

The homologies of this element are indeed problematical, particularly in the absence of the other dermal snout bones. Because it is median, tooth-supporting, canal-bearing and shows no evidence of an orbital margin, identification in terms of Gardiner's (1963) criteria is difficult. As the bone belonged to a mature individual, fusion of premaxillae is possible. Patterson (1975, fig. 138) has noted this condition in an East Greenland specimen of *Perleidus*. An additional "fusion," with the canal-bearing rostral, could produce a single, median rostromaxilla. The Lueders element also resembles the median rostromethmoid of *Pachycormus curtus* (Patterson, 1975, fig. 139), but as the presence of separate premaxillae cannot be demonstrated in the former, further speculation about its identity seems pointless.

SYSTEMATICS

On the basis of available evidence it is not possible to formulate a hypothesis of relationship for the fish represented by the Lueders braincase and rostral element. It is probably a palaeoniscoid, which means only that it has numerous primitive actinopterygian neurocranial characters, including a sutureless braincase, a notochordal canal that extends forward to the ventral otic fissure, and an undivided, oblique or nearly vertical hyoman-dibular facet. However, comparison at a broader level, with other paleopterygian neurocrania, supports the opinion that it has certain unique derived characters that favor formal taxonomic treatment, as follows:

CLASS OSTEICHTHYES
SUBCLASS ACTINOPTERYGII
ORDER PALAEONISCIFORMES (PALAEONISCIDA),
INCERTAE SEDIS
LUEDERIA,¹ NEW GENUS

TYPE SPECIES: *Luederia kempfi*.

DISTRIBUTION: Baylor County, Texas. Lower Permian (Leonardian) Lueders Formation, Maybelle Aa2 Limestone Member.

DIAGNOSIS: Large palaeonisciform approx-

¹For the Lueders Formation.

imating size of *Scanilepis dubia* (Woodward) on basis of braincase dimensions. Neurocranium differs from that of other palaeonisciforms in having well-defined ethmoid articular processes for the autopalatines, aortic grooves, and articulations for the first infrapharyngobranchials situated lateral to the posterior extension of the parasphenoid, well-defined sub-epiotic fossae that are bordered ventrolaterally by strong craniospinal processes, and in having an associated median rostral element that is tooth-supporting, canal bearing, and without orbital margins.

Luederia kempii,¹ new species

Figures 1-7

HOLOTYPE: AMNH 8998, complete braincase and associated median rostral element. Only known specimen.

HORIZON AND LOCALITY: Lueders Formation, Maybelle Aa2 Limestone Member, Lower Permian (Leonardian), about 200 m. south of south end of the Lake Kemp Dam, Baylor County, Texas (locality 2 of Berman, 1970, fig. 2).

DIAGNOSIS: Same as for genus.

**COMMENTS ON THE CRANIAL
FISSURES AND THE POSTERIOR
MYODOME**

In order to distinguish between the primitive and the derived aspects of the palaeoniscoid braincase, outgroup comparison at various levels of universality is obviously necessary. In this regard Patterson (1975) has provided a detailed comparison of paleopterygian and neopterygian neurocrania with emphasis on the origin and fate of the ventral otic fissure, the otico-occipital fissure, the vestibular fontanelle and the posterior myodome. More recently Gardiner and Bartram (1977) have discussed the homologies of the ventral otic fissure in palaeoniscoids and in the rhipidistian *Eusthenopteron* and *Glyptolepis*. Although the relationships of the acanthodians are still somewhat controversial (Jarvik, 1977), we believe that the hypothesis of a sister group relationship with the Osteichthyes has not been falsified. Accord-

ingly, we are following Miles (1973, p. 74) in grouping the acanthodians and osteichthyans in the category Teleostomi. In this same paper, Miles (pp. 85-89) discussed the components of the *Acanthodes* basicranium (also Moy-Thomas and Miles, 1971, p. 66) and compared the fissures between these components with the lateral occipital fissure and the ventral otic fissure of primitive actinopterygians and crossopterygians.

The possibility of inferring some embryonic chondrocranial features from the braincase of an extinct, adult osteichthyan depends on the presence of morphological landmarks that can also be identified in the developing and mature neurocrania of related living forms. The basitrabecular (basipterygoid) process, the lateral commissure, the ventral otic and otico-occipital (metotic) fissures, the vestibular fontanelle and various canals and foramina (along with their topographic relationships) represent such landmarks. The developmental basis for differences in the relationships of these fissures with each other and with the vestibular fontanelle in adult extinct paleopterygians and early neopterygians remains problematical, but some inferences can be derived from living forms. A perusal of DeBeer (1937) indicates that the lateral auditory wall in the vicinity of the foramina for the facial, glossopharyngeal, and vagus nerves has a fairly uniform development. The cartilaginous wall becomes perichondrally and sometimes endochondrally ossified without any significant changes in topography except for those related to increase in size.

Romer (1937, pp. 39-43) was apparently the first to deduce the embryonic components of an extinct osteichthyan neurocranium, in this instance for the rhipidistian *Ectosteorhachis* (non-*Megalichthys*). He concluded that the trabeculae formed the basal part of the ethmosphenoid moiety and the parachordals the same for the otico-occipital portion. Romer also compared the *Ectosteorhachis* braincase with Watson's (1925) "Palaeoniscoid A" and "Palaeoniscoid B," which have been subsequently redescribed by Poplin (1974). Although Watson (1925, p. 837) figured the ventral otic fissure of "B," this fissure was not discussed by him, and Romer (1937, p. 57) made no comparison with the rhipidistian condition. Jarvik (1954, p.

¹For Lake Kemp, Baylor County, Texas.

7), as pointed out by Gardiner and Bartram (1977), apparently confused the ventral otic fissure in *Pteronisculus* (Nielsen, 1942) with a vaguely defined, inconstant furrow in *Eus-thenopteron* that runs transversely from the vestibular fontanelles to the U-shaped gap in the floor of the notochordal canal. Schaeffer (1968) and Gardiner and Bartram (1977) have suggested that the lower part of the intracranial joint in crossopterygians is the developmental homologue of the ventral otic fissure in the primitive actinopterygians for reasons that are discussed in their respective papers.

In *Polypterus*, *Acipenser*, *Lepisosteus*, *Amia*, and various teleosts the anteroventral part of the metotic fissure (which housed the vagus nerve) becomes incorporated into the basicapsular fenestra through the orientation of the basicapsular commissure as it fuses with the parachordal (DeBeer, 1937, p. 399). During subsequent growth of the auditory capsule, of the basal plate and of the anterior and posterior basicapsular commissures, the foramina for the facial, glossopharyngeal and vagus nerves acquire their adult spatial relationships. Although these foramina are usually well separated, the ninth and tenth cranial nerves in, for example, *Clupea* (*?harengus*) emerge through the same foramen, and the posterior basicapsular commissure is apparently absent (DeBeer, 1937, p. 132). The anterior and posterior commissures obviously play an important role in the development of the lateral auditory wall. Although they cannot be observed *per se* in the adult chondrified or ossified neurocranium, their condition in the developing chondrocranium (including their absence) can frequently be inferred by the relationships of the relevant foramina and fissures.

The ventral otic fissure in adult palaeoniscoids (fig. 6) is usually interpreted as a persistently cartilaginous zone between the basisphenoid and basioccipital ossifications (the fissure is thus a synchondrosis), which may be near or at the junction of the prechordal and chordal components of the basal plate (Schaeffer, 1968, p. 13; Gardiner, 1973, p. 106; Patterson, 1975, p. 416, 466; Gardiner and Bartram, 1977, pp. 239-240, 241-242). However, if the basiptyergoid processes mark the posterior limit of the prechordal basicranium (De-

Beer, 1937, p. 391), the persistent ventral otic fissure in adult teleostomes may be behind rather than at the actual embryonic chordal-prechordal junction. As noted by Patterson, the fissure cartilage may ossify in some specimens of *Boreosomus* and this may be the case in *Luederia*. The fissure may also disappear in *Saurichthys* (Stensiö, 1925), in *Perleidus* (Lehman, 1952), in the parasemionotids, in some caturids, in *Dapedium* and in "early" pholidophorids and leptolepids (Patterson, 1975). In some forms the closure of the ventral otic fissure may be age-related, but out-group comparison suggests that the presence of cartilage in the adult fissure is primitive. In advanced actinopterygians the prootics have grown downward between the basisphenoid and the basioccipital, but the fissure persists as a synchondrosis between the basioccipital and the prootic according to Patterson (1975). In regard to the acanthodians, Miles (1973, p. 89; 1977, p. 49) has noted that the cleft between the posterior margin of the basisphenoid and the middle ventral ossification in *Acanthodes* is topographically in the position of the actinopterygian ventral otic fissure (see also Patterson, 1975, pp. 537-538). Although this deduction is based only on external molds of the *Acanthodes* braincase, it is the most parsimonious explanation. As preserved in the negative, the several components of the braincase in *Acanthodes* were presumably separated by areas of cartilage; there is no evidence of fusion between them. It is also possible that the cartilage-filled ventral otic fissure opened into the rear of the orbit in *Acanthodes*, as in *Mimia*. At least there is no ossification that would prevent this in the adult *Acanthodes* (Miles, 1973, fig. 4).

The otico-occipital fissure requires only brief comment as we are not concerned here with ways in which it is eliminated in higher actinopterygians. It represents the embryonic metotic fissure between the auditory capsule and the occipital arch, and its position is readily determined by the location of the vagal foramen, which in living immature actinopterygians is always situated in the fissure. As in actinopterygians that retain the otico-occipital fissure in the adult stage, the apparently homologous fissure in *Acanthodes* may be lined

with perichondral bone (Miles, 1973, p. 89; 1977, p. 49) which indicates the absence of cartilage. In crossopterygians, the auditory capsule and the occipital arch are generally fused in the mature neurocranium, although Jarvik (1954, p. 7) has found a more or less separate supravagal portion in some specimens of *Eusthenopteron*, and there is indication of a fissure around the vagal foramen in *Ectosterorhachis* (Romer, 1937, fig. 21). The otico-occipital fissure and the ventral otic fissure are confluent and cartilage-filled in the Devonian dipnoans from Australia (Miles, 1977, p. 49), but the vestibular fontanelle is absent.

The vestibular fontanelle, derived ontogenetically from the basicapsular fenestra, is present in several groups of adult living teleosts as a membrane- or cartilage-filled space between the otic and occipital ossifications (Patterson, 1975, p. 428). Closure of the fontanelle with cartilage must mean that this hiatus is eliminated before ossification begins, and in this case, that the fontanelle represents a part of the chondrocranial wall that has failed to ossify. The absence of perichondral bone around the edge of the vestibular fontanelle, as in *Pachycormus* (Patterson, 1975, fig. 106), implies that this area was filled with cartilage. In *Perleidus* the vestibular fontanelle is variously developed in the adult; it was presumably cartilage filled when not closed by bone (Lehman, 1952). Patterson has noted that the differences in the expression of the fissure and the fontanelle may be, in part, age related, which seems to be the case in *Luederia*. Incidentally, the term "fontanelle" is usually defined as a membrane-covered (but not cartilage filled) space in the chondrocranium or between neighboring dermal or endoskeletal ossifications.

As implied above, "confluence" of the ventral otic fissure or of the otico-occipital fissure with the vestibular fontanelle means only that they are not separated by areas or bridges of bone. Embryological evidence indicates that ossification in the lateral wall of the auditory region follows closely the final pattern of the chondrocranium. Absence of the anterior or the posterior basicapsular commissures, or failure of either to fuse with the parachordal, will apparently influence the configuration of the

ossified auditory wall and the related foramina.

In Patterson's (1975, p. 416) opinion, the primitive state for the actinopterygian ventral otic fissure includes; (1) a bony separation between it and the otico-occipital fissure; (2) continuation of the fissure cartilage to the orbit, and (3) a position definitely anterior to the vestibular fontanelle. This hypothesis is difficult to test by comparison with the rhipidistian condition because of the marked differences in the cranial wall around the trigeminal nerve. In the rhipidistians, the ventral otic and otico-occipital fissures are well separated, and the ventral otic fissure is some distance in front of the vestibular fontanelle (Jarvik, 1954, fig. 11). These modifications are presumably related to the intracranial joint rather than only to ossification of the anterior basicapsular commissure and related areas. The otico-occipital fissure and the fontanelle are absent in the actinistians. The presence of a continuous cranial fissure, without an intervening fontanelle in some Devonian dipnoans (Miles, 1977) neither falsifies nor corroborates the above hypothesis.

Patterson (1975) has rightly emphasized that the ventral otic fissure and the otico-occipital fissure have separate origins and different fates, which is generally true for the teleostomes. The ultimate reason for the persistence or disappearance of a particular fissure, or part thereof, and of the vestibular fontanelle, may represent a compromise between the constraints of phylogeny, the demands of function, and the effects of aging.

A particularly interesting aspect of the primitive actinopterygian basicranium involves the relative position of the ventral otic fissure. Gardiner (1973, p. 109), Patterson (1975, p. 543), and Gardiner and Bartram (1977, p. 242) have suggested that an increase in the size of the posterior myodome is responsible for a posterior migration of this fissure. In a succinct summary of posterior myodome history, Patterson (1975, p. 543) noted that it is absent in some Devonian actinopterygians (e.g., *Mimia*). In *Kentuckia* (Rayner, 1951), a Mississippian genus, the paired myodomies are separated by a bony partition of the basisphenoid but are joined by the canal for the pituitary vein, which passes transversely through the partition. Bjerring (1977, p. 169) claimed that the posterior

myodomies of *Kentuckia* are only parts of the respective trigeminofacialis chambers, but aside from being paired, they resemble the myodomies of *Pteronisculus* in most respects (figs. 8, 9). In *Luederia*, as in *Pteronisculus*, and most other actinopterygians, there is a single median posterior myodome that is joined to the pituitary space dorsally and includes the path of the pituitary vein. The recess for the sacculus vasculosus is also dorsal to the median myodome, and the bucco-hypophyseal canal passes through the anterior part of the myodome to its opening in the basicranium.

Gardiner (1973), Patterson (1975), and Gardiner and Bartram (1977) have concluded that, along with enlargement of the myodome and consequent atrophy of the front of the notochord, the ventral otic fissure migrated posteriorly from its primitive position anterior to the vestibular fontanelle to a location within the chordal part of the basal plate. As interpreted by Gardiner and Bartram (1977, pp. 241-242), the position of the ventral otic fissure in palaeoniscoids varies from an anterior one, where the ventral fissure is confluent with the orbit, to a posterior location where it "passes through the base of the otic region and runs into the vestibular fontanelles." In spite of this presumed migration, these authors list certain constant topographical relationships between the ventral fissure and certain other structures, including (a) the anterior tip of the notochord; (b) the partition between the auditory and cranial cavities; (c) the level of the origin of the orbital arteries, and (d) the place where the lateral commissures join the basicranium. In addition, they found constant relationships between the position of the fissure in *Mimia* and in embryos of *Acipenser*, *Lepisosteus*, and *Exocoetus* in relation to the transverse pituitary vein, the foramina for the palatine branch of the facial nerve and the openings for the orbito-nasal arteries as they pass into the orbit (see DeBeer, 1937, pl. 30, fig. 1; pl. 38, fig. 1; p. 50, fig. 3).

In order to interpret some of the structures visible in the midsagittal section of the *Luederia* braincase we have compared it with sagittal sections of other palaeoniscoid neurocrania (fig. 8) and, where possible, with the topographical relationships of the ventral otic

fissure to the various landmarks discussed by Gardiner and Bartram (1977) plus additional features such as the basiptyergoid process, the foramina for the oculomotor and the glossopharyngeal nerves, the utricular recess and the canal for the internal carotid artery. As noted above, *Luederia* has a large posterior myodome that is anteroventral to the prootic bridge and to the partition in front of the ventral otic fissure. In most ways it agrees with the situation in *Pteronisculus* (Nielsen, 1942, fig. 9).

As a result of this comparison, we can find little evidence that the ventral otic fissure between the basisphenoid anteriorly and the basioccipital posteriorly has migrated or been pushed backward in the palaeopterygians. If the occipital segment of the basicranium is drawn to unit size in *Mimia*, *Kentuckia*, *Kansasiella*, *Pteronisculus*, and *Luederia* (fig. 8), it is evident that the landmarks mentioned above have about the same spatial relationships with each other and with the ventral otic fissure. In the neopterygians, however, the prootics have enlarged and separated the basisphenoid from the basioccipital. The basisphenoid has become relatively smaller (C. Patterson, personal commun.) and most of the posterior myodome floor is formed by the prootics. The ventral otic fissure is now bordered anteriorly by the prootics, which, through their increase in size, have apparently moved the fissure into a relatively more posterior position.

In order to appreciate the meaning of these changes it should be recalled that the external recti muscles differentiate before the posterior myodome is actually formed and while the lateral chondrocranial wall is still membranous (see DeBeer, 1937, p. 428; pl. 35, fig. 1; pl. 47, fig. 2; Bjerring, 1967, fig. 18). The position and length of the posterior myodome (and, in fact, of the other myodomies) is thus related to the position and the length of the external recti (or other eye muscles). Increase in the length of the obliquely oriented external recti muscles (fig. 9) is a derived condition in the actinopterygians that initially resulted in shallow, paired myodomies and eventually in a single posterior myodome that finally extended into the basioccipital. It thus appears to us that the enlargement of the myodome in the advanced

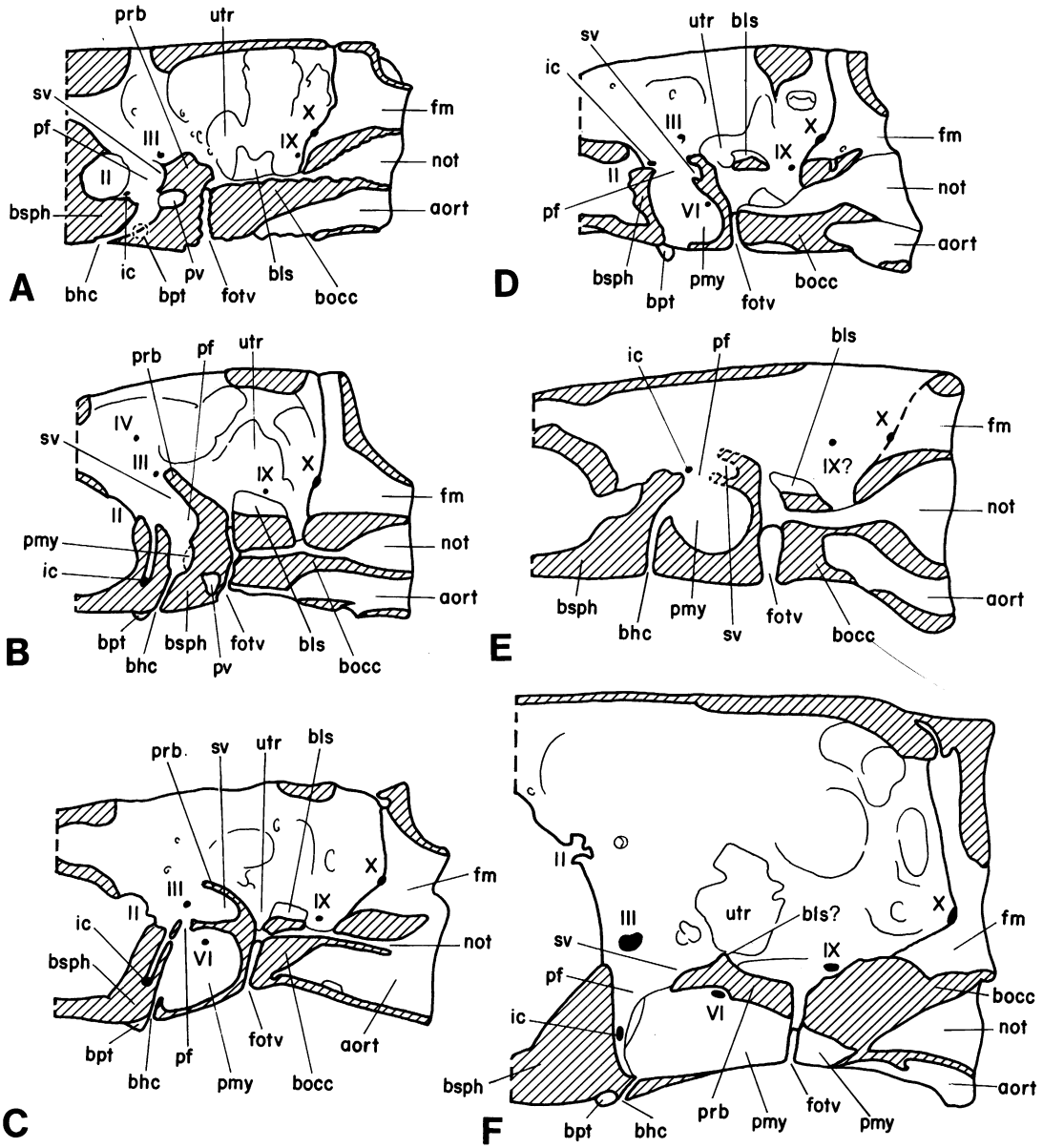


FIG. 8. Postorbital portion of the neurocranium in sagittal section in various palaeonisciforms and in a pholidophorid. The basicranial part of the occipital segment is the same length in all figures. A. *Mimia toombsi*, after Gardiner and Bartram, 1977. B. *Kentuckia deani*, after Rayner, 1951. C. *Kansasiella eatoni*, after Poplin, 1974. D. *Pteronisculus stensiöi*, after Nielsen, 1942. E. *Luederia kempi*. F. *Pholidophorus bechei*, after Patterson, 1975.

actinopterygians involved reduction in or the absence of chondrification and ossification around the elongating external recti muscles as

well as some backward displacement of the fissure. As noted by Patterson (1975) enlargement of the pituitary vein canal was not in-

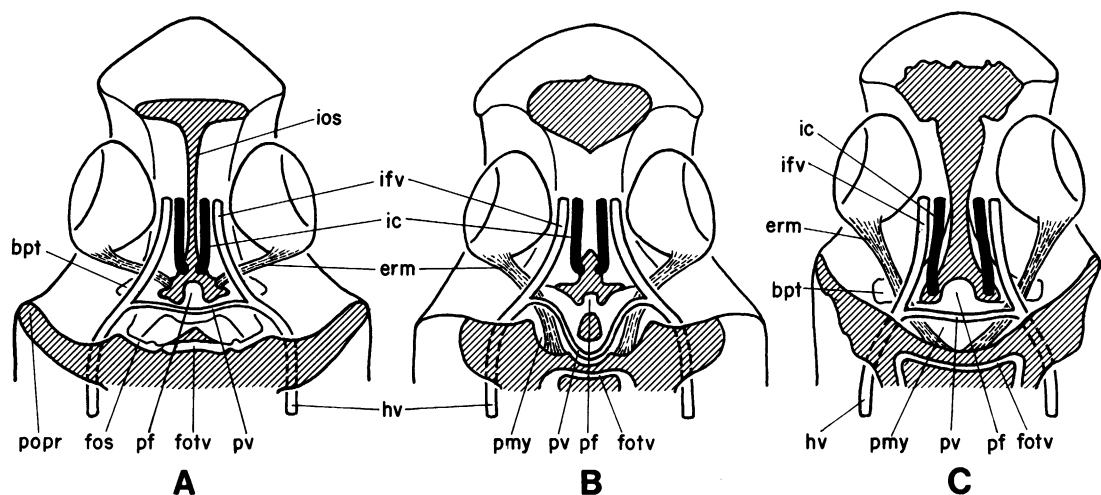


FIG. 9. Schematic reconstructions of palaeonisciform neurocrania in dorsal aspect to show the development of the posterior myodome in relation to the elongation of the external recti muscles. A. Posterior myodomes not developed as in *Mimia toombsi* (Gardiner and Bartram, 1977). B. Separate posterior myodome for each external rectus muscle, as in *Kentuckia deani* (Rayner, 1951). C. Single posterior myodome for both external recti muscles, as in *Pteronisculus stenstiöi* (Nielsen, 1942) and most other actinopterygians.

volved, at least initially. Nevertheless, the canal and the incipient myodomes were in close association, and the median myodome incorporates the pituitary vein.

According to our scenario reconstruction of posterior myodome history, which agrees in most respects with that of Patterson (1975, pp. 540-544), the external recti muscles primitively were attached to the surface of the basisphenoid portion of the postorbital wall at the level of the pituitary fossa (fig. 9). As some Devonian palaeoniscoids had no myodomes, it follows that their external recti muscles were short and contained within the orbit. This was apparently the primitive gnathostome condition. Elongation of the external recti muscles obviously occurred among the palaeoniscoids, resulting in the paired myodomes of *Kentuckia* and in the single posterior myodome of most actinopterygians that is also confluent with the pituitary fossa.

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