THE BRAINCASE ANATOMY OF *LAWRENCIELLA SCHAEFFERI,* ACTINOPTERYGIAN FROM THE UPPER CARBONIFEROUS OF KANSAS (USA)

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ABSTRACT—A full description and diagnosis are given of *Lawrenciella schaefferi* Poplin 1984, from the Pennsylvanian
(Late Carboniferous) of Kansas, U.S.A. This taxon is only known by braincases and associated parasphenoids, which are
exceptionally well preserved as phosphatic nodules. The external and internal morphology of the endocrania were studied
from serial sectionings which allowed detailed three-dimensional reconstructions. The study shows that, besides synapo-
morphies inherent to basal actinopterans, *L. schaefferi* displays a set of very peculiar features such as prespiracular fossae,
intracranial ossicles, and paired anterior myodomes for nonocular eye muscles. Another conspicuous feature, the noto-
chordal canal ending blindly anteriorly, has been observed until now only in more advanced Triassic actinopterans. The
anatomical characters of *L. schaefferi* indicate, in the light of recent cladistic analyses, that this Carboniferous taxon is a
relatively advanced actinopteran compared to basal forms such as *Kentuckia*, *Mimia*, or *Moythomasia*.

INTRODUCTION

The Upper Pennsylvanian of Kansas has provided fossil bear-
ing nodules in which actinopterygian remains are preserved as
complete and uncrushed endocrania. They pertain to three kinds
which were first designated as 'Palaeoniscid A, B, and C' in
studies from Moodie (1915, 1920), Watson (1925, 1928), and
Rayner (1951). More recently, *Kansasiella eatoni* Poplin 1974
(Watson's 'Palaeoniscid A') has been described in detail, and
Lawrenciella schaefferi Poplin 1984 (Watson's 'Palaeoniscid B')
was the subject of a brief description and of a preliminary diag-
nosis. The aim of the present paper is to provide an accurate
anatomical study and a new diagnosis of the latter.

These nodules are of an exceptional interest because they con-
tain a large amount of tridimensionally preserved endocrania.
Such endocrania are rarely preserved in the fossil actinoptery-
gian record, so that our knowledge about these internal struc-
tures is quite limited with regard to that about the exoskeleton.
Thus, studies of this material from Kansas bring important con-
tributions for the understanding of the anatomy and early evo-
lution of the actinopterygian braincase. However, these studies
encounter a major problem due to the fact that these endocrania
are isolated and never associated with any part of the exoskele-
ton, save the parasphenoid, which is sometimes preserved on
their ventral face. Therefore, their head and body dermal anato-
mies being unknown, discussions about the relationships of these
fishes within the fossil Actinopterygii are limited to those rare
taxa the endocranium of which has been investigated. Below we
propose an overview of the endocranial synapomorphies shared
by *L. schaefferi* and other basal actinopterygians, as a prelimi-
nary to a wider and future synthesis in preparation by one of us
(M.-H. H). Comments and discussions about some unexpected
and unique features of this lower actinopteran are also included.

Anatomical Abbreviations—**a.fb**, anterior fossa bridgei;
ant.amp, anterior ampulla; **ant.asc.p**, anterior ascending process;
ant.c.v, foramen or canal for the anterior cerebral vein; **ant.
d.fon**, anterior dorsal fontanelle; **ant.my.n.m**, anterior myodome
for a nonocular muscle; **ant.s.c**, anterior semicircular canal; **ao.c**,
anterior foramen of the aortic canal; **a.octl**, area octavolateralis;
aort, aortic canal or its posterior opening; **art.1.i**, articular facet
for the first infrapharyngobranchial; **art.1.s**, articular facet for
the first suprapharyngobranchial; **art.p**, articular facet for the
palatoquadrate; **aur**, cerebellar auricle; **bhc**, bucco-hypophysial
canal or its ventral opening; **b.oc.a1, b.oc.a2**, foramina or canals
for branches of the occipital artery; **b.p**, basipterygoid process;
bsph, pars basisphenoidea; **c.c**, crus commune; **ccc**, communica-
tion between the notochordal canal and the cranial cavity; **cr.csp**,
crista above the posterior semicircular canal; **c.r.d**, canal for
branches of the superficial ophthalmic nerves; **cr.o**, crista occipi-
talis; **crs.p**, craniospinal process; **d.ant.my**, dorsal anterior my-
odome; **d.ao**, dorsal aorta; **die**, diencephalon; **e.hy.a**, efferent
hyoidean artery; **epi**, epiphysial part of the anterior dorsal fon-
tanelle; **epi.a**, foramen for epibranchial arteries; **epiI, II, III, IV**,
epibranchial arteries I, II, III, and IV; **e.ps.a**, efferent pseudo-
branchial artery, or its groove or notch; **ext.amp**, external am-
pulla; **ext.s.c**, external semicircular canal; **f.hm**, articular facet for
the hyomandibular; **f.m**, foramen magnum; **f.ram.dors**, foramina
for branches of the ramus ophthalmicus superficialis trigemini,
the ramus ophthalmicus lateralis and vessels; **f.r.d**, foramina for
branches of the superficial ophthalmic nerves; **g.o.a**, groove for
the orbital artery; **g.oph.a**, great ophthalmic artery, or its groove;
hy.o.a, hyo-opercular artery; **int.car**, internal carotid artery, or
its foramen, groove or notch; **iorb.s**, interorbital septum; **ir.int.
cav**, irregular intracranial cavities; **j.c**, jugular canal or its ante-
rior opening; **j.d**, jugular depression; **j.v**, jugular vein; **l.ao**, lateral
aorta, or its groove; **l.c**, lateral commissure; **l.cr.c**, lateral cranial
canal; **l.d.v**, longitudinal dorsal vein; **l.ex.oc**, dorso-lateral promi-
nence of the occipital ossification; **l.r**, lateral ridges; **l.sl**, longitu-
dinal slit; **l.st.a**, longitudinally striated area overhanging the pos-
terior dorsal fontanelle; **md.c.v**, middle cerebral vein; **m.ex.oc**,
median extension of the occipital ossification; **m.r**, median ridge;
my, posterior myodome; **mye**, myelencephalon; **not**, notochordal
canal, or its posterior opening; **n.p**, nasal pit; **o.a**, orbital artery,
or its foramen; **oc.a**, occipital artery, or its foramen and groove;

o.dhc.m, insertion area of a dorsal hyoid constrictor muscle; **oims1**, **oims2**, areas of insertion of the first and second intermuscular septa; **olf.b**, olfactive bulbs; **opt.a**, optic artery, or its groove; **opt.fen**, optic fenestra; **opt.l**, optic lobe; **orb**, orbit; **o.rec.m**, insertion of the superior, inferior, and internal recti muscles; **ot.oc.f**, otico-occipital fissure; **pal.a**, palatine artery, or grooves for the palatine artery and nerve; **p.fb**, posterior fossa bridgei; **pit**, hypophysial recess; **pit.fon**, pituitary fontanelle; **pit.v**, pituitary vein, or its groove; **p.n.w**, postnasal wall; **po.p**, postorbital process; **post.amp**, posterior ampulla; **post.asc.p**, posterior ascending process; **post.d.fon**, posterior dorsal fontanelle; **post.s.c**, posterior semicircular canal; **pr.b**, prootic bridge; **psph**, parasphenoid; **p.spi.f**, prespiracular fossa; **q**, canal from the irregular intracranial cavities to the spiracular canal; **r.gass.lat.g**, recessus for the gasserian and lateralis ganglia; **r.gen.g**, recessus for the geniculate ganglion; **sac**, saccular recess; **s.n**, septum nasi; **s.oph.a**, small ophthalmic artery, or its foramen; **spic**, spiracular canal, or its ventral opening; **spi.g**, spiracular groove; **spio**, spinooccipital nerve, or its foramen; **sr**, supraorbital ridge; **s.su**, sinus superior; **s.vasc**, space for the saccus vasculosus; **tel**, telencephalon; **tr.f.ch**, trigeminofacialis chamber; **utr**, utricular recess; **v.ant.my**, ventral anterior myodome; **v.font**, vestibular fontanelle; **v.ot.f**, ventral otic fissure; **zy**, zygal plate; **I**, canal or foramen for the olfactive nerves; **II**, canal or foramen for the optic nerves; **III**, canal or foramina for the oculomotor nerve; **IV**, canal or foramen for the trochlear nerve; **V**, canal for the trigeminal nerve; **Vo**, canal or foramen for the profundus nerve; **V+VII lat**, foramen for the trigeminal and the lateralis trunk of the facial nerve; **VI₁**, **VI₂**, foramina or canals for the abducens nerve; **VII**, canal for the facial nerve; **VIIhy**, hyomandibular trunk of the facial nerve; **VII lat**, canal for the lateralis trunk of the facial nerve; **VIIop**, opercular branch of the facial nerve; **VIIot**, canal for otic branch of the facial nerve; **VIIpal**, palatine nerve, or its canal or foramen; **IX**, glossopharyngeal nerve, or its canal or foramen; **IXst**, supratemporal branch of the glossopharyngeal nerve, or its foramen or groove; **X**, vagus nerve, or its foramen.

MATERIAL AND METHODS

The isolated braincases of *Lawrenciella schaefferi* are enclosed in ovoid phosphatic nodules the size of which varies from 1.5 cm to 3.5 cm in width, and 2.5 cm to 5 cm in height. They consist in three-dimensionally preserved, generally complete, endocrania and their natural endocasts, which allow a detailed description of their external and internal anatomies.

The material comprises a total of 87 specimens, with 76 specimens (numbered 'UK') from the Museum of Natural History, University of Kansas, Lawrence (USA), and 11 specimens (numbered 'ANP') from the Muséum national d'Histoire naturelle, Paris, France.

The specimen UK 21755 is a complete endocranium which was serially sectioned by one of us (C. P.) with a microtome (Poplin and De Ricqlès, 1970; Poplin, 1977). A total of 1437, 20 μm thick, sections were mounted between two glass slides and photographed (fig 1). Thanks to this technique, the endocranial cavities could be investigated in detail, and two kinds of tridimensional (3D) models of the endocranium were constructed.

The first 3D models are wax reproduction of the external and internal anatomies of the endocranium (Fig. 1B). The other 3D models (Fig. 1C) are computer models of the same structures, using a program ('Reconstruct') that reconstructs objects from serial section images. This free software, developed by the Boston University (Fiala, 2005), provides practical tools for aligning the sections and for tracing the profiles of each anatomical structure. These 3D models, surfaced from the traces, were afterward virtually dissected and new structures, hidden in the fossils, could be easily observed. The reconstruction drawings were made by
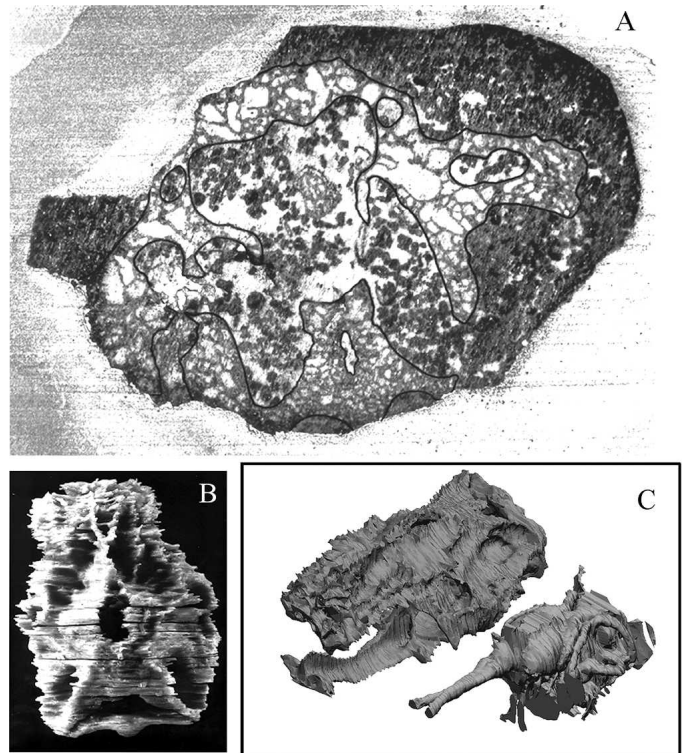

FIGURE 1.   **A**, 20-μm thick microtome section of the specimen UK 21755 for the 3D reconstructions of *Lawrenciella schaefferi*; **B**, wax model made by C. Poplin; **C**, three-dimensional virtual models made by M.-H. Hamel.

Mr. C. Salgueiro, who was artist at the Naturhistoriska Riksmuseet, Stockholm (Sweden).

LOCALITY AND HORIZON

The nodules were collected in a concretion-rich area that was first reported and studied by Twenhofel and Dunbar (1914). An extensive paleoecological, stratigraphical and geochemical study about these nodules was later undertaken by Miller and Swineford (1957), and the following information is mainly based on this work.

The outcrops that yielded the nodules are located in about thirty different localities situated approximately 150 km southeast of Kansas City, between Lawrence, upon the Kansas River, and Baldwin (Fig. 2). The nodules occur in a thin bed of yellowish-gray shale, lying immediately above the Haskell limestones, which are of marine origin, and at the base of the Robbins shale originated in brackish waters. This sequence is part of the Douglas Group, which is placed at the base of the Virgil Series, Upper Pennsylvanian (Fig. 3).

The nodules are mainly composed of apatite, concentrated outside the fossil, and crystalline calcite, which replaced the original bone. The matrix also shows quartz grains and minute blotches of organic mater. No pyrite nor marcassite were detected.

The fossil content of the nodules, besides the Actinopterygian remains, also includes Chondrichthyan remains (*Ctenacanthus, Cladodus*), Brachiopods (Orbiculoidea), Cephalopods (Goniatites, Nautiloids, Orthocerids), Arthropods (Idiotheca, Phyllopod ?), fossil wood and fish coprolites. As Twenhofel and Dunbar (1914) associated the nodules with the Robbins shale, they considered the environment of deposition as a brackish-water bay or estuary. However, according to Miller and Swineford (1957), the nodules are genetically linked to the Haskell lime-
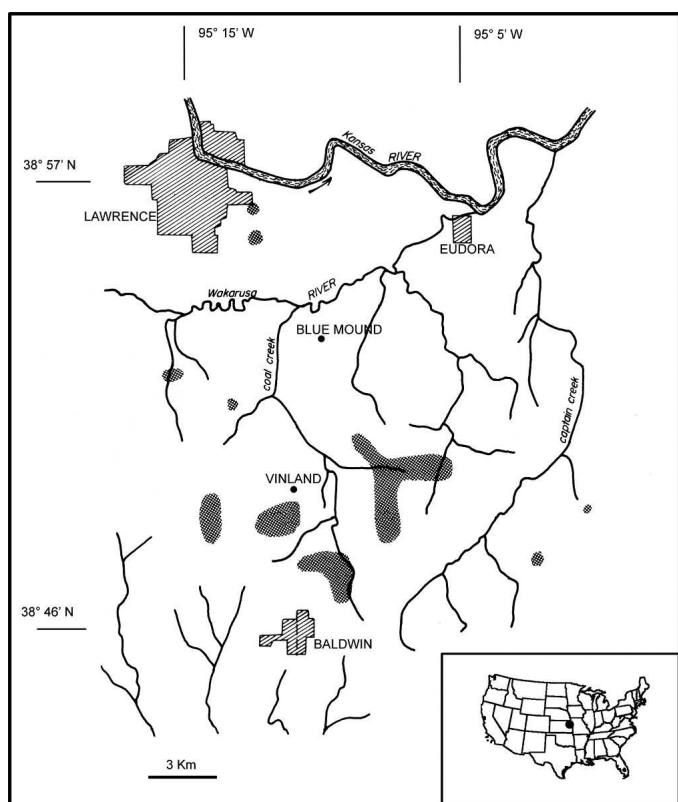
FIGURE 2. Map of outcrops where the nodules have been found (reticulate zones) near Lawrence (Kansas, U.S.A.). Modified from Miller and Swineford (1957).
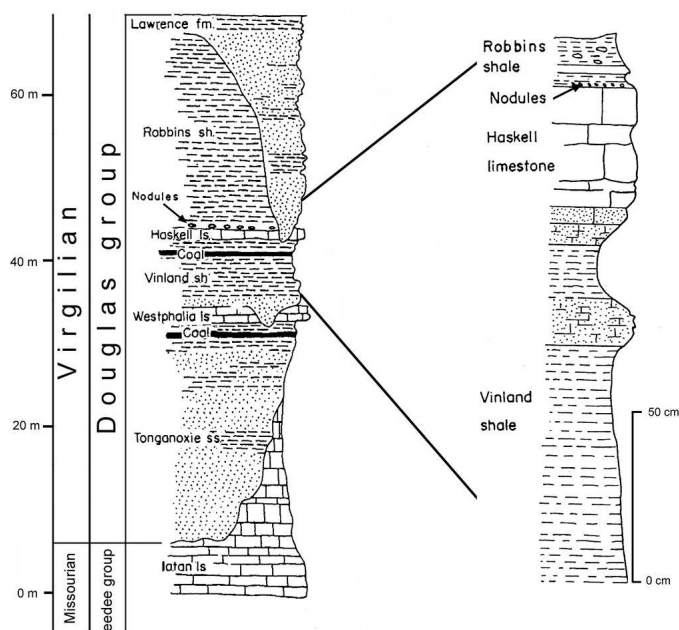

FIGURE 3. Generalized columnar section of lower Virgilian rocks (left) and section of a quarry situated East of Lawrence (Kansas, U.S.A.) (right). The position of the nodulose level is indicated by arrows. Modified from Miller and Swineford (1957).

stone and the fossils fauna is different from that in the Robbins shale. They concluded that the nodules were formed in a near shore environment, probably within shallow marine basins formed in a subtropical and humid area. The bottom condition of these basins was probably quiet, anoxic, without strong currents nor overturning at the time the nodules formed. These conditions explain the remarkable abundance and exceptional preservation of the fish remains. However, the taphocoenosis is especially marked by the fact that the actinopterygian remains are almost exclusively isolated endocrania. This taphofacies is quite different from those observed in other paleontological deposits in which the fish braincases preserved are articulated with the dermal bones: e.g. Eotriassic from Madagascar (Lehman, 1952), Triassic from East Greenland (Nielsen 1942, 1949) or Upper Devonian from Western Australia (Gardiner, 1984). Poplin (1986) interpreted these isolated endocrania of Kansas as regurgitation contents of Chondrichthyans. Another possible explanation would be the mechanical action of selective currents which, previous to burial, were able to carry within a limited zone endocrania resulting from scattered carcasses which were in an advanced decomposition stage. Nevertheless, in absence of detailed biostratinomic data, it is impossible to verify these hypotheses.

SYSTEMATIC PALEONTOLOGY

OSTEICHTHYES Huxley, 1880
ACTINOPTERYGII Cope, 1887
ACTINOPTERI Cope, 1871
Genus *LAWRENCIELLA* Poplin, 1984

Type Species—Lawrenciella schaefferi Poplin, 1984.
Diagnosis—As for the type species, by monotypy.

Etymology—From Lawrence, Kansas, U.S.A, where the material of the type species was collected.

LAWRENCIELLA SCHAEFFERI Poplin, 1984
(Figs. 4–21)

Synonymy—'Palaeoniscid B' Watson, 1925
Holotype—UK 21942, Museum of Natural History, the University of Kansas, Lawrence, Kansas, U.S.A.
Paratypes—UK 56371, 56372, 56373, 56374, 56375, 56376, 56377, 21984, and 22010.
Horizon and Locality—Upper Pennsylvanian, Douglas Group, Lawrence Formation, Haskell Limestone Member. Douglas County near Lawrence, Kansas, U.S.A.
Diagnosis—(emended after Poplin 1984) Lower actinopterygian endocranium about 32 mm long, 19 mm wide at the level of the postorbital processes, and 15 mm high at the level of the basipterygoid processes; presence of paired prespiracular fossae; anterior edge of the posterior dorsal fontanelle overhanged by the tip of a medial bony prominence; posterior fossa bridgei without intramural diverticuli; ventral otic fissure separated from the vestibular fontanelle by a bony bridge; paired anterior myodomes for nonocular muscles below the olfactive nerve canal; single median anterior myodome for ocular muscles; posterior myodome unpaired, large and without a ventral fenestra; lateral cranial canals bulging blindly through the loop of the posterior semicircular canals; dorsal aortic canal extending from the occipital face to a level just behind the ventral otic fissure, with a single median bilobate anterior foramen for the lateral dorsal aortae and, at mid length, with a median opening for efferent branchial arteries; notochordal canal ending blindly, without reaching the ventral otic fissure; walls of the diencephalic and mesencephalic regions often internally covered by paired intracranial ossicles; presence of wide and irregular intracranial cavities lateral to each jugular canal; absence of a cerebellar corpus at the metencephalic region of the braincast; optic nerves leaving the cranial cavity through a single foramen; canal for the lateralis

nerve incompletely separated from the trigeminal canal; profundus nerve canal independent from the trigeminofacialis complex; absence of a distinct canal for the superficial ophthalmic branch of the facial nerve in the posterior wall of the orbit; no palatine foramen in the floor of the jugular canal; internal carotids penetrating into the braincase through two separate canals; anterior cerebral veins leaving the endocranial cavity at the level of the diencephalon, the left one always through an independent bony canal toward the left orbital cavity; inner wall of the unpaired posterior myodome with lateral deep grooves for the pituitary veins; parasphenoid extending posteriorly to a short distance in front of the ventral otic fissure, with very short anterior ascending processes, and large and long posterior ascending processes reaching the spiracular canals.

NEUROCRANIUM

External Anatomy

General Features—Among the three types of endocrania from the Upper Carboniferous of Kansas, those of *L. schaefferi* have an intermediate size between those of the large *Kansasiella eatoni* and those of the small 'Palaeoniscid C'. Most endocrania are 32 mm long, 19mm wide at the level of the postorbital processes, and 15mm high at the level of the basipterygoid processes. As for most other lower actinopterans, the neurocranium of *L. schaefferi* is fully ossified, except for the nasal capsules. Like the two other genera from Kansas, it has no sutures suggesting ossification boundaries, but the neurocranium is much more massive. It comprises two large parts, separated by the posterior dorsal fontanelle, the otico-occipital fissure, the vestibular fontanelles and the ventral otic fissure: (1) the anterior one with the ethmoidal, the orbitotemporal regions, and the upper part of the otic region; (2) the posterior one with the lower part of the otic region and the occipital region.

Ethmoidal Region—(Figs. 4, 5, 7) This region is incompletely ossified and the best information is provided by the serially sectioned specimen and three-dimensional models. From the ethmoidal region, only the dorso-medial and ventro-medial parts of the *planum antorbitale*, or 'postnasal wall' (p.n.w), are preserved, the intermediate part presumably being cartilaginous.

The dorso-posterior face of the postnasal wall is grooved by the anterior myodomes and its anterior face bears the posterior wall of the nasal pits (*n.p*) and a fragment of the median septum nasi (*s.n*). *L. schaefferi* has three distinguishable depressions in the posterior face of the postnasal wall: (1) The anterodorsal depressions are paired and deep, and are separated by the interorbital septum (*iorb.s*). They are probably the dorsal anterior
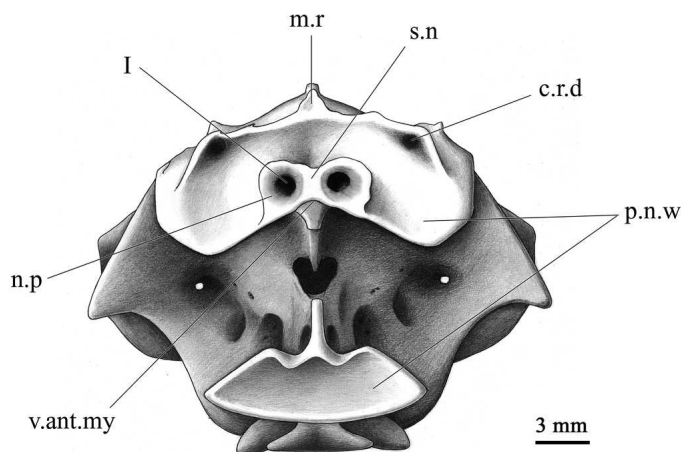

FIGURE 4. *Lawrenciella schaefferi* Poplin 1984: Reconstruction of the endocranium in anterior view.
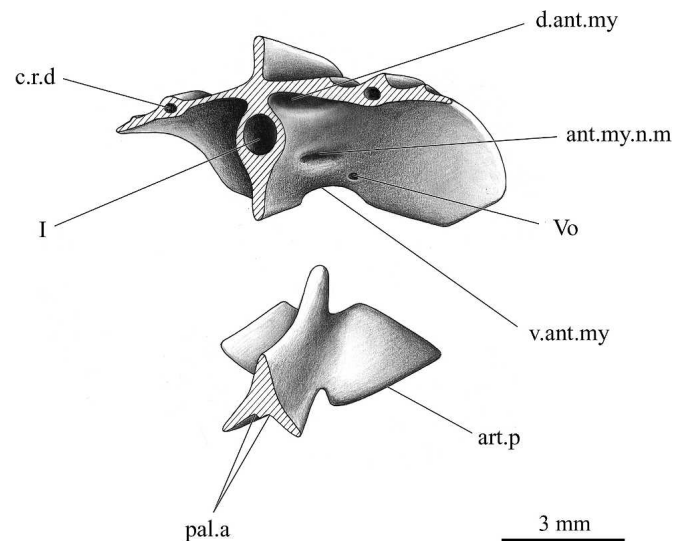

FIGURE 5. *Lawrenciella schaefferi* Poplin 1984: Reconstruction of the orbital face of the postnasal wall in posterolateral view. Bone sections hatched.

myodomes (*d.ant.my*) for the superior oblique muscles. (2) Below the olfactive nerve canal (*I*) lies another pair of shallow and shorter depressions (*ant.my.n.m*). A possible interpretation for these structures can be found in the early development of *Amia calva*. Bjerring (1977, p.140) mentioned an aberrant nonocular muscle in *Amia* 22-mm embryos, the anterior insertion of which lies immediately below that of the superior oblique eye muscle. This nonocular muscle is found only inside the right orbit and its posterior attachment is adjacent to the internal, inferior and superior recti muscles. According to Bjerring's segmentalist model, this muscle, innervated by the oculomotor nerve, is the basicranial muscle of the second metamere. Based on this anatomical peculiarity of *Amia calva,* we propose that *L. schaefferi* has, inside both orbits, nonocular muscles homologous to the basicranial muscle, with similarly placed anterior insertions: the anterior myodomes for nonocular muscles. (3) Regarding the inferior oblique muscles, they are housed in a single median ventral anterior myodome, which lies below the olfactory canal. Only the roof of this myodome is preserved and, as in *Kansasiella* (Poplin 1974:fig. 18), it displays a median longitudinal ridge.

After a course in a median bony canal, the olfactive nerves (*I*) diverge and enter the ethmoidal region through the postnasal wall by two distinct nasal foramina. The large canals which transmitted the branches of the superficial ophthalmic nerves (*c.r.d*) penetrate the *planum antorbitale* laterally to the anterior dorsal myodomes and open into the nasal capsule dorso-laterally to the foramina for the olfactory nerves. More ventrally, another paired canal (*Vo*) passes through the *planum antorbitale* between the median ventral anterior myodome and the anterior myodomes for nonocular muscles. This canal, which leads to the posteroventral wall of the nasal capsule, could carried the profundus nerve.

At the anterior extremity of the base of the cranium, the ventral-medial part of the *planum antorbitale* widens laterally into two bony wings (*art.p*). The high axial ridge between them separates the orbits. The ventral edges of these wings constitute two posterolaterally directed processes against which the palatoquadrate probably articulated. No canals or notches for the maxillary branch of the trigeminal nerve and the buccal branch of the facial nerve were preserved on the studied specimens.

Orbitotemporal and Upper Part of the Otic Regions—(Figs. 6–11; 20A, 20B, 20C; 21C) These two regions form a single,

well-ossified unit. In dorsal view (Figs. 6, 7) the orbital part comprises very wide supraorbital ridges (*s.r*) overhanging the eyeball and ending by massive postorbital processes (*po.p*). Medially is a very wide anterior dorsal fontanelle (*ant.d. fon*), as in *Kansasiella eatoni* (Poplin 1974:fig. 12), *Pteronisculus stensiöi* (Nielsen, 1942:fig. 12) and *Kentuckia deani* (Rayner, 1951:fig. 6). It extends from the anterior level of the articular facet for the hyomandibular to that of the postorbital process. A slight anterior constriction (*epi*) indicates the epiphysial part of the fontanelle. It is not perichondrally lined and was probably cartilage-filled during life. Its edges are raised above the endocranial surface of the neurocranium and continue forwards as a long median ridge (*m.r*) that extends to the ethmoidal region, and which is flanked by two paired lateral ridges (*l.r*). The orbital portion of the dorsal face of the braincase is marked by the presence of numerous irregular pits and foramina for branches of the ramus ophthalmicus superficialis trigemini, the ramus ophthalmicus lateralis and vessels (*f.ram.dors*).

The otic portion of the dorsal part displays, on each side, three large and distinct pits. The anteriomost pit is the prespiracular fossa (*p.spi.f*), which is a large, blind-ending depression lying medial to the postorbital process. This fossa has no homologue in any other basal actinopterygians, and its exact function is unclear. Behind and below the prespiracular fossa lies the anterior fossa bridgei (*a.fb*) into which opens the spiracular canal. The third pit is the posterior fossa bridgei (*p.fb*) which is very large and deep but without intramural diverticuli. The two last fossae are separated by a convexity produced by the underlying external ampulla. Laterally to the posterior fossa bridgei is the foramen for the suprapemoral branch of the glossopharyngeal nerve (*IXst*). The dorsal surface of the otic region bears on each side a prominent *crista* (*cr.csp*), which lies above the posterior semicircular canal.
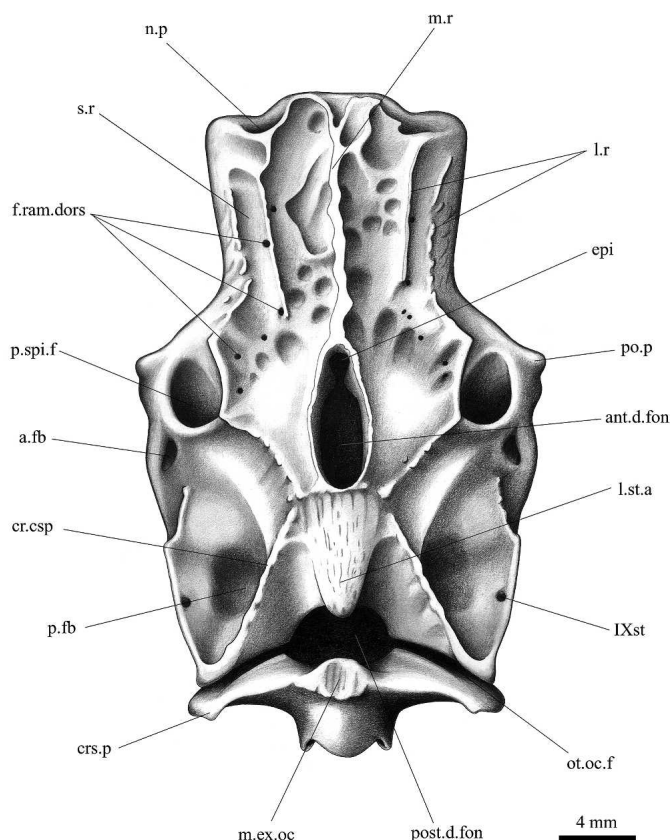
The posterior dorsal fontanelle (*post.d.fon*), which communicates laterally with the otico-occipital fissures, has roughly the same size as that of *Kansasiella eatoni*. The tip of a longitudinally striated area (*l.st.a*), peculiar to *L. schaefferi*, overhangs its anterior edge. Posteriorly, a small median projection from the upper margin of the occipital region (*m.ex.oc*) also overhangs it. A similar extension of the occipital area is present in *K. eatoni* (Poplin 1974:fig. 12) and, according to Gardiner (1984), may represent a median supraoccipital in these forms.

In lateral view (Fig. 7) the orbital part comprises a large optic fenestra (*opt.fen*) as in *K. eatoni* but with a deeper interorbital septum (*iorb.s*). The postorbital process is pierced vertically by a short spiracular canal (*spic*) as in *Pteronisculus stensiöi* (Nielsen, 1942: Fig. 11) and *K. eatoni* (Poplin 1974:fig. 13). This canal opens dorsally within the anterior fossa bridgei. In the rear of the lateral commissure (*lc*) is the non-perichondrally lined articular facet for the hyomandibula (*f.hm*), which is elongate and oblique. The entrance of the orbital artery (*o.a*) lies immediately below it. The long jugular canal traverses the lateral commissure and leaves it posteriorly, immediately behind the posterior edge of the articular facet for the hyomandibula. Ventral and lateral to the posterior opening of the jugular canal lie two smaller foramina for the hyomandibular and the opercular branches of the facial nerve (cf. *VIIhy*, *VIIop* in Fig. 17).

The lateral face of the otic region shows a deep longitudinal gutter-like jugular depression (*j.d*) joining the posterior opening of the jugular canal and the exit of the vagus nerve (*X*). At its postero-ventral edge lies the foramen for the glossopharyngeal nerve (*IX*). Below it and above the vestibular fontanelle are two distincts tuberosities forming the crescent-shaped articular facet for the first suprapharyngobranchial (*art.1.s*).

A stout ridge, which covers the horizontal semicircular canal, overhangs the jugular depression. In *L. schaefferi*, this elongate area is only interrupted by a well-marked groove for the supratemporal branch of the glossopharyngeal nerve (*IXst*). Above this ridge there is a muscle scar (*o.dhc.m*) that, according to Gardiner's interpretation (1984) for the Gogo "Palaeonisciformes," marks the insertion area of an undifferentiated dorsal hyoid constrictor muscle as in living chondrosteans.

On both sides, the otico-occipital fissure (*ot.oc.f*) is perichondrally lined throughout and widens laterally to allow the vagus nerve (*X*), and probably the posterior cerebral vein, to pass. It terminates anteriorly and ventrally into the oval shaped vestibular fontanelle (*v.font*) which is very large and similar in shape to that of *Coccocephalus wildi* (Poplin and Véran, 1996:fig. 7). This fontanelle is perichondrally lined, and not confluent with the ventral otic fissure as in most early actinopterans.

In ventral view (Figs. 8, 9), the supraorbital ridges are pierced by numerous foramina for the passage of branches of the superficial ophthalmic nerves (*f.r.d*). The ventral otic fissure (*v.ot.f*) is separated from the vestibular fontanelle by a large bony bridge as in several other forms, such as Gogo 'Palaeonisciformes' (Gardiner, 1984:figs. 7, 50), *Coccocephalus wildi* (Poplin and Véran, 1996:fig. 7), *Kansasiella eatoni* (Poplin, 1974:fig. 14), *Pteronisculus macropterus* (Beltan, 1968:fig. 2) and *Boreosomus piveteaui* (Nielsen, 1942:fig. 63). The ventral otic fissure seems to have been filled with cartilage during life.

On the ventral face of the otic region are foramina and well-marked grooves for the orbital arteries (*o.a* and *g.o.a*). The latter are given off from each lateral aorta, behind the ventral otic fissure. After a short course forward, each orbital artery bends outward and backward, passes in front of the articular facet for the first infrapharyngobranchial (*art.1.i*), and penetrates the endocranium through the large foramen that lies under the hyomandibular facet. More posteriorly, the aortic canal opens on the ventral surface by a single large foramen for epibranchial arteries (*epi.a*). Two symmetric slight grooves probably mark the bifurcation of the two posterior pairs, III and IV (*epi III*, *epi IV*). At

FIGURE 6. *Lawrenciella schaefferi* Poplin 1984: Reconstruction of the endocranium in dorsal view.
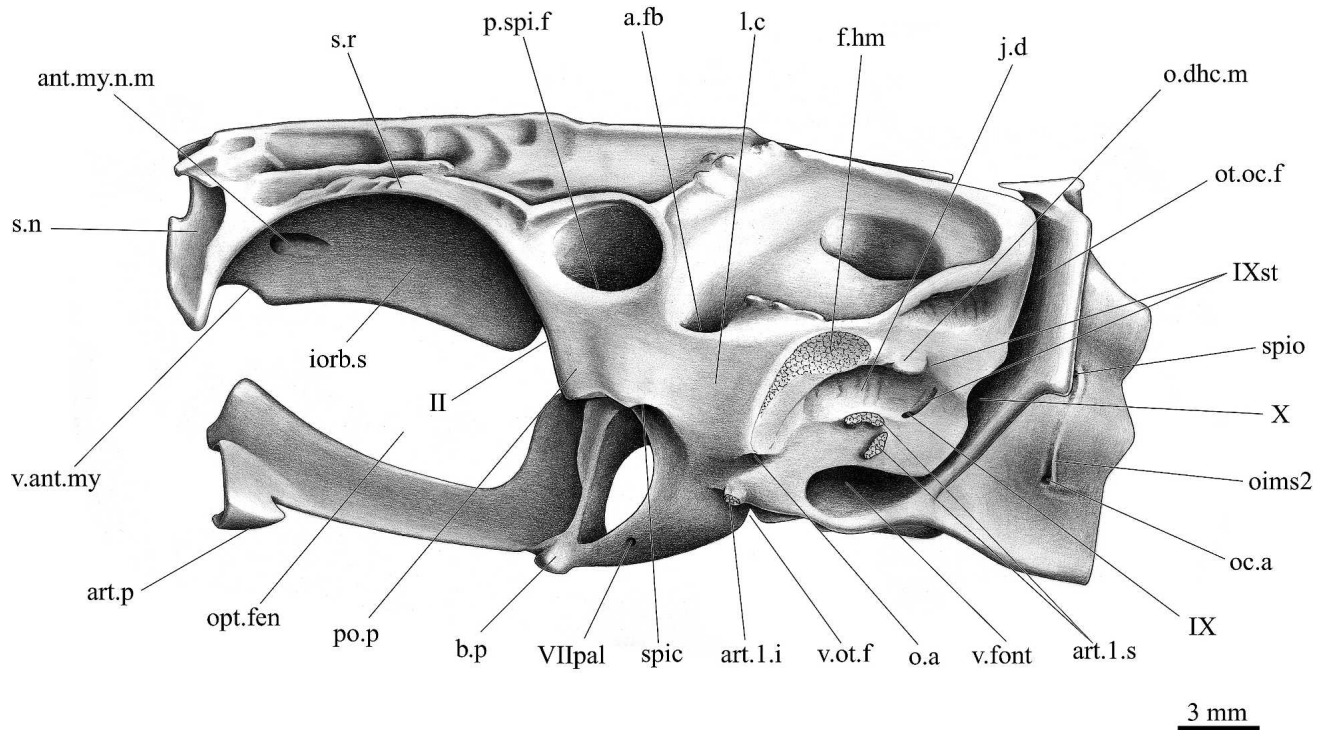
FIGURE 7. *Lawrenciella schaefferi* Poplin 1984: Reconstruction of the endocranium in lateral view. Reticulated areas: not perichondrally lined surfaces.

its anterior extremity, the aortic canal exits through a single bilobate opening (*ao.c*), for the lateral aortae, which lies behind the ventral otic fissure. These conditions differ from those of *Kansasiella eatoni*, which has paired exits for the epibranchial arteries and the lateral aortae. After leaving the aortic canal, each lateral aorta could have immediately given off the epibranchial arteries I and II (*epiI*, *epiII*), and anteriorly the efferent hyoidean artery (*e.hy.a*) and the orbital artery (*o.a*).

Lateral to the posterior myodome, are two foramina that directly communicate with its floor (*VIIpal*). After leaving the trigeminofacialis chamber (see text below for details), the palatine branches of the facial nerve passed through these foramina to exit on the ventral face of the cranium. We can also assume, as observed in embryos of *Lepisosteus* and *Salmo* (De Beer, 1927, 1937), that these foramina may have also transmitted the orbitonasal arteries which are given off from the internal carotids as the latter pass under the pars basisphenoidea. The palatine nerves pass through the floor of the posterior myodome in a similar position in *Kansasiella eatoni* (Poplin, 1974:Pl. XX fig. 2).

The basipterygoid processes (*bp*) are massive but relatively less developed than in *Kansasiella eatoni* (Poplin, 1974:fig. 14) or *Pteronisculus stensiöi* (Nielsen, 1942:fig. 6). Medially to each, on the ventral face, there is a V-shaped groove formed by two distinct grooves joining each other laterally to a large opening at the base of the pars basisphenoidea (*bsph*). At this level, the internal carotid (*int.car*), housed in the posterior groove, gave off laterally the efferent pseudobranchial artery (*e.ps.a*) housed in the anterior groove; and, anteriorly, the palatine artery (*pal.a*) (see also Fig. 14A). The latter and its ramifications lay forwards in grooves on the ventral face of the orbital region. The palatine nerve (*VIIpal*) was probably parallel to the artery in this region.

The ventral surface of the posterior myodome is perforated by the opening for the bucco-hypophysial canal (*bhc*). As in *K. eatoni*, this canal is particularly short. It is orientated upwards and backwards through the pars basisphenoidea and exits

into the anterior part of the unpaired posterior myodome (*my*) (Fig. 11).

The posterior part of the orbital cavity (Fig. 10) displays the high pars basisphenoidea which divides the anterior opening of the posterior myodome into two large symmetric and rounded fenestrae. In contrast to *K. eatoni* (Poplin, 1974:fig. 15), the *pars basisphenoïdea* has no symmetric apertures communicating with the posterior myodome. At its base are two deep, cup-shaped depressions which probably are the right and left insertions of the superior, inferior and internal recti muscles (*o.rec.m*). On its anterior face are two vertical and parallel grooves which housed the internal carotids between the floor of the endocranium and the braincase cavity. Unlike *K. eatoni*, the internal carotids (*int. car*) penetrated the braincase through two separate canals opening anteriorly to the pituitary fossa (see also Fig. 11). The external edge of each vertical groove of the pars basisphenoidea is notched by a short perpendicular groove which is probably the passage of the great ophthalmic artery (*g.oph.a*). This arterial arrangement differs from that of *K. eatoni*, the ophthalmic artery of which separates from the internal carotid near to its union with the efferent pseudobranchial artery (Poplin, 1974:Pl. 26, fig. 1).

Above the entrances of the internal carotids, two small grooves extend up on both sides of the optic foramen. They mark the passage of other collaterals of the internal carotids, the optic arteries (*opt.a*), which should probably extend forwards, alongside the ocular tract before entering the eyeball (see also Fig. 14A).

The braincase displays two symmetric small foramina (*s.oph.a*) dorsally and laterally to the optic foramen. Such foramina or notches have been described as external openings for the optic arteries in *Pteronisculus* (Nielsen, 1942:figs. 10, 16), *Coccocephalus* (Poplin and Véran, 1996:fig. 7) and in *Kentuckia* (Rayner, 1951:fig. 7, 9). However, the optic artery (=central retinal artery) in *Amia* arises from the anterior cerebral artery rather in a
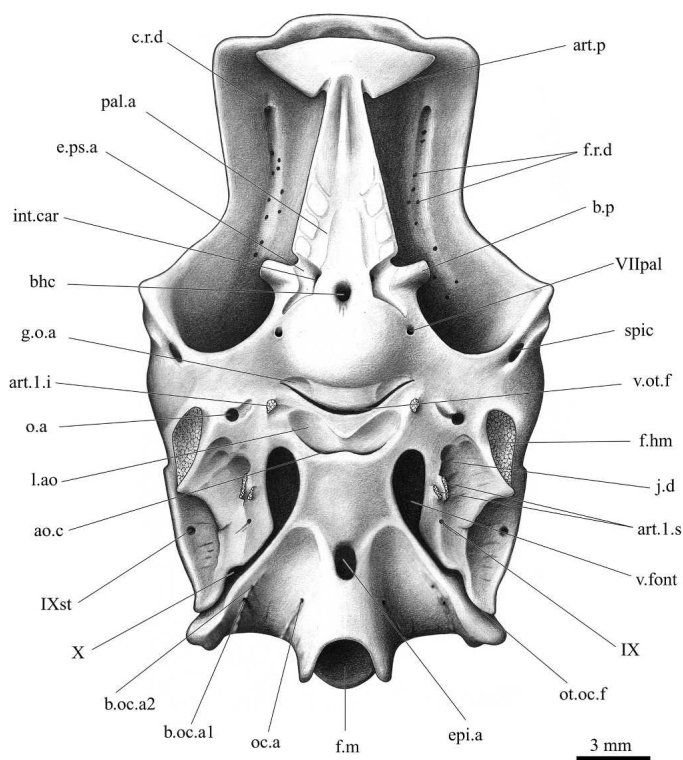
FIGURE 8. *Lawrenciella schaefferi* Poplin 1984: Reconstruction of the endocranium in ventral view. Reticulated areas: not perichondrally lined surfaces.
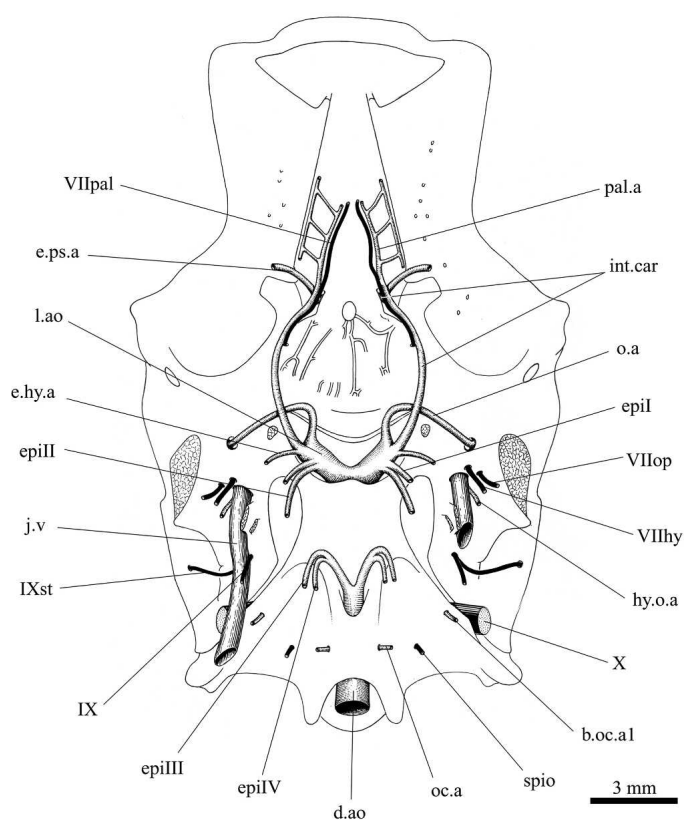

FIGURE 9. *Lawrenciella schaefferi* Poplin 1984: Reconstruction of the cephalic blood supply and cranial nerves in ventral view.

more ventro-lateral position relative to the ocular tract (De Beer, 1937). This is also the case in teleosts (Zwehl, 1961). We suggest, based on the arrangement in *Amia* (Bjerring, 1977), that in *L. schaefferi*, these foramina transmitted a branch of the anterior cerebral artery, i.e, the small ophthalmic artery, which arises and emerges into the orbit above the optic tract.

On the sidewall of the braincase, the orbital openings for the profundus (*Vo*) and oculomotor (*III*) nerves lie midway between the exit of the trigeminofacialis chamber and the optic foramen. Generally, *L. schaefferi* has a double exit for the oculomotor nerve, in front of that of the profundus foramen (see below). The trochlear nerve (*IV*) issues as usual in a high position, slightly in front of the oculomotor foramina. The external opening for the anterior cerebral vein (*ant.c.v*: Figs. 11, 13, 14A) lies well forward, on the left side only as in *K. eatoni*.

The gaping anterior aperture of the jugular canal (*j.c*) lies in a relatively high position. The medial wall of the jugular canal, just behind the ridge between the trigemino-facialis chamber (*tr.f.ch*) and the myodome (*my*), has a deep irregular recess that housed the geniculate ganglion (*r.gen.g*). The roof of the opening also shows a large recess for the gasserian and lateralis ganglia (*r.gass.lat.g*) (see details below).

In sagittal view (Fig. 11) the prootic bridge (*pr.b*) constitutes the median part of the roof of the posterior myodome (*my*), the wall which covers spaces for the pituitary (*pit*), and the saccus vasculosus (*s.vasc*). The deep, unpaired and large posterior myodome housed left and right external recti muscles. The myodome has no ventral fenestra and, compared to that of *K. eatoni*, is deeper and its posterior extremity is more rounded. Its roof is pierced by a large pituitary fontanelle (*pit.fon*). Behind this, the roof of the myodome has a medial short crest. The abducens nerve penetrates the posterior wall of the myodome through an anterolaterally directed canal (*VI$_2$*). This canal displays in some specimens a distinct widening before its entrance

into the myodome. This feature probably indicates that the abducens nerve entered the myodome as two or more separated branches. Below and in front of the exit of the abducens nerve lies a deep, antero-ventrally directed groove (*pit.v*) which probably marks the path of the pituitary vein (see also Fig. 14A). Having drained the hypophysial area, this vein probably ran dorsally and laterally to the external rectus muscle before emptying
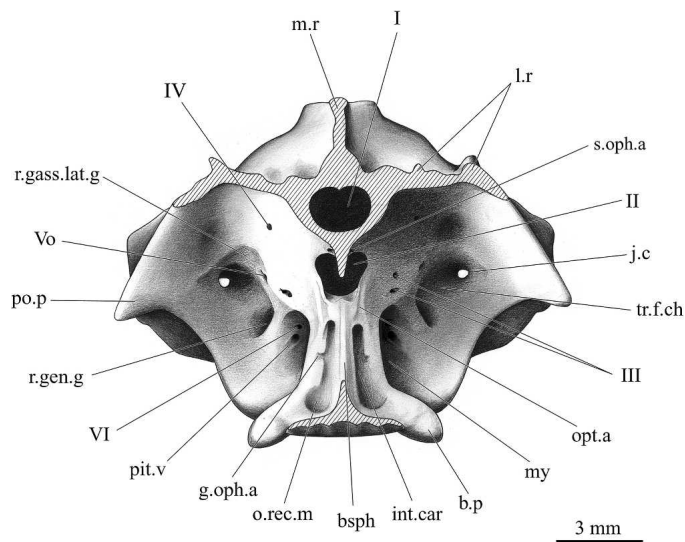

FIGURE 10. *Lawrenciella schaefferi* Poplin 1984: Reconstruction of the posterior part of the orbitotemporal region in anterior view. Bone sections hatched.
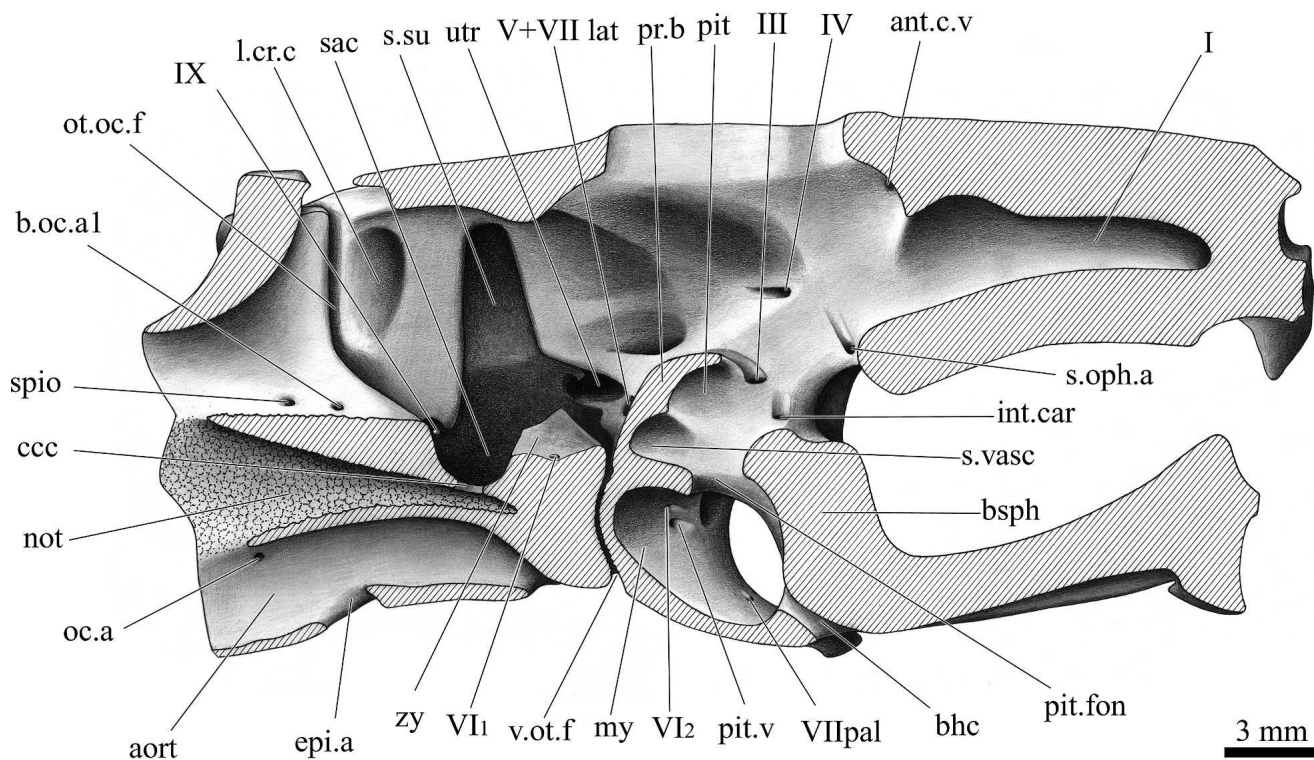
FIGURE 11.   *Lawrenciella schaefferi* Poplin 1984: Reconstruction of the braincase in longitudinal section. Reticulated area: not perichondrally lined surface. Bone sections hatched.

into the jugular vein. These grooves seem to be homologous to similarly directed grooves in the posterior myodome of *K. eatoni* (Poplin, 1974: Pl. XVII fig. 4), which were interpreted as passages for the palatine nerves.

Occipital Region—The occipital region is similar to that of *K. eatoni*; however, more stout and wider (Figs. 7, 11, 12, 20C, 20D).

Posteriorly (Fig. 12), the occiput is pierced by a diamond-shaped aperture, which contains three superimposed openings: the foramen magnum on top (*fm*), the posterior opening of the notochordal canal below (*not*), and the opening of the aortic canal ventrally (*aort*). The foramen magnum is large and trian-
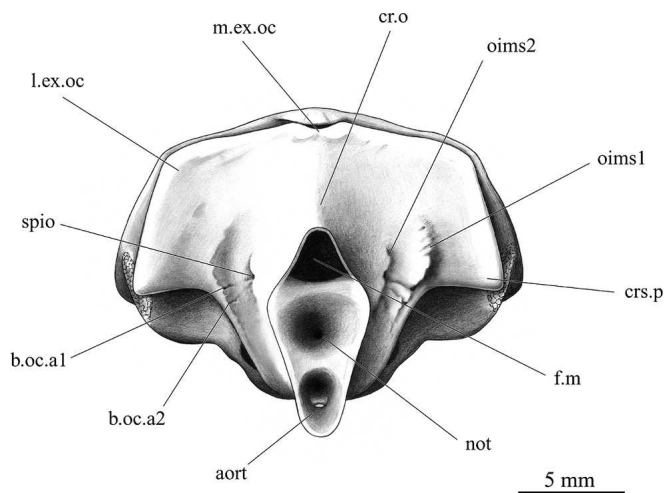

FIGURE 12.   *Lawrenciella schaefferi* Poplin 1984: Reconstruction of the endocranium in posterior view. Reticulated areas: not perichondrally lined surfaces.

gular. Above, lies the sagittal *crista occipitalis* (*cr.o*) which is not very prominent. On the dorsal edge of the occipital ossification are two dorso-lateral prominences (*l.ex.oc*), which might correspond to epioccipitals (cf. Patterson, 1975). On the lateral edges arise two craniospinal processes (*crs.p*). On each side of the median aperture lie two vertical ridges. The lateral one (*oims1*) rises on a level with the aortic canal, thickens gradually upward at the craniospinal process level and fades out a little above the foramen magnum. The medial ridge (*oims2*) is shorter and rises behind the foramen for the occipital artery (Fig. 7). Then it extends vertically toward the distal opening of the spino-occipital nerve (*spio*) and terminates posterodorsally to it. These ridges correspond respectively to the areas for the insertion of the first and the second intermuscular septa.

In front of the area of insertion of the second intermuscular septum lies a groove for the occipital artery (*oc.a*). The path of the occipital arteries on the lateral and dorsal surfaces of the occiput are almost similar to those described in *Mimia toombsi* (Gardiner, 1984:figs. 4–6). As for *Mimia*, a groove leads up from the foramen for the occipital artery to the foramen of the spino-occipital nerve (*spio*). Just below the latter, the groove bifurcates (Fig. 12). Its dorsal branch leads, through a gap in the area of insertion for the first intermuscular septum (*oims1*) to a small foramen (*b.oc.a1*) which is the distal opening of a canal that leads to the anterior floor of the foramen magnum. This canal, also present in Gogo 'Palaeonisciformes' (Gardiner, 1984:fig. 26) and in *Kansasiella eatoni* (Poplin, 1974:fig. 20), probably transmitted a branch of the occipital artery. From this small foramen, the groove continues and passes up toward the top of the occiput just in front of the area of insertion for the first intermuscular septum. This part of the groove probably marks the path of a dorsal branch of the occipital artery, which should have supplied blood to the first trunk muscle. The second branch of the groove leads to a more ventral gap where lies a second smaller foramen

(*b.oc.a2*), which is presumably a passage for another branch of the occipital artery, but it was not possible to establish where the canal leads.

On each side of the inner wall of the foramen magnum (Fig. 11), there are two small foramina. The posterior one (*spio*) is the proximal opening of a dorsolaterally directed canal that probably housed a spino-occipital nerve. The anterior one (*b.oc.a1*) is the proximal opening of a canal which probably transmitted a branch of the occipital artery. The posterior entrance of the aortic canal (*aort*) is narrow, slightly shorter than in *K. eatoni*, and coalescent with the entrance of the notochordal canal (*not*). The walls of the aortic canal are pierced by single dorsolaterally directed canals (*oc.a*) for the occipital arteries.

The notochordal canal (*not*) is conical and not perichondrally lined. Unlike the other basal actinopterans where this canal is known, its anterior extremity ends blindly in the bone, behind the ventral otic fissure. The roof is pierced by a large opening towards the endocranial cavity (*ccc*). This unossified area has been observed in all palaeoniscoid braincases known so far and it was possibly closed by cartilage during life.

The zygal plates (*zy*) correspond to a median ossification formed by two blades arising laterally on the anterior roof of the notochordal canal. The blades are thin and roughly triangular in shape. They are covered with perichondral bone dorsally and are fused to the underlying basioccipital ossification. Medially, each blade is pierced by a small foramen for the abducens nerve. The course of the abducens nerve through the occipital ossification could be traced mainly from the three-dimensional models. Forwardly it penetrates at first into the single foramen (*VI₁*), which lies on the medial surface of the zygal plate as indicated previously. Then it passes down through the occipital ossification via

an antero-ventro-laterally directed canal which opens into the saccular cavity. At this point, it goes forwards through the sacculus against its inner wall where it digs a deep and narrow groove (*VI₁*, Fig. 13B). Having crossed the sacculus, the abducens passes forwards across the ventral otic fissure and enters the posterior wall of the prootic bridge (*VI₂*, Figs. 11, 13B). A similar passage through the basioccipital ossification has been reported in *Mimia* (Gardiner, 1984:fig. 25). The abducens nerve penetrates the zygal plates also in *K. deani* (Rayner, 1951:fig. 10) and possibly in the 'Palaeoniscid C.'

Internal Anatomy

The "Brain Cast"—The cranial cavity is small and the brain was probably very closely surrounded by bone since the various portions of the brain are easily distinguishable on the natural endocasts (Figs. 13–15, 21A, 21B).

The telencephalic part (*tel*) includes the telencephalon, which corresponds to an unpaired small swelling bounded posteriorly by the epiphysial part of the anterior fontanelle and anteriorly by the paired olfactory bulbs (*olf.b*). The telencephalon and the olfactory bulbs are clearly distinct. The telencephalon is separated from the diencephalon (*die*) behind by a very light constriction visible in dorsal and ventral views. The telencephalon is very small, like in all lower actinopterans in which this structure could be observed, as it is narrower than the olfactory bulbs. The two olfactory nerves (*I*) extend from the olfactory bulbs to the ethmoidal region through a bony canal that bifurcates before its entrance into the nasal cavity. The anterior cerebral vein (*ant.c.v*) is visible on the left side only, in front of the anterior dorsal fontanelle, as in *Kansasiella*. From this point, its short
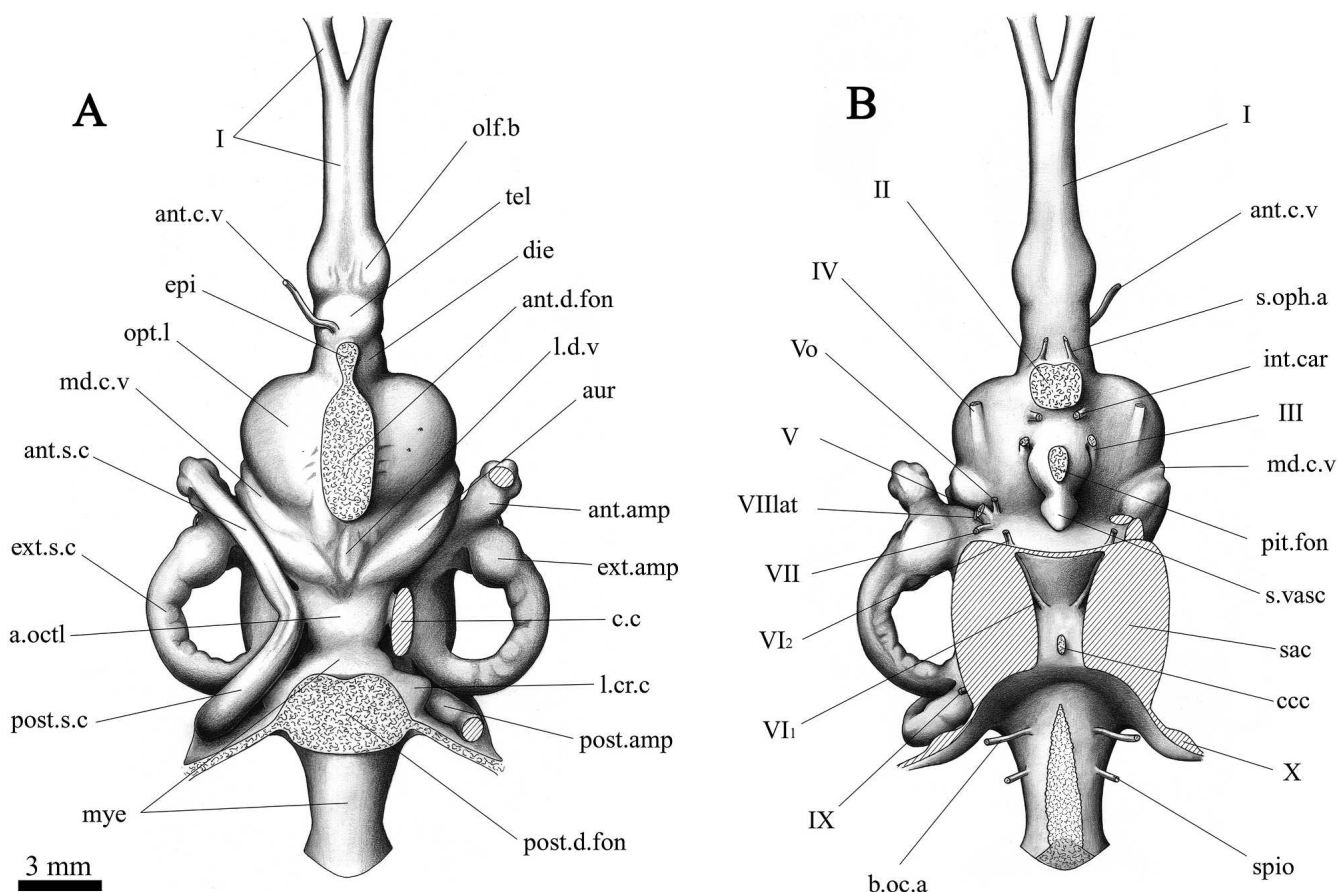

FIGURE 13. *Lawrenciella schaefferi* Poplin 1984: Reconstruction of the cast of the cranial cavity in dorsal (**A**) and ventral (**B**) views. Cast sections hatched.
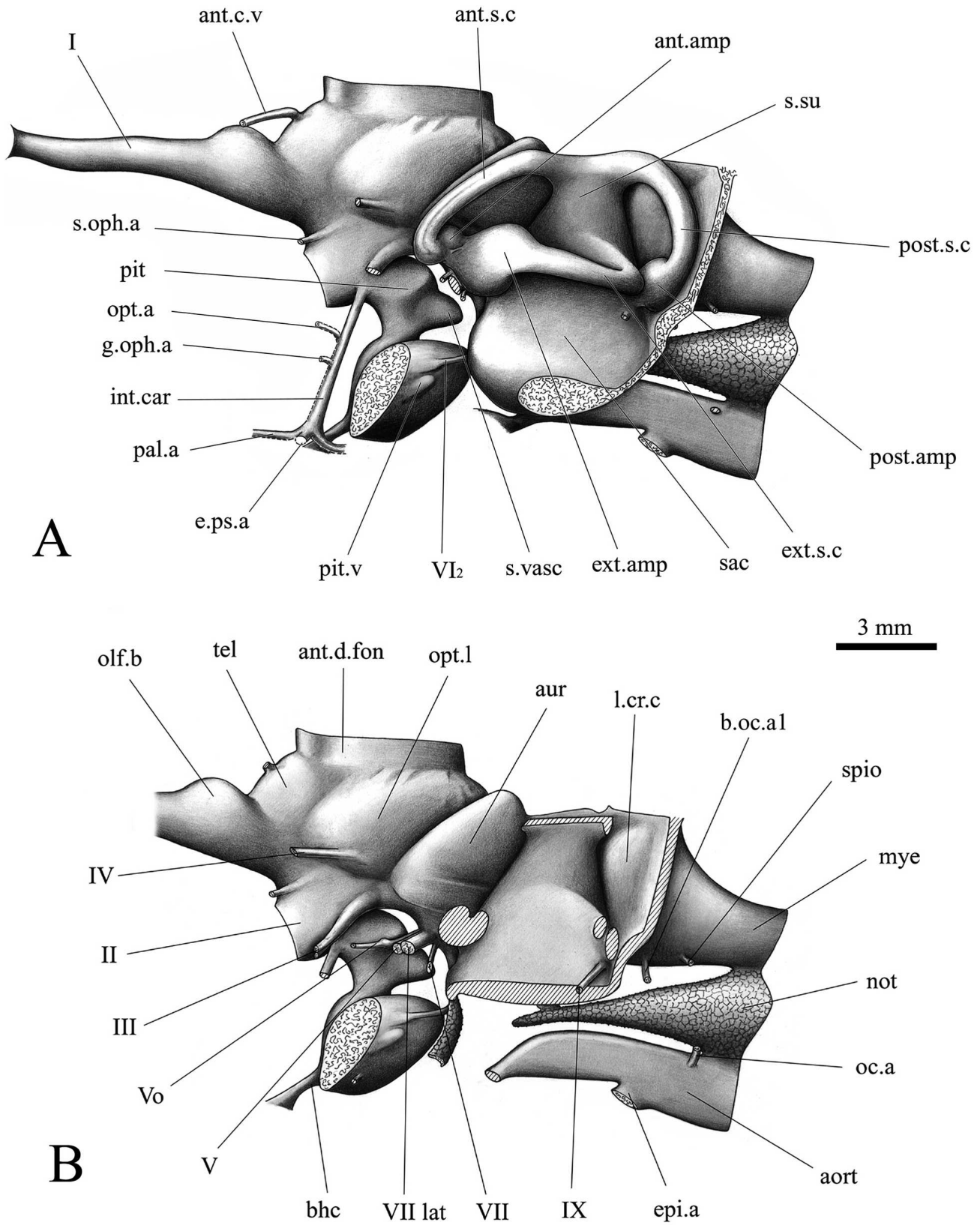
FIGURE 14. *Lawrenciella schaefferi* Poplin 1984: Reconstructions of the cast of the cranial cavity in lateral views: (**A**) with the otic labyrinth; (**B**) otic labyrinth removed. Cast sections hatched.
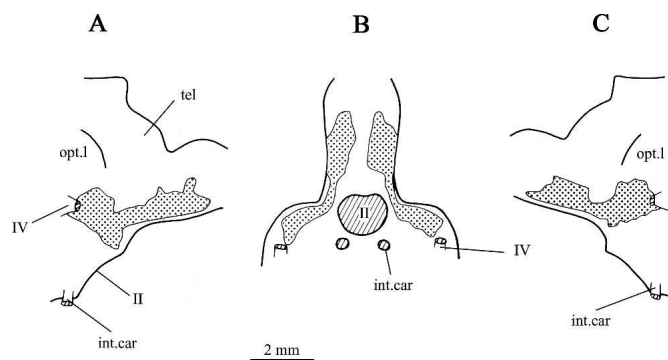
FIGURE 15. *Lawrenciella schaefferi* Poplin 1984: Schematic reconstruction of intracranial ossicles on a natural cast of the endocranial cavity (after UK 56374). Stippled areas: ossicles; **A**, right lateral view; **B**, ventral view; **C**, left lateral view. Modified from Poplin (1982).

FIGURE 16. *Lawrenciella schaefferi* Poplin 1984: Reconstruction of the cast of the orbito-temporal region with the trigeminofacialis chamber and posterior face of the orbit (viewed from above) mainly after UK 56372.

canal runs in an antero-latero-ventral direction and emerges in the orbit well in front of the foramen for the trochlear nerve.

In dorsal view, the diencephalic region (*die*) is restricted to the short part placed immediately in front of the optic lobes (*opt.l*), and beneath the epiphysial part of the anterior dorsal fontanelle. The diencephalon probably extended backward under the mesencephalon as in extant actinopterygians. The floor of the diencephalon extends deeply downward, but no inferior lobes can be distinguished. The floor is pierced by the two narrow canals for the small ophthalmic arteries (*s.oph.a*) and, immediately behind them, by the single optical foramen (*II*) followed by the internal carotid arteries (*int.car*), the large hypophysial recess (*pit*) and the saccus vasculosus (*s.vasc*). The hypophysial recess (*pit*), which opens in the roof of the posterior myodome through an ovoid pituitary fontanelle (*pit.fon*), is more conspicuous in *L. schaefferi* than in *Kansasiella eatoni*, and is very similar to that of *Mesopoma planti* (Coates, 1999:fig. 6). The saccus vasculosus (*s.vasc*) is pear shaped and shorter than that of *K. eatoni*. It communicates forward with the hypophysial recess through a wide aperture.

In many specimens, the wall of the diencephalic and the mesencephalic regions is internally covered by paired intracranial ossicles which lie laterally and in front of the optic foramen (Fig. 15). Their function, if they had any, remains unclear. According to Poplin (1982) they may be derived from dorsal arcual elements.

The mesencephalic region is well developed with two large optic lobes (*opt.l*). They are wider and more spherical than those of *K. eatoni* and, in lateral view, are easily distinguishable from the diencephalic part. Their bipartition is hidden by the anterior dorsal fontanelle. The floor of the mesencephalic region is pierced by the canals for the trochlear nerves (*IV*). The oculomotor canal (*III*) arises on both sides of the hypophysial recess. The nerve is directed antero-ventro-laterally to the posterodorsal wall of the orbit. The oculomotor canal generally is divided into dorsal and ventral branches before reaching the orbit (Fig. 16). The dorsal canal probably transmitted branches of the oculomotor nerve which innervate the superior and internal recti muscles, whereas the ventral one transmitted branches for the inferior rectus and inferior oblique muscles. These two orbital openings lie one above the other, the ventral one in front of the exit of the profundus nerve (Fig. 10).

Behind the optic lobes is the cast of paired large cerebellar auricles (*aur*), which constitute the main part of the metencephalic region. As in the other Kansas forms, the *corpus cerebelli* could not be identified. Between the cerebellar auricles there is a longitudinal ridge marking the position of a median venous sinus (*l.d.v*), which extends between the optic lobes. A
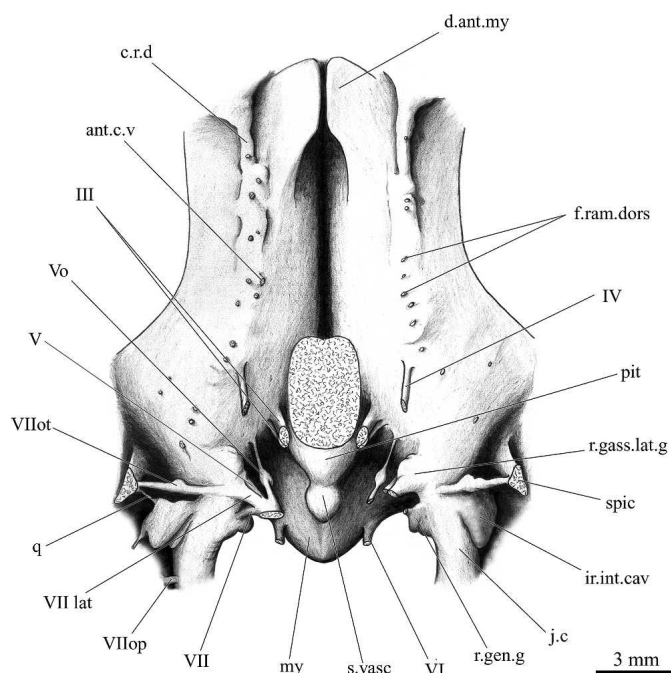
similar vessel has been reported in 'Palaeoniscid C' (Moodie, 1915:fig. 15) and in *Mesopoma planti* (Coates, 1999:Fig. 6). According to Coates, this vessel corresponds to the longitudinal dorsal vein (according to Zwehl, 1961). The courses of the middle cerebral veins (*md.c.v*) are preserved as ridges along the anterodorsal part of the cerebellar auricles. These ridges extend down to the anteroventral corners of the cerebellum. From these points (Fig. 13B), the middle cerebral veins probably entered the cranial wall to exit into the orbit a little forward as in *K. eatoni* (Poplin, 1974:'v,' fig. 20; Pl. XXV, fig. 2). Ventrally to the auricles and to the utricular recesses, emerge four distinct canals for the profundus (*Vo*), trigeminal (*V*), facial (*VII*) and lateralis (*VII lat*) nerves. The long and narrow canal for the profondus nerve (*Vo*) originates near the trigeminal canal and emerges by a separate foramen more or less near the exit of the oculomotor nerve (*III*), according to the specimens. A swelling in the middle of the canal indicates the position of the profundus ganglion (Fig. 16). Unlike *K. eatoni*, this canal is never confluent with the canal for the trigeminal nerve. The paths of the trigeminal and facial nerves are described below. The posterior portion of the metencephalic region is pierced by the roots of the abducens nerve (*VI*) between the two saccular recesses (*sac*).

In Actinopterygians, the myelencephalon is not clearly distinct from the metencephalon and, for this reason this region in *L. schaefferi* is difficult to interpret. Coates (1999) proposed that, in *Mesopoma planti*, the swelling behind the cerebellar auricles, divided by a medial groove, corresponds to the *corpus cerebelli*. The endocast of *L. schaefferi* presents an equivalent bulging, although less prominent, in a similar position (*a.octl*). However, following the interpretations made of *K. eatoni* (Poplin, 1974), *Pteronisculus* (Nielsen, 1942), *Boreosomus reuterskiöldi* (Véran, 1971), and 'Palaeoniscid C' (Moodie, 1915), we think that this swelling in *L. schaefferi* corresponds rather to the area octavolateralis of the rhombencephalon, which receives the acoustic nerve and lateral line roots. In recent Actinopterygians, this particular region of the rhombencephalon is characterized by the

presence of tubercles (*tubercula acoustica*). Moodie (1915) identified these structures on the endocasts of *Kentuckia deani* and of 'Palaeoniscid C.' However, unlike these genera, the area octavolateralis of *L. schaefferi* shows no lobes or ridges. There is only a smooth surface in continuity with that of the cerebellum, which is compressed laterally between the utricular sinuses and widened backward to form a light convexity in front of the posterior dorsal fontanelle. Behind the latter, the myelenphalon recovers a cylindrical shape, its diameter decreases gradually back to the foramen magnum. The floor of the myencephalic region is pierced by the roots of the canals for the spino-occipital nerves (*spio*) and for branches of the occipital arteries (*b.oc.a*). The lateral cranial canal (*l.cr.c*) is a small intramural pocket projected through the loop of the posterior semicircular canal. It communicates posteriorly with the myelencephalic cavity, in front of the otico-occipital fissure through a large, oval and high aperture. The lateral cranial canal never communicates with the posterior fossa bridgei.

Labyrinth—The endocast of the labyrinth region, visible in many specimens, is particularly well preserved on specimen UK 21984 (Figs. 11, 13, 14, 21F). The inner ear has the typical actinopterygian morphology: three semicircular canals, a utriculus situated in the crus commune of the anterior and horizontal semicircular canals, and a saccular (or sacculo-lagenar) pouch.

The saccular recess (*sac*) is deep and wide, almost squared in lateral view. No distinct lagena is visible in the casts.

The sinus superior (*s.su*) and the utricular recess (*utr*) largely communicate with the myelencephalic cavity (Fig. 11). The three semicircular canals (anterior, external, posterior), their respective ampullae, and the sinus superior are rather similar to those of *K. eatoni*. The only notable difference are that, in *L. schaefferi*, the sinus superior is longer, the crus commune lying just below the endocranial roof, and the utricular recess is more conspicuous. The anterior semicircular canal is slightly longer and less curved compared to that of other basal actinopterans.

No otoliths nor otoconia have been preserved. Presumably the large saccular recess could have contained at least one large polycrystalline otolith. The presence of an endolymphatic duct could not be determined.

Lateral Commissure and Trigeminofacialis Chamber—The lateral commissure encloses a long jugular canal (*j.c*) (Figs. 16, 17, 20E, 21E). The posterior part of this canal is perforated ventrally by the large canal for the orbital artery (*o.a*), while the antero-mesial part is pierced by the facial (*VII*) and trigeminal (*V*) canals that originate medially to the utricular recess.

In basal actinopterans such as *Kansasiella eatoni* (Poplin 1974:fig. 24) or *Pteronisculus stensiöi* (Nielsen, 1942:fig. 15), there are two distinct canals coming from the cerebral cavity down to the trigeminofacialis chamber. The first of them, the widest, opens into the anterodorsal part of the chamber, and transmitted both the trigeminal nerve and the lateralis branches of the facial nerve (superficial ophthalmic, buccal and otic branches). The second canal opens posteroventrally to the former and serves for the palatine, hyomandibular and opercular trunks of the facial nerve. In many natural endocasts of *L. schaefferi* the first canal mentioned above shows an incomplete horizontal splitting. Very likely, the dorsal wide canal, originated from this division, transmitted the lateralis branches of the facial nerve (*VII lat*), whereas the ventral canal, narrower and placed a little forward, should have transmitted the trigeminal nerve (*V*). At the posterior part of the trigeminofacialis chamber opens a third canal (*VII*), narrow and posteroventrally directed, which should have served for the facial nerve. *L. schaefferi* displays no distinct canal for the superficial ophthalmic branch of the facial nerve leading to the posterior wall of the orbit.

The ganglia of the trigeminal, facial and lateralis nerves were clearly extracranial as they were lodged in unusually deep recesses onto the roof and floor of the trigeminofacialis chamber.
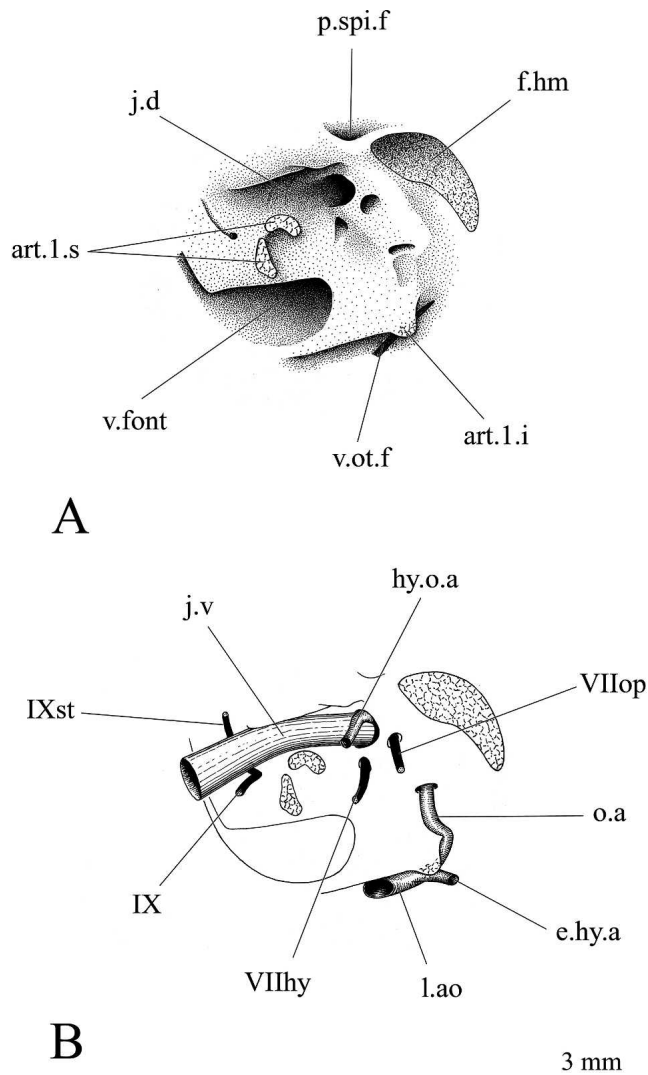

FIGURE 17. *Lawrenciella schaefferi* Poplin 1984: The posterior opening of the right jugular canal in posterolateral view. **A**, endocranial surface; **B**, with blood supply and nerves.

In *Amia* (Norris, 1925: Fig. 13) and *Polypteus* (Allis, 1922; Piotrowski and Northcutt, 1996: Fig. 6), there is a distinct lateralis ganglion (facial nerve) which lies above the gasserian ganglion (trigeminal nerve). By comparison to these taxa, we infer that the large anterior swelling below the roof of the trigeminofacialis chamber housed both ganglia, in similar positions (*r.gass.lat.g*). The recessus for the geniculate ganglion (*r.gen.g*) lies posteriorly on the floor of the jugular canal, in front of the issue of the facial nerve. From this ganglion, the palatine branch of the facial nerve was directed forward toward the orbit, whereas the hyomandibular and opercular trunks (*VIIhy*, *VIIop*) were directed backwards and left the jugular canal by two separate posterior openings. These two openings are placed ventral and lateral to the entrance of the jugular canal (Fig. 17). Natural casts of the canals issuing in these foramina are visible in the specimen UK 22-46 (Fig. 21E).

The otic canal (*VIIot*) originates laterally under the roof of the trigeminofacialis chamber, opposite to the issue of the lateralis canal, and opens into the top of the spiracular canal (*spic*). It often communicates or is incorporated into wide and unusual intramural cavities (*ir.int.cav*) the interpretation of which will be discussed further below.

In *L. schaefferi*, as in all lower actinopterans, except *Moythomasia* (Gardiner 1984:fig. 29), there is no palatine foramen in the floor of the jugular canal. The palatine nerve passed through the orbital opening of the jugular canal and directly entered the passage into the floor of the myodome toward the parabasal canal (*VIIpal*:fig. 9).

The hyo-opercular artery (*hy.o.a*), branched from the orbital artery (*o.a*), probably went out from the jugular canal through its posterior opening.

Lateral to each jugular canal, *L. schaefferi* displays wide and irregular intracranial cavities (*ir.int.cav*: Figs. 16, 20E). They communicate with the jugular canal, behind and below the origin of the VIIot canal, and with the spiracular canal via a separate canal (*q*) which, in some specimens, seems to have merged with the VIIot canal. These intracranial cavities also communicate with the lower part of the facet for the hyomandibula. Poplin (1974:Pl. XXV, fig. 1,*VIIop* or *a.hy.o?*) noticed in *K. eatoni* the presence of a short and sinuous canal that originates on the jugular canal, behind the otic canal, and exits on the posterior edge of the jugular canal. From this canal emanates a narrow distinct canal (*b*) that joins the otic canal near to the spiracular canal. These sinuous and rectilinear canals seem to be homologous with the intracranial cavities associated with canaliculi found in *L. schaefferi*. The irregular aspect of these intracranial spaces excludes the possibility that they housed arteries or nerves. They rather housed dilated canals of the lymphatic or venous system. In *Amia*, the middle cephalic lymph sinus (Bjerring, 1977:figs 2b, 3) is a dilated part of the lymphatic system that empties into the jugular vein in a similar position with the cavities described above. However, these cephalic sinuses are extracranial structures, which are interposed between the endocranium and the hyomandibula. Another possibility is that hemopoietic organs filled these spaces in *L. schaefferi* but, among osteichthyans, such organs have never been found in this position.

PARASPHENOID

The parasphenoid (Figs. 18, 20A, 21D), is the only dermal bone preserved. It is known mainly from isolated, fragmentary specimens. Some of these are partially preserved on the ventral face of the endocranium.

The anterior ascending processes (*ant.asc.p*) are faint and cover only the base of the endocranial basipterygoid processes. Their anterior margin display a notch and a short groove for the passage of the efferent pseudobranchial artery (*e.ps.a*). Each posterior ascending processes (*post.asc.p*) extends as far as the lateral commissure and terminates in front of the lower openings of the spiracular canals. Behind the posterior ascending pro-

cesses and below the posterior myodome, the parasphenoid is short, rounded and reaches the ventral otic fissure without covering it. It covers the internal carotids, the palatine branches of the facial nerves and possibly part of the orbital arteries.

Ventrally (Fig. 18A), the parasphenoid displays a narrow median area bearing numerous small teeth, and which extends back to the anterior half of the area covering the posterior myodome. Two deep spiracular grooves (*spi.g*) run along the posterior ascending processes.

Dorsally (Fig. 18B), at the level of the endocranial opening of the bucco-hypophysial canal, the parasphenoid bears an irregular lump similar to that of *Kansasiella eatoni* (Poplin, 1974:fig. 8B). In other basal actinopterans, the parasphenoid displays in the same place a small depression or an opening for the buccohypophysial duct into the roof of the mouth. From this bony lump extends forwards a stout median ridge bearing anteriorly a longitudinal slit (*l.sl*), which fits with the narrow ridge rising on the ventral surface of the endocranium

DISCUSSION

Because the aim of the present paper is not to propose a new phylogenetic hypothesis for Actinopterygii, we will use the recent works devoted to actinopterygian relationships to determine the possible relationships of *Lawrenciella schaefferi*.

The systematic position of *L. schaefferi* has been previously discussed by Poplin (1984). That author concluded that *L. schaefferi* is closely related to the order of 'Palaeonisciforms,' but the monophyly of this group is not established. That author also reported the difficulties in establishing the systematic status of this taxon, as it is only known by its braincase and parasphenoid. Indeed most of the characters used in phylogenetic studies concerning lower actinopterygians are based mainly on the exoskeletal osteology (for historical review see Cloutier & Arratia, 2004). In fossil actinopterygians, the endoskeletal features, particularly the braincase, are generally not, or poorly preserved, or hidden by the exoskeleton. This explains the limited number of taxa the endocranium of which is known: i.e., only 18 stemactinopterans taxa according to the phylogeny proposed by Gardiner and Schaeffer (1989). Furthermore, their descriptions are often incomplete: the detailed study of three dimensional structures often requires the use of modern methods of investigation as well as preparation of three-dimensional models, and, of course, such methods were not at hand in former times. Despite these limitations, it is possible to determine a more accurate position for *L. schaefferi* within the current actinopterygian phylogenies.

Because we are mainly concerned with endoskeletal features, we will only consider here the lower actinopterygians phylogenies in which neurocranial characters were included. Among the recent works using such characters, we can mention: Coates (1999), Cloutier and Arratia (2004), and Gardiner et al. (2005). The latter is a concise analysis based on 14 taxa only and 38 characters, among which 10 characters concern the braincase. This is basically an update of Gardiner and Schaeffer's (1989) analysis. The study from Cloutier and Arratia (2004) deals with 185 characters and a diversified range of lower actinopterygians including Devonian forms such as *Dialipina*. However only 8 neurocranial characters have been used and none of them represent an original contribution to the studies quoted above. The most complete work dealing with the taxonomy and phylogeny of actinopterygians including neurocranial features was made by Coates (1999). He used, for the first time, a significant number of endoskeletal features for inferring phylogenetic relationships: 10 characters originally used by Gardiner (1984) and Gardiner and Schaeffer (1989), and 7 new characters. In addition, Coates coded 9 new characters of the endocast, which were considered
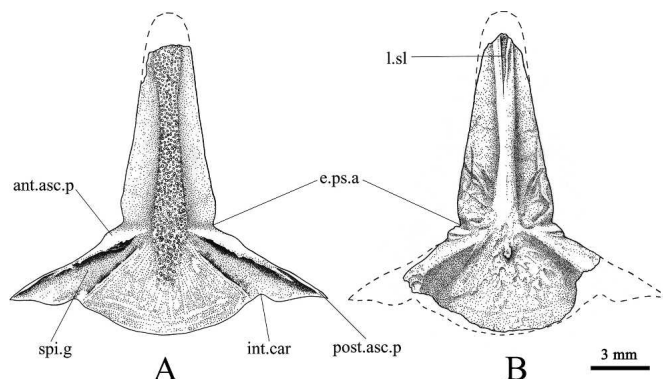

FIGURE 18. *Lawrenciella schaefferi* Poplin 1984: Reconstruction of the parasphenoid in ventral (**A**) and dorsal (**B**) views, mainly after UK 56377, UK 56379 and UK 56382.
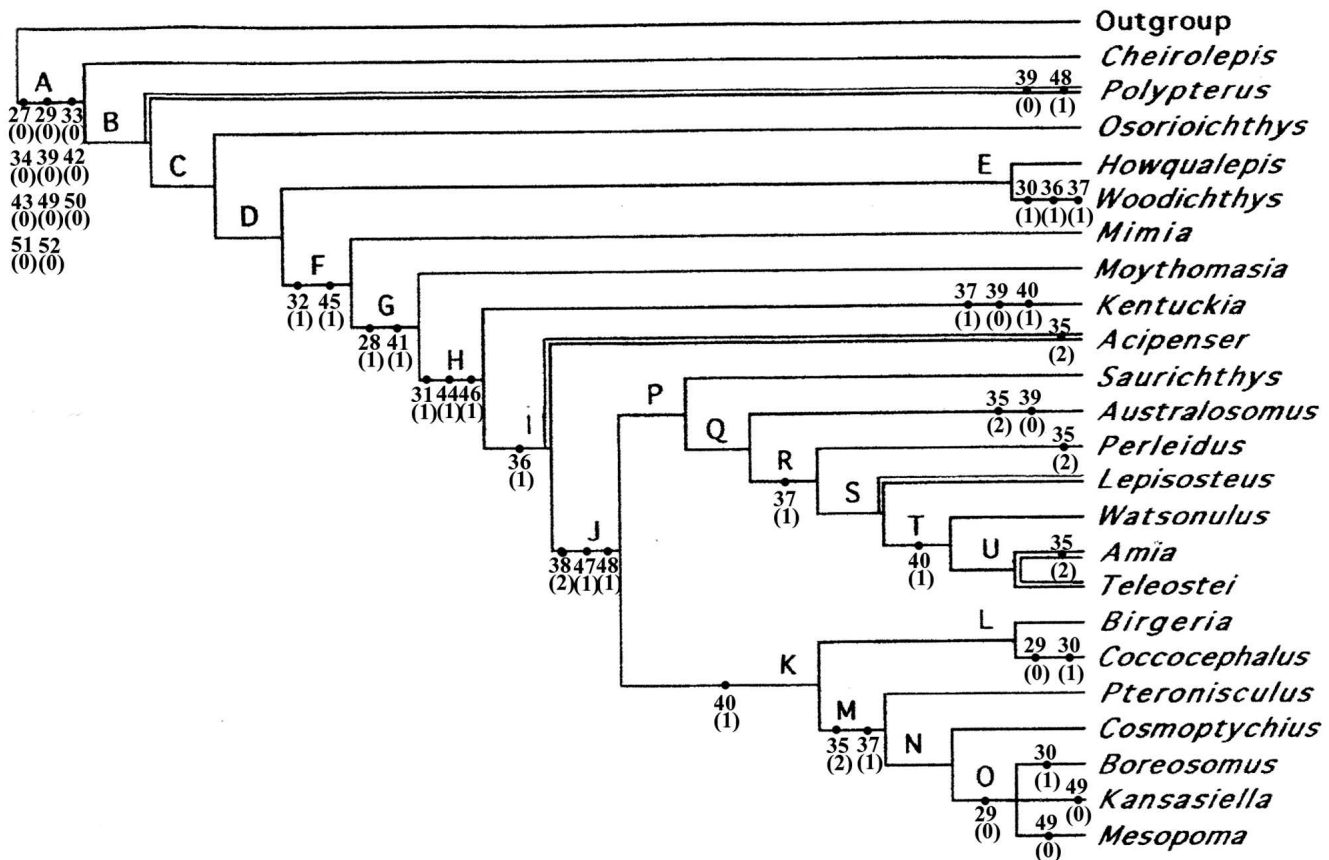
FIGURE 19. Coates' (1999:fig. 9) phylogenetic hypotheses of lower actinopterygians. In the cladogram are indicated the nodal positions and states of the characters present in *L. schaefferi* (see text).

as a reproduction of the gross morphology of the brain. A total of 64 anatomical characters were compiled for 23 taxa of extant and fossil actinopterygians. The tree was rooted on a hypothetical outgroup composed by primitive states were inferred from acanthodians, chondrichthyans and sarcopterygians.

Based on this latter analysis, we will try to determine the possible relationships of *L. schaefferi* among lower actinopterygians. Of course, the purpose of the following approach is not to include *L. schaefferi* into Coates's (1999) cladogram. This would be problematic due to the very large number of missing data. However, this approach shows the synapormophies shared by *L. schaefferi,* and may allow this taxon to be placed into the evolutionary scenario proposed by Coates. The characters present in *L. schaefferi* are listed below with using Coates' (1999) definitions, numbers and states. Their nodal position and states are represented on Figure 19.

Node A—The neurocranium of *L. schaefferi* and its endocast display the following primitive characters for actinopterygians: hyoid facet directed posteroventrally (27-0); ventral cranial-otic fissure separate from lateral-otico-occipital fissure (29-0); absence of post-temporal fossa (33-0); absence of dilatator fossa (34-0); absence of ventrally directed canal for palatine branch of facial nerve in the roof of posterior myodome (39-0); paired anterodorsal myodome (42-0); distinct dorsal and ventral anterior myodomes (43-0); hypophysial body, or cast of enclosing chamber, projects posteroventrally (49-0); cerebellar corpus divided into bilateral halves (50-0); cerebellar corpus enters fourth ventricle (51-0) and absence of cerebellar corpus with median anteriorly directed portion (52-0).

Node F—*L. schaefferi* shares the following synapomorphies with the actinopteran-stem lineage: lateral cranial canal present

(32-1) and orbit extending anteriorly relative to the olfactory bulb (45-1).

Node G—Spiracular groove enclosed within canal (28-1), and abducens foramen in dorsal position, level with dorsoventral midpoint of optic foramen (41-1).

Node H—*L. schaefferi* shares: fossa bridgei present (31-1); brain compact, with anteriorly directed parallel olfactive nerves (44-1) and optic tectum larger than telencephalon (46-1).

Node I—The parasphenoid of *L. schaefferi* shares the following character with the actinopteran crown-group: parasphenoid posteriorly expanded and reaching the ventral otic fissure without covering it (36-1). This differs from Coates' coding in which state 1 corresponds to "parasphenoid posterior expanded to cover ventral otic fissure." We adopt this coding here as it is more 'appropriate' than the other states.

Node J—*L. schaefferi* shares the following synapomorphies with the clade which originates here: canal for pituitary vein obliterated (38-2); olfactory bulb of similar size of the telencephalon (47-1) and optic tectum divided into bilateral halves (48-1) (called above 'optic lobes'). The latter character is also shared by *Polypterus*. It is interesting to notice here that, the chondrostean-neopterygian split proposed by Coates is mainly based in the gross features of the actinopterygian brain morphology.

Node P—This clade comprises neopterygians and fossil relatives.

Node K—This clade is composed of [*Birgeria+Coccocephalus*] and a 'palaeoniscid' clade, which includes *Pteronisculus*, *Cosmoptychius*, *Boreosomus*, *Kansasiella,* and *Mesopoma*. The neurocranial characters shared by *Lawrenciella* at these last two nodes are unfortunately all homoplasic. We cannot thus establish a hypothetical relationship with any taxa of these clades.
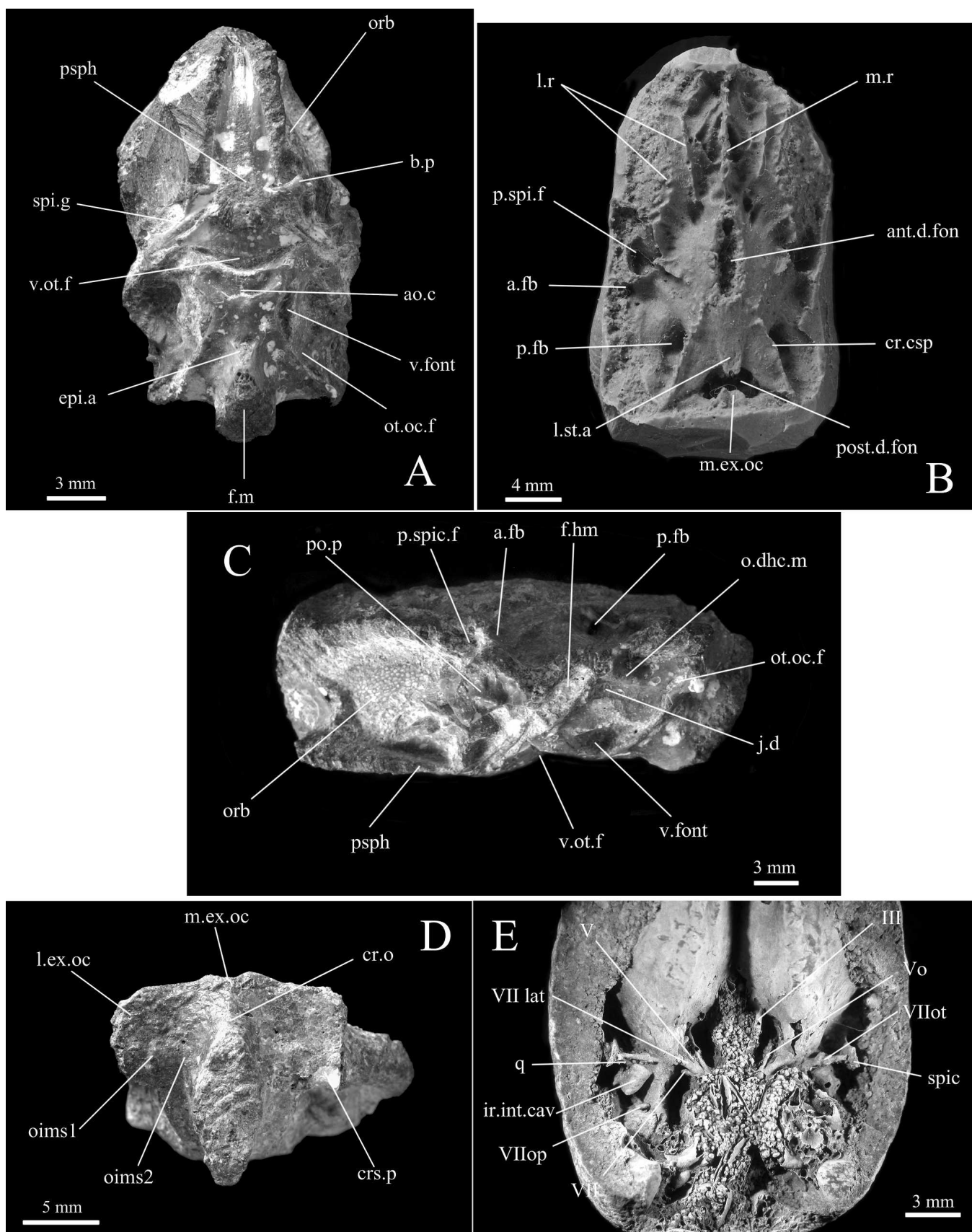
FIGURE 20. *Lawrenciella schaefferi* Poplin 1984: **A**, holotype UK 21942 in ventral view; **B**, specimen UK 56395, elastomere cast of the dorsal face; **C**, holotype UK 21942 in lateral view; **D**, specimen UK 21624 in posterior view; **E**, paratype UK 56372, natural cast of the posterior face of the orbit and of the trigeminofacialis chamber.
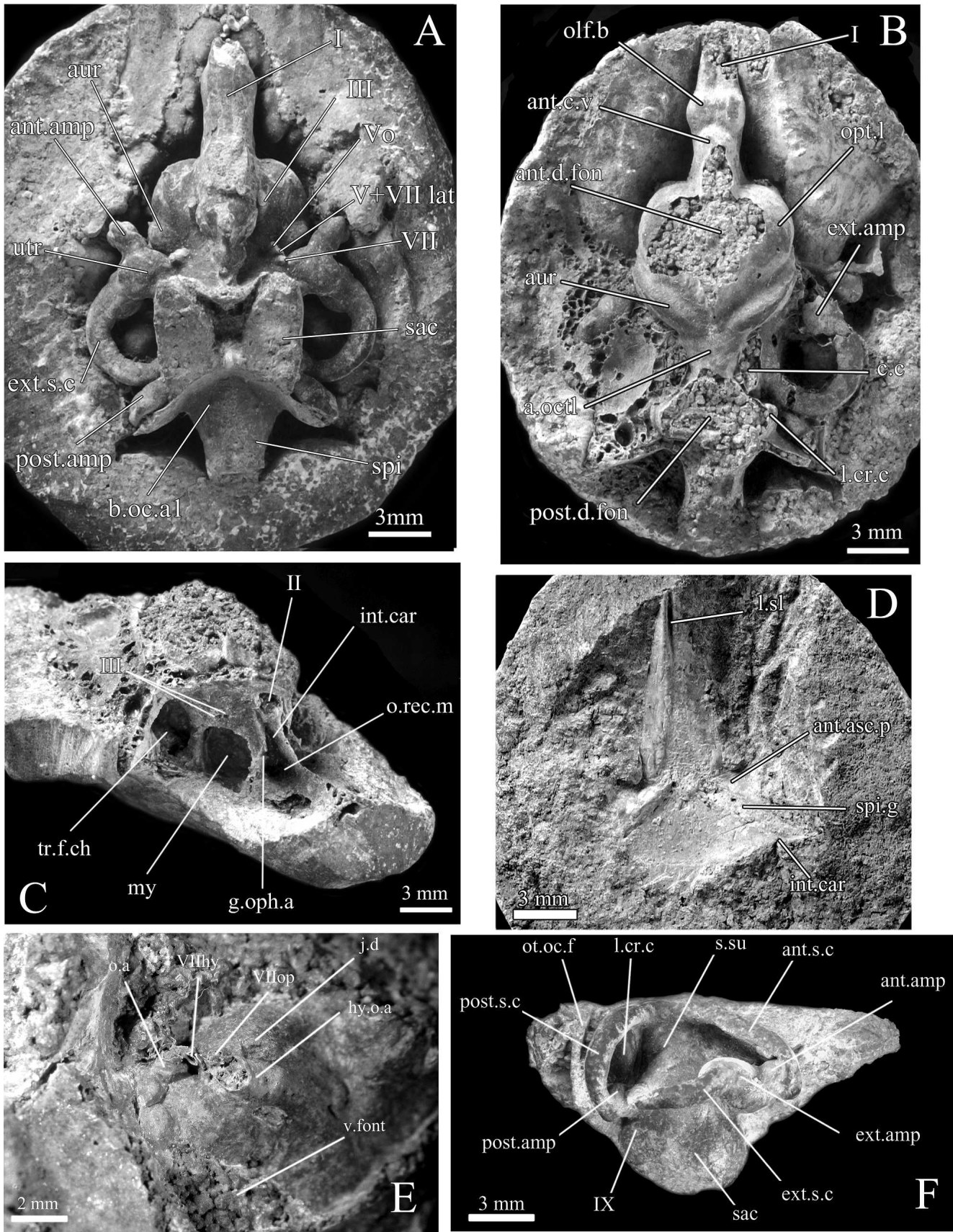
FIGURE 21. *Lawrenciella schaefferi* Poplin 1984: **A**, paratype UK 56374, natural cast of the cranial cavity in ventral view; **B**, paratype UK 56373, natural cast of the cranial cavity in dorsal view; **C**, paratype UK 56375, posterior part of the orbitotemporal region in perspective view; **D**, specimen UK 56385, natural cast of the ventral face of the parasphenoid; **E**, specimen ANP 117, natural cast of the posterior portion of the right jugular canal; **F**, paratype UK 21984, natural cast of the right labyrinth in lateral view.

The distribution of these homoplasic characters across the tree appears as follows:

○ (40-1) Anterior boundary to posterior myodome marked by ridge from basisphenoid pillar to basipterygoid process is present at nodes K, T and in *Kentuckia*;

○ (35-2) Parasphenoid with ascending process reaching spiracular canal is present at node M and in *Acipenser*, *Amia*, *Australosomus* and *Perleidus*;

○ (37-1) Dermal basipterygoid process is present at nodes M, R, and in *Kentuckia* and *Woodichthys*;

○ (30-1) Canal for dorsal aorta with wide anterior opening, bifurcation point partly concealed and median opening for efferent branchial arteries is present in *Boreosomus*, *Coccocephalus* and *Woodichthys*.

Finally *Lawrenciella* shares the two following primitive (interpreted here as reversal) features: (29-0), ventral otic fissure separate from otico-occipital fissure, with *Coccocephalus Boreosomus*, *Kansasiella* and *Mesopoma*; and (49-0), hypophyseal body projects posteroventrally, with the two latter genera as well as with the stem-actinopteran taxa.

According to this analysis, we tentatively conclude that *L. schaefferi* could be either a primitive stem-neopterygian (sensu Coates, 1999:455), together with other forms from the Upper Carboniferous, namely *Coccocephalus*, *Kansasiella* and *Mesopoma*. Without discussing here whether the divergence of chondrosteans and neopterygians really occurred within the lower Carboniferous, we can at least assert that *Lawrenciella schaefferi* is a relatively advanced actinopteran, which can be distinguished from more primitive forms, such as *Kentuckia*, *Mimia* or *Moythomasia*, especially by the presence of a median posterior myodome.

Lawrenciella schaefferi also presents autapomorphies, which distinguishes it from the other basal actinopterans: prespiracular fossae; intracranial ossicles on the wall of the diencephalic and the mesencephalic regions; anterior edge of the posterior dorsal fontanelle overhanged by the tip of a striated bony projection; notochordal canal ending blindly anteriorly; irregular intracranial cavities lateral to each jugular canal; paired anterior myodomes for nonocular eye muscles.

Other characters occur in *L. schaefferi* that are infrequently observed in the braincase of other basal actinopterans: presence of a lateralis canal incompletely separated from the trigeminal one; grooves for pituitary vein in the inner wall of the posterior myodome as in *Kansasiella*, and absence of distinct canal for the superficial ophthalmic branch of the facial nerve. To date we cannot determine whether these characters are phylogenetically significant.

Among these characters, the presence of a relatively short notochordal canal, ending blindly into the occipital ossification, was unexpected in a Carboniferous actinopteran. The notochordal canal generally reaches the ventral otic fissure in lower actinopterans. The notochordal space shows a progressive occlusion only in more advanced forms such as the pholidopleurid *Australosomus* (Nielsen, 1949), Pholidophorids and in Leptolepids (Patterson, 1975). The backward migration of the anterior tip of the notochord is one of the major evolutionary trends of the actinopterygian neurocranium. Gardiner (1973), Patterson (1975), Gardiner and Bartram (1977) and Gardiner (1984) have concluded that the regression of the notochordal canal is concomitant with the increase in size of the posterior myodome. According to these authors, along with the lengthening of the myodome the front of the notochord has become atrophied and the ventral otic fissure has migrated posteriorly. However, *L. schaefferi* has a posterior myodome of equivalent size to those of *Kansasiella* or *Pteronisculus*, the notochord of which reaches the ventral otic fissure. Also, we observe that the ventral otic fissure is placed in a similar position in all these taxa, when we compare

it and the various morphological landmarks used by Schaeffer and Dalquest (1978) in their comparative study of the cranial fissures and the posterior myodome in 'palaeonisciforms'. Schaeffer and Dalquest assert, contra Gardiner (1984), that the location of the fissure is not correlated with the development of the posterior myodome in actinopterygians. *L. schaefferi* shows, in the same way, that the regression of the notochordal canal is not correlated with lengthening of the posterior myodome. We conclude, based on our observation of *L. schaefferi*, that in basal actinopterans, there is no evolutionary relationship between the increase in posterior myodome size, the apparent backward migration of the ventral otic fissure and the regression of the notochordal canal.

CONCLUSION

At present, neurocranial characters alone are insufficient to resolve the position of *Lawrenciella schaefferi* within the basal actinopterygian phylogenies proposed by previous authors and a review of the previously published cladistic analyses is beyond the scope of the present paper. Consequently, we leave *Lawrenciella* as *incertae sedis* within the basal actinopterans sensu Gardiner and Schaeffer (1989).

Although the phylogenetic position of *L .schaefferi* is unresolved, the detailed study of this fossil adds substantial new knowledge about primitive actinopterygian neurocrania. Only 18 basal actinopteran braincases have been described to date and, morever, the endocranial cavities of only few species have been investigated. However, the current improvements of investigating techniques (e.g., computed tomography scan) open up the possibility of increasing the availability of the data about their internal morphology. We can thus expect that future works devoted to actinopterygian relationships may integrate and test completely new phylogenetically informative data as the cranial nerves courses, the trigeminofacialis chamber arrangement or the skeletal labyrinth morphology. This could prove decisive for understanding the interrelationships and evolutionary trends of the lower actinopterygians.

ACKNOWLEDGMENTS

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