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Authors: Giles, Sam, and Friedman, Matt

VIRTUAL RECONSTRUCTION OF ENDOCAST ANATOMY IN EARLY RAY-FINNED FISHES (OSTEICHTHYES, ACTINOPTERYGII)

SAM GILES AND MATT FRIEDMAN

Department of Earth Sciences, University of Oxford, Oxford OX1 3AN, UK, <sam.giles@earth.ox.ac.uk> and <mattf@earth.ox.ac.uk>

ABSTRACT—Cranial endocasts, infillings of the skeletal void that once contained the brain and associated soft tissues, represent detailed anatomical structures that have long been the focus of paleontological investigation. We applied computed tomographics (CTs) in order to generate endocast models for the Paleozoic actinopterygian fishes *Mimipiscis* and *Kentuckia*, which serve as key representatives of anatomically primitive, early ray fins in analyses of early vertebrate relationships. The resultant endocranial models generally corroborate existing accounts of endocranial anatomy in these genera, drawn from descriptions of the inner face of the brain cavity. However, the endocasts also provide new anatomical details, the most significant of which are the presence in *Mimipiscis* of widely divergent olfactory tracts, small optic lobes, and anterior and posterior semicircular canals that extend dorsal to the roof of the endocranial chamber. By contrast, *Kentuckia* possesses a single, straight olfactory tract, wide optic lobes, and anterior and posterior semicircular canals that do not reach the dorsal surface of the endocast. In each of these features, *Kentuckia* resembles stratigraphically younger actinopterygians such as *Lawrenciella* and *Kansasiella*, whereas *Mimipiscis* more closely resembles sarcopterygians and other outgroups. This character distribution provides further support for earlier phylogenetic interpretations of these genera.

INTRODUCTION

THE OCCURRENCE of so-called "fossil brains" has fascinated vertebrate paleontologists since the earliest reports of such structures in the 1800s (e.g., Owen, 1841; Marsh, 1874; Owen, 1875; Moodie, 1915). When found, preserved brain and other nervous tissues are rich sources of morphological information, but such remains are exceedingly rare in the fossil record and sometimes difficult to interpret (Trinajstic et al., 2007; Pradel et al., 2009; Pradel, 2010). More typically, the sediment-filled void within the neurocranium provides the only clues about gross brain architecture. Such endocasts have been described for a diversity of groups (see discussion in Jerison, 1973; Coates, 1999; Walsh and Knoll, 2011), with Paleozoic fishes receiving considerable attention due to the early application of tomographic techniques by Erik Stensiö and other members of the 'Stockholm school' to a range of early vertebrate fossils (Stensiö, 1927, 1963a, 1963b; Jarvik, 1980).

Two key limitations apply to the study of neuroanatomy through the use of endocasts. The first of these arises from the mismatch between the endocast and brain in many groups of vertebrates. The brains of modern chondrichthyans and lobe-finned fishes can occupy as little as 1% of their associated cavities (Millot and Anthony, 1965; Kruska, 1988; Pradel, 2010), suggesting this disagreement might be primitive for jawed vertebrates. Important exceptions to this generality include birds, mammals, and, apparently, early ray-finned fishes (Edinger, 1929; Jerison, 1973). The high fidelity of brain anatomy captured by fossil actinopterygian endocasts is thought to reflect the presence of only a single layer of meningeal tissue separating the brain from the surrounding bone (Bjerring, 1991; Coates, 1999). This arrangement, combined with a relative abundance of well-preserved braincases (e.g., Nielsen, 1942; Rayner, 1951; Poplin, 1974; Schaeffer and Dalquest, 1978; Gardiner, 1984; Coates, 1998; Hamel, 2005), makes stratigraphically early fossil ray-finned fishes ideal targets for neuroanatomical study.

The second limitation associated with the study of vertebrate endocasts reflects the logistical difficulty in obtaining them. In the case of early ray-finned fishes, previous studies have often relied on the chance finding of ideally positioned or preserved specimens (e.g., Eastman, 1908; Moodie, 1915; Rayner, 1951; Coates, 1999). Although this permits description without recourse to more invasive procedures, such circumstances often allow only a cursory description of one face of the endocast or internal wall of the endocranial cavity (e.g., Eastman, 1908). More detailed approaches available to past researchers required a fossil to be serially destroyed and studied either through Sollas' grinding method (Sollas, 1904) or Poplin's more recent microtome technique (Poplin and de Ricqlès, 1970). In addition to being time-consuming, the destructive nature of these methods means that the specimen cannot be revisited, and the author's anatomical interpretations can only be corroborated through examination of original sections or associated photographs. Furthermore, such records are fragile and are prone to damage, as are the large wax models that are based upon them.

Virtual paleontology, through the use of computed tomographic (CT) techniques, provides a solution to the problems associated with mechanical tomographic techniques. Non-destructive CT methods generate datasets and resulting models that are long-lasting and portable (providing the files are stored in a way that can be accessible in the long term; Sutton et al., 2012). The results of such techniques are repeatable in the sense that the data can be revisited and the resultant hypotheses retested, and models can be digitally manipulated, sectioned and redescribed, with the ability to return to the original material as required. Furthermore, CT methods can be used to reinvestigate taxa previously studied via destructive or non-invasive methods, and to test existing interpretations in the literature (e.g., Gai et al., 2011). Importantly, specimens that were previously dismissed as too rare or fragile for destructive investigation can now be "virtually" dissected and studied, all in a process that takes days rather than decades.
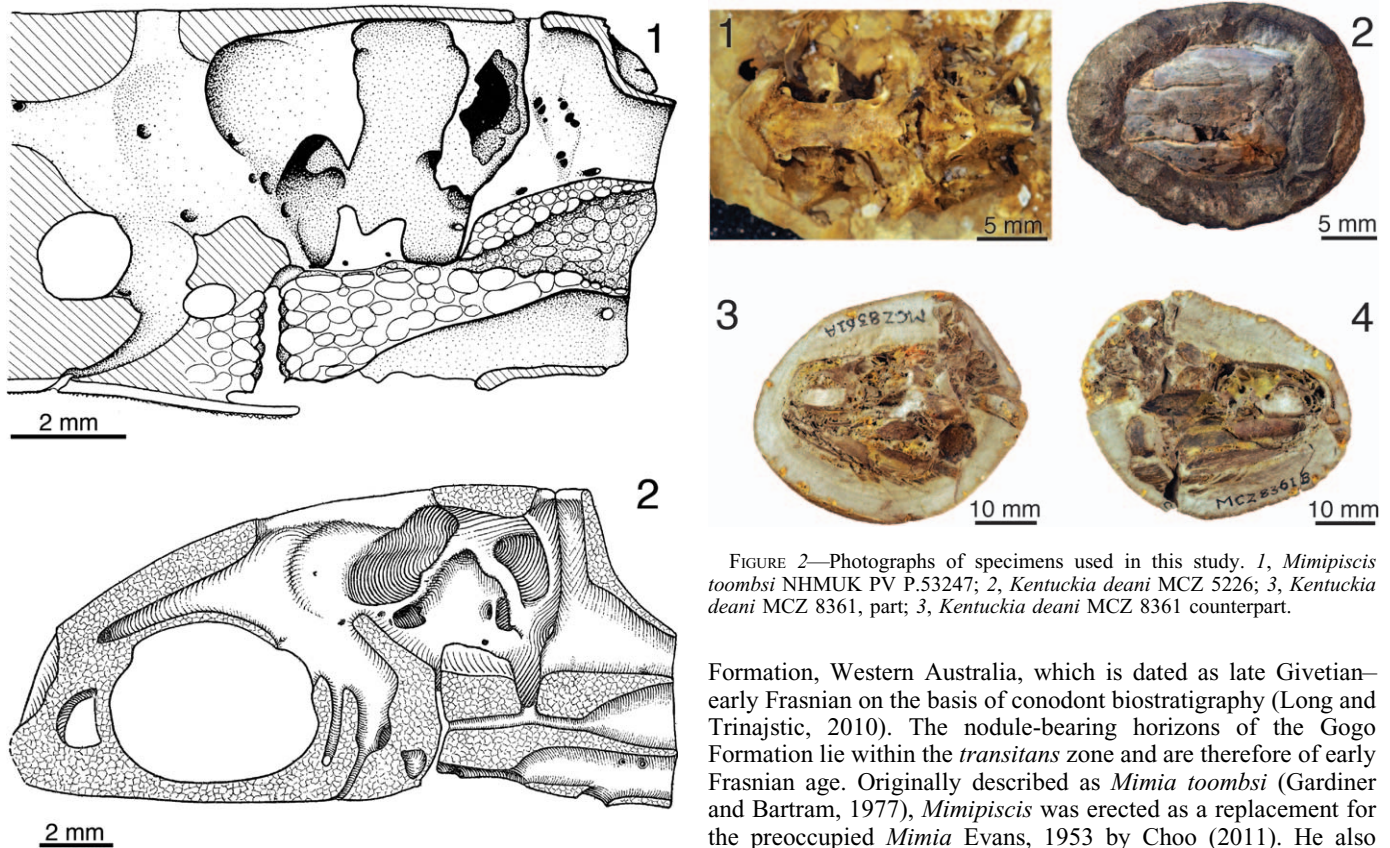
FIGURE 1—Existing illustrations of the cranial cavity of *Mimipiscis toombsi* Gardiner and Bartram, 1977 and *Kentuckia deani* Eastman, 1908. *1*, sagittal section through post-ethmoid region of neurocranium of *Mimipiscis toombsi*; from Gardiner (1984, fig. 26); *2*, sagittal section through neurocranium of *Kentuckia deani*; modified from Rayner (1951, fig. 9).

FIGURE 2—Photographs of specimens used in this study. *1*, *Mimipiscis toombsi* NHMUK PV P.53247; *2*, *Kentuckia deani* MCZ 5226; *3*, *Kentuckia deani* MCZ 8361, part; *3*, *Kentuckia deani* MCZ 8361 counterpart.

Here we apply CT techniques to *Mimipiscis toombsi* Gardiner and Bartram, 1977, and *Kentuckia deani* Eastman, 1908, two Paleozoic ray-finned fishes that serve as key exemplars in analyses of interrelationships among early actinopterygians (Gardiner, 1984; Gardiner and Schaeffer, 1989; Coates, 1999; Arratia and Cloutier, 2004; Gardiner et al., 2005; Friedman and Blom, 2006; Long et al., 2008; Choo, 2011) and among Paleozoic gnathostomes more generally (Zhu et al., 1999, 2006; Friedman, 2007; Brazeau, 2009; Zhu et al., 2009; Davis et al., 2012). This prominence in phylogenetic analyses stems from the Late Devonian (Frasnian) and Mississippian (Tournaisian–Visean) age of these species, along with the fact that both preserve endoskeletal and dermal components of the skull in great detail.

The endocranial cavities of *Mimipiscis* Choo, 2011 and *Kentuckia* Rayner, 1951 have previously been described in the literature, and mid-sagittal sections through the endocavity have been presented for both (Fig. 1). This contribution provides the first endocast reconstructions for these taxa, which serve as a check on previous structural accounts (online Supplemental Data file 1) and the phylogenetic interpretations drawn from them.

MATERIALS AND METHODS

Materials and taxonomic background.—The first specimen examined is the near-complete skull roof and braincase of a large individual of *Mimipiscis* (Natural History Museum, London, 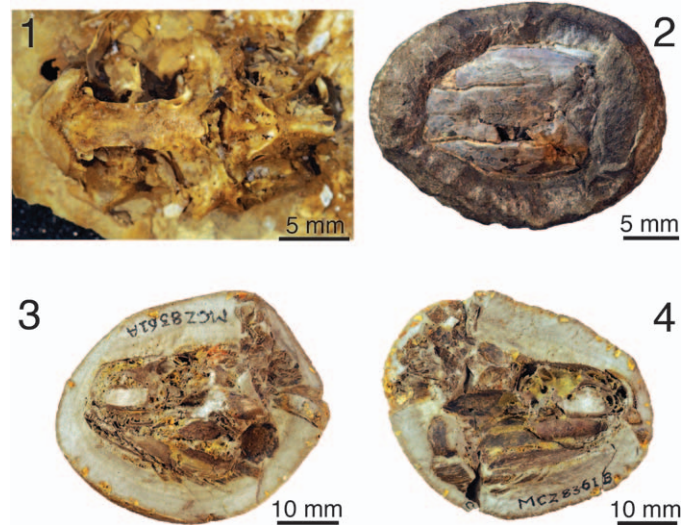UK [NHMUK] PV P.53247). The specimen is from the Gogo Formation, Western Australia, which is dated as late Givetian–early Frasnian on the basis of conodont biostratigraphy (Long and Trinajstic, 2010). The nodule-bearing horizons of the Gogo Formation lie within the *transitans* zone and are therefore of early Frasnian age. Originally described as *Mimia toombsi* (Gardiner and Bartram, 1977), *Mimipiscis* was erected as a replacement for the preoccupied *Mimia* Evans, 1953 by Choo (2011). He also recognized two distinct species of *Mimipiscis*: the type species *M. toombsi*, and the new species *M. bartrami* Choo, 2011. In his review of Gogo actinopterygian material housed at NHMUK, Choo regarded NHMUK PV P.53247 as *M. toombsi*. The specimen measures approximately 25 mm in length from snout to back of occiput and 15 mm at its widest point (Fig. 2.1). The specimen was previously acid prepared to remove surrounding matrix, and its dorsal surface embedded in a thin resin block. Although some sediment remains in the dorsal-most parts, the brain cavity itself is largely free of infillings and is preserved as void space.

Two individuals of *Kentuckia deani* were examined, both of which are deposited at Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. (MCZ). These specimens derive from the New Providence Shale Member of the Stockdale Formation of Kentucky, U.S.A., which is referred to as the Waverley Shales in older accounts. This unit has been dated to the latest Tournaisian or early Visean on the basis of ammonoids and conodonts (Work and Mason, 2003). First named as *Rhadinichthys deani* Eastman, 1908, actinopterygians from the New Providence Shale Member were subsequently transferred to the new genus *Kentuckia* by Rayner (1951). She referred all but one of the specimens to *K. deani*, with one larger individual (MCZ 5257) identified as *Kentuckia* sp. A further species, *K. hlavini* Dunkle, 1964, was placed in the genus based on an articulated specimen from the Late Devonian (Famennian) Cleveland Shale Member of the Ohio Shale Formation. Dunkle (1964) himself noted that this attribution was far from certain, and we note that there are conspicuous differences between this older species and specimens from the Stockdale Formation. Following Friedman and Blom (2006), we do not regard *K. hlavini* as belonging to the genus *Kentuckia*, and advise against the use of composite codings for the genus that draws on evidence from both species (e.g., Arratia and Cloutier, 2004).

The first specimen of *Kentuckia* studied here (MCZ 8361) is contained within a broken nodule, splitting the fossil along an oblique mid-sagittal plane (Fig. 2.3, 2.4). The fossil represents a large individual, measuring 30 mm from the snout to the back of the skull. As internal parts of the cranium are visible, this specimen was one of two used by Rayner (1951) to describe the cranial cavity of *Kentuckia*. The second specimen (MCZ 5226) is contained within an unbroken nodule, the top of which has been prepared away to reveal the dorsal surface of the skull roof (Fig. 2.2). This individual is smaller than the first. The exposed part of the skull roof (from anterior margin of frontals to posterior margin of dermopterotics) measures 15 mm. A complete braincase and parasphenoid is preserved within the nodule. The two specimens exhibit clear morphological differences (see below), but we retain them within *Kentuckia* pending a much-needed taxonomic review of the genus. Specimen numbers are used when describing to morphological differences between these individuals.

Tomographic methods.—All three specimens were scanned at the Imaging and Analysis Centre of NHMUK using a Metris X-Tek HMX ST 225 CT System with a 2,000 × 2,000 pixel detector panel. The two halves of the nodule comprising MCZ 8361 were secured together with a rubber band during scanning and 3,142 projections were made for each specimen. Other scan parameters are as follows: NHMUK PV P.53247: 150 kV, 169 µA, 1 mm thick copper filter, voxel size 27 µm; MCZ 8361: 210 kV, 200 µA, 2 mm thick copper filter, voxel size 26.5 µm; MCZ 5226: 210 kV, 200 µA, 2 mm thick copper filter, voxel size 14.5 µm.

Data segmentation and three-dimensional rendering.—Following scanning, the resulting files ("vol") were manipulated in Avizo 7.1 (VSG Inc., Burlington, Massachusetts, U.S.A.). A workflow for the following method is provided in online Supplemental Data file 2. The segmentation editor in Avizo was used to generate a new label field. Bone material, distinguishable from the surrounding air by its different X-ray attenuation, visible as gray-values, was selected and added to a new mask. The mask was then locked, and the blow tool used to segment the void space representing the endocast, cranial nerves and canals. As this tool is semi-automated, it removes an element of worker subjectivity. This method can only be used where the tissue of interest is well mineralized and of a sufficiently different contrast than the surrounding matrix. Where this is not the case, as in some parts of MCZ 5226, segmentation must be completed by hand.

Once segmentation was complete, three-dimensional rendering was achieved by generating a surface view. The data object was saved ("ply" file) and exported to Blender (blender.org) for image and video acquisition (Garwood and Dunlop, 2014). The right side of the endocast of MCZ 5226 was resolved to a higher degree of completeness, but in order to follow standard practice when imaging endocasts this image has been flipped horizontally so as to resemble the left side of the endocast. Interpretive diagrams were drafted from virtual models. An animation of the endocast of *Mimipiscis* NHMUK PV P.53247 (online Supplemental Data file 3) and of *Kentuckia* MCZ 8361 (online Supplemental Data file 4) is provided. PLY 3D files of the endocast surfaces are also available (*Mimipiscis* NHMUK PV P.53247, online Supplemental Data file 5; *Kentuckia* MCZ 8361, online Supplemental Data file 6; *Kentuckia* MCZ 8361, online Supplemental Data file 7). Such files can be easily viewed and manipulated in free programs such as Meshlab (www.meshlab.sourceforge.net; Cignoni et al., 2008).

Comparative materials.—The morphology of the endocasts of *Mimipiscis* and *Kentuckia* was compared with descriptive accounts of this structure in other extinct and extant jawed vertebrates (online Supplemental Data file 1). Particular emphasis was placed on Paleozoic actinopterygians: *Kansasiella* Poplin,

1974, *Lawrenciella* Poplin, 1984 (Hamel, 2005; Hamel and Poplin, 2008), *Mesopoma* Traquair, 1890 (Coates, 1999) and Paleozoic sarcopterygian fishes: *Diplocercides* Stensiö, 1922 (Jarvik, 1954; Stensiö, 1963b; Jarvik, 1980), *Dipnorhynchus* Jaekel, 1927 (Thomson and Campbell, 1971; Campbell and Barwick, 1982, 2000), *Ectosteorachis* Cope, 1880 (Romer, 1937), *Eusthenopteron* Whiteaves, 1881 (Bjerring, 1971; Jarvik, 1980); *Youngolepis* Chang and Yu, 1981 (Chang, 1982). Extant actinopterygians used for comparison are *Polypterus* Lacépède, 1803 (Senn, 1976; Nieuwenhuys, 1982); *Acipenser* Linneaus, 1758 (Nieuwenhuys, 1982; Rupp and Northcutt, 1998; Gómez et al., 2009); *Amia* Linneaus, 1766 (Nieuwenhuys, 1982); and *Lepisosteus* Linneaus, 1758 (Balfour and Parker, 1882).

Anatomical abbreviations.—acv, canal for anterior cerebral vein; ant.amp, ampulla of anterior semicircular canal; asc, anterior semicircular canal; aur, cerebellar auricle; bhc, bucco-hypophysial canal; b.oc.a, canal for branch of occipital artery; c.c, crus commune; ccc, communication between cranial cavity and notochordal canal; c.co, cerebellar corpus; die, diencephalon; esc, external semicircular canal; ext.amp, ampulla of external semicircular canal; ica, canal for internal carotid artery; l.c.c, lateral cranial canal; ldv, canal for longitudinal dorsal vein; mcv, canal for middle cerebral vein; nc, nasal capsule; olf.b, olfactory bulb; oof, otico-occipital fissure; opt.f, optic fenestra; opt.l, optic lobe; pdf, posterior dorsal fontanelle; pin.f, pineal foramen (anterior dorsal fontanelle); pit.f, pituitary fenestra; post.amp, ampulla of posterior semicircular canal; psc, posterior semicircular canal; sac, sacculus; s.oph.a, canal for small ophthalmic artery (branch of anterior cerebral artery); spio, canal for spino-occipital nerve; s.su, sinus superior; s.v, saccus vasculosus; tel, telencephalon; v.fon, vestibular fontanelle; I, canal for olfactory nerve; III, canal for oculomotor nerve; IV, canal for trochlear nerve; V, canal for trigeminal nerve; Vprof, canal for profundus nerve; VI, canal for abducens nerve; VII, canal for facial nerve; VIIlat, canal for lateralis branch of facial nerve; IX, canal for glossopharyngeal nerve; X, canal for vagus nerve. Dotted lines in figures indicate unresolved regions.

ANATOMICAL DESCRIPTION: *MIMIPISCIS*

General endocast morphology.—The endocast is long and narrow, with elongate, anterolaterally-directed olfactory tracts (I, Figs. 3–5). The endocast of *Mimipiscis* has unusual proportions relative to that of other early extant and extinct actinopterygians listed above. The forebrain (excluding olfactory tracts) accounts for less than 20% of the total length, as opposed to the more usual 25–30%, and the hindbrain takes up over 60% of total brain length rather than around 50%.

Forebrain.—This region of the endocast corresponds to the diencephalon, telencephalon and olfactory bulbs. The separation between the diencephalon (die) and the mesencephalon (mes) is marked by a constriction dorsally and laterally (Figs. 3, 4), and the diencephalon and telencephalon (tel) are continuous. As in most primitive extant and extinct actinopterygians, such as *Polypterus*, *Acipenser*, and *Lawrenciella*, the olfactory bulbs (olf.b, Figs. 3–5) are confluent with the telencephalon. However, it is almost impossible to distinguish two olfactory bulbs in *Mimipiscis*. This contrasts with the situation in the fossil taxa *Lawrenciella* and *Mesopoma*, as well as many extant chondrosteans and neopterygians, where the olfactory bulbs are well developed and clearly divided. The region of the olfactory bulbs is confined to the posterior part of the orbit (Coates, 1999). The roof of the telencephalic region is perforated by a single foramen for the anterior cerebral vein (acv, Figs. 3, 4). This anterior exit is unusual, as the more standard early actinopterygian arrangement is for it to exit from the roof of the diencephalon as in *Lawrenciella*, *Kentuckia*, and *Kansasiella*.

The diencephalon in NHMUK PV P.53247 is visible dorsally only as a slight swelling. Ventrally, however, it extends
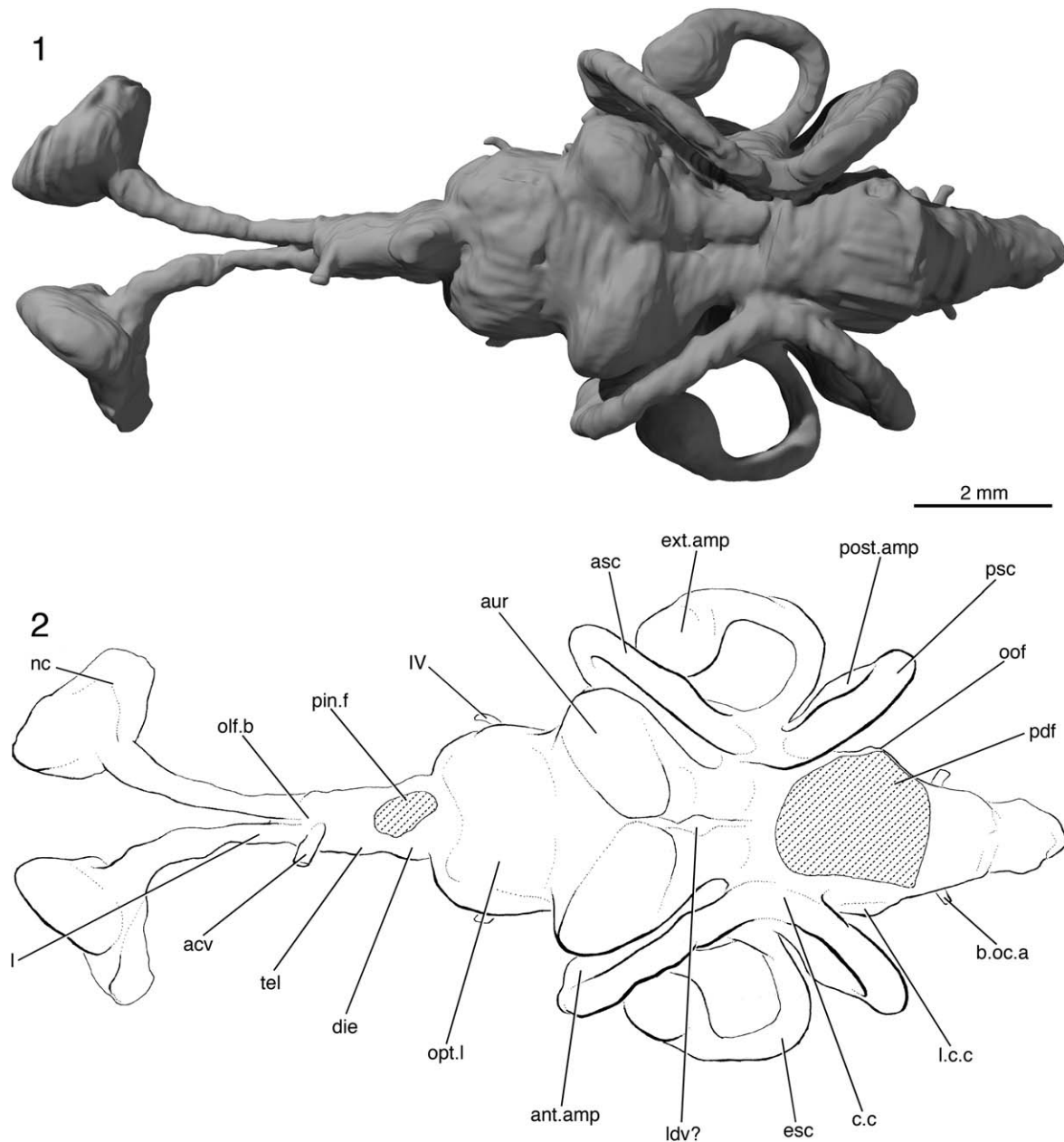
FIGURE 3—Reconstruction of the endocast of *Mimipiscis toombsi*, NHMUK PV P.53247, in dorsal view. *1*, three-dimensional rendering of endocast; *2*, interpretive drawing of endocast.

downwards and slightly posteriorly under the mesencephalon (die, Fig. 4), in a similar orientation to that of *Acipenser*. The diencephalon is mostly confined beneath the optic lobes, unlike in *Lawrenciella*, *Mesopoma*, and *Polypterus*, where it extends posteriorly beneath the cerebellar auricles. Anteriorly, the interorbital wall is unfinished and thus does not delimit the endocast (opt.f, Figs. 4, 5). The optic (II) nerves were likely transmitted through this opening, and foramina for the internal carotids are visible just beneath (ica, Fig. 5). Unlike in *Lawrenciella*, there is no groove or foramen for the small ophthalmic artery; the apparent opening in this region illustrated (but not identified) by Gardiner (1984, fig. 13) does not penetrate the bone. The hypophysial canal, carrying the pituitary vein, extends ventrally into the diencephalon. The saccus vasculosus is developed as a somewhat dorsally directed pouch on the caudal face of the diencephalon (s.v, Figs. 4, 5), and is of a similar

relative size to that of *Lawrenciella* and *Kansasiella*, but smaller than that of *Mesopoma*. An anterior prolongation at the bottom of the diencephalic region marks the passage of the bucco-hypophysial canal through the parasphenoid (bhc, Figs. 4, 5).

As a whole, the endocranial cast of the forebrain in *Mimipiscis* is very narrow, being barely wider than the olfactory tracts. These tracts, transmitting the olfactory (I) nerves, diverge almost immediately upon leaving the olfactory bulbs and extend anterolaterally towards the nasal sacs (Figs. 3, 5). This differs from the condition seen in the fossils of almost all other early actinopterygians, where the two nerves share a common canal for most of their length. The anterolateral orientation of the tracts is also unusual, but is similar to that seen in sarcopterygian fishes such as *Youngolepis* and *Ectosteorachis*, as well as extant chondrosteans.

Midbrain.—The mesencephalic region in *Mimipiscis* is about twice the width of the forebrain, but does not reach the maximum
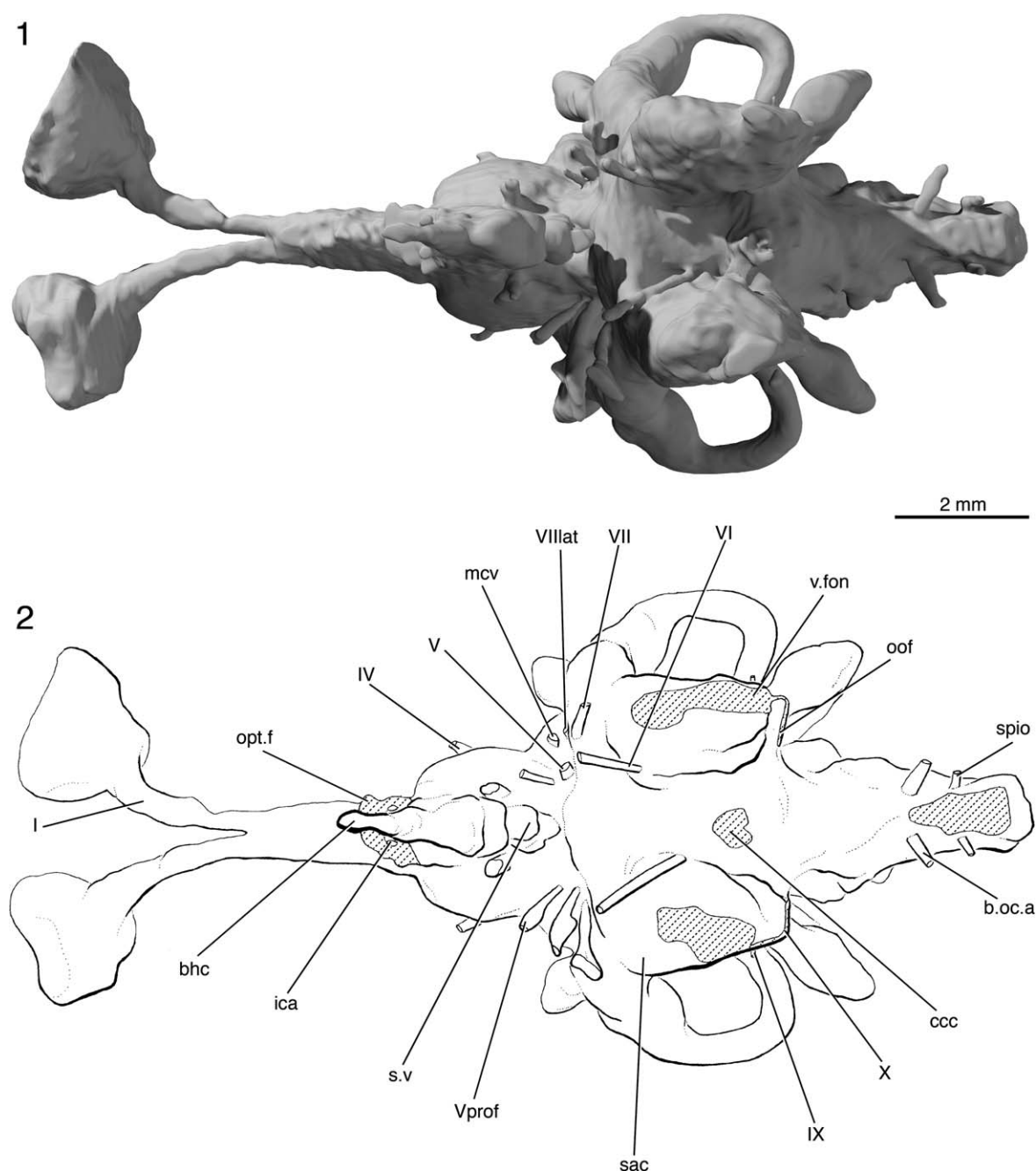
FIGURE *4*—Reconstruction of the endocast of *Mimipiscis toombsi*, NHMUK PV P.53247, in left lateral view. *1*, three-dimensional rendering of endocast; *2*, interpretive drawing of endocast. The lateral cranial canal has been only been partially filled so as to avoid obscuring details of the labyrinth.

width of the cerebellum (Fig. 3). As with *Acipenser*, the two optic lobes (opt.l, Figs. 3–5) lack a well-defined median groove. In comparison to Carboniferous ray fins, the optic lobes of *Mimpiscis* are poorly developed. The root of the trochlear (IV) nerve pierces the lateral limit of each lobe (Fig. 4), a position somewhat higher than the corresponding foramen in *Lawren-ciella*, *Mesopoma*, and *Kansasiella*. The oculomotor (III) nerve leaves the floor of each optic lobe and, as in *Lawrenciella*, bifurcates almost immediately to enter the orbit through two closely spaced foramina (III, Fig. 4).

Hindbrain.—This region of the endocast relates to the cerebellum and rhombencephalon. In *Mimipiscis*, the cerebellar auricles resemble those of *Acipenser* in being robust but short (aur, Figs. 3, 4). As in *Lawrenciella*, *Kansasiella*, and extant chondrosteans, they are separated from the optic lobes by a deep sulcus. In *Lawrenciella*, dorsal ridges within the sulcus are thought to be related to the middle cerebral vein. No such ridges are present in *Mimipiscis*; instead, a canal that exits from the bottom of the auricle and extends ventrally has been suggested to carry this vessel (Gardiner, 1984). A similar canal is reported in *Pteronisculus* White, 1933 (Nielsen, 1942), where it leaves the auricle and passes directly into the orbit above the trigeminofacialis chamber. Somewhat unusually, the canal in *Mimipiscis* appears to enter the trigeminofacialis chamber (mcv, Figs. 4, 5).

Gardiner (1984) commented upon a similarly close relationship between the middle cerebral vein and trigeminal (V) nerve in teleosts, and it is likely that in *Mimipiscis* the vein entered the chamber and exited again almost immediately by way of an anterodorsally directed canal.

Relative to the placement seen in other ray fins, the auricles in *Mimipiscis* are positioned far anteriorly, with the anterior limits level with the ampulla of the anterior semicircular canal and the posterior extent no further than the external ampulla (Fig. 3). Dorsally, the auricles stand proud of the rest of the endocast, a condition uncommon in early fossil ray fins, as well as extant chondrosteans and neopterygians. It is hard to compare this with the condition seen in actinopterygian outgroups as the endocranial cavity typically does not conform well to the shape of the brain in this region. However, in *Ectosteorachis* and *Youngolepis*, there is a suggestion of an increase in depth of the endocavity in the region of the cerebellum. Similarly, in *Latimeria* Smith 1939, the cerebellum extends above the rest of the brain, although the auricles sit somewhat lower (Northcutt et al., 1978).

Beneath the auricles, the lateral limits of the endocast slope inwards to meet a short distance above the saccus vasculosus. This lateral wall is pierced by two foramina: the more medial for the anteriorly directed profundus (Vprof) nerve canal, and the

FIGURE 5—Reconstruction of the endocast of *Mimipiscis toombsi*, NHMUK PV P.53247, in ventral view. *1*, three-dimensional rendering of endocast; *2*, interpretive drawing of endocast.

more lateral for the trigeminal (V) nerve canal (Figs. 4, 5). The canal for the trigeminal nerve travels laterally to enter the trigeminofacialis chamber, intercepting and carrying the middle cerebral vein en route (see above). Lateral and slightly ventral to these two openings are two additional foramina. The more dorsal of these most likely transmitted the lateralis branch of the facial (VIIlat) nerve, which also travels into the trigeminofacialis chamber. The more ventral transmitted the facialis (VII) nerve ventrolaterally. The canal for the abducens (VI) nerve pierces the zygal plates and extends anterolaterally along the medial boundaries of the saccular recesses (Fig. 5). The glossopharyngeal (IX) nerve leaves the sacculus ventral to the ampulla for the posterior semicircular canal (Fig. 4).

A deep groove between the two auricles presumably marked the course of the longitudinal dorsal vein (ldv, Fig. 3; Coates, 1999). This groove extends posteriorly, but does not appear to continue forwards between the optic lobes, unlike the condition inferred for *Mesopoma*. There is no obvious cerebellar corpus projecting behind the auricles. The region posterior to the auricles is elongate and bilobed, and may represent the area octavolateralis. The lateral wall of the endocast between the sinus superior and oticocippital fissure is interrupted by a large foramen for the lateral cranial canal (l.c.c, Fig. 4). Although the canals are complete in the specimen, they have only been partially segmented so as to avoid obscuring any parts of the labyrinth. Behind the fissure the endocast sloped downwards to assume a

cylindrical shape, from which canals issue for branches of the occipital arteries (b.oc.a, Figs. 3–5) and, further posteriorly, the spino-occipital nerves (spio, Figs. 3–5).

Labyrinth.—The overall morphology of the labyrinth region in *Mimipiscis* is as expected for an early actinopterygian (Figs. 3–5). The three semicircular canals (anterior, posterior, and external) are robust, with a relatively large separation between them and the lateral walls of the endocast. The sinus superior (s.su, Fig. 4) is wide and is underlain by a large saccular recess that lacks an obvious lagena (sac, Fig. 4). Despite being widespread among vertebrates, a separate lagenar pouch is also unknown in all other early actinopterygians, as well as in the extant *Acipenser*, *Amia*, and *Lepisosteus* (Popper, 1978; Mathiesen and Popper, 1987; Lovell et al., 2005). Its absence in early members of other groups, for example in some sarcopterygians (Jarvik, 1980; Platt et al., 2004) and chondrichthyans (de Burlet, 1934; Gauldie et al., 1987; Maisey, 2005, 2007; Pradel, 2010), suggests that a distinct lagenar pouch may have arisen independently several times in vertebrates. No otoliths are preserved within the saccular chambers of *Mimipiscis*, and were presumably dissolved during acid preparation, as otoliths have been found in other material examined by Gardiner (1984, p. 227). The curvature of the anterior and posterior canals is such that they rise above the level of the hindbrain, causing the crus commune to sit just above the level of the endocast roof (c.c, Fig. 4).

ANATOMICAL DESCRIPTION: *KENTUCKIA*

General endocast morphology.—In both MCZ 5226 and MCZ 6381, the endocast is markedly less slender than that of *Mimipiscis* (Figs. 6–10). The relative proportions assumed are more typical of previously described endocasts of primitive extant and extinct ray-finned fishes (see references above); the forebrain constitutes around 25% of the total brain length and the hindbrain around 50%. Although the endocasts of the two specimens agree in these general proportions, they differ in a series of more specific features: the optic lobes are better developed and more spherical in MCZ 5226 than in MCZ 8361; the cerebellar auricles are proportionally longer in MCZ 5226 than in MCZ 8361; the posterior semicircular canal is more tightly curved and thus shorter in MCZ 8361 than MCZ 5226; and the canal for the third cranial nerve bifurcates in MCZ 5226 but remains undivided in MCZ 8361. These are reviewed in more detail in the relevant sections below.

Forebrain.—Similar to in *Mimipiscis*, *Lawrenciella*, and *Kansasiella*, the cast of the forebrain of *Kentuckia* is narrow. The separation between the diencephalon (die) and the mesencephalon (mes) is marked by a constriction dorsally and laterally (Figs. 3, 4). As in *Mimipiscis*, olfactory bulbs cannot be identified in either MCZ 5226 or MCZ 8361, and it is difficult to distinguish between the diencephalon and telencephalon (Figs. 6, 9). The telencephalon can be identified with confidence only in MCZ 5226, where a slight bulge is visible laterally (tel, Fig. 10). In both *Kentuckia* specimens, the dorsal limit of the endocast is uncertain immediately in advance of the anterior dorsal fontanelle (pin.f, Fig. 9), and it seems likely that this region of the brain was not closely applied to the walls of the endocranial chamber. In MCZ 8361, a canal exits from the top of the diencephalic region. This corresponds to the single foramen for the anterior cerebral vein (acv, Figs. 6, 7). The bone in MCZ 5226 is poorly mineralized in this region, and no such passage is visible. In both specimens, the olfactory (I) nerves are carried through a single tract, which travels anteriorly before diverging into two anterolateral canals immediately before reaching the nasal capsules (Figs. 6, 9). Curiously, the shared tract extends ventrally as well as anteriorly (I, Figs. 7, 10). This is not reported in any other fossil actinopterygian, but is very similar to the condition in *Acipenser*.

The ventral portion of the diencephalon is poorly preserved in MCZ 8361, but can be described in more detail from MCZ 5226.

A shared opening for the optic (II) nerves is visible anteriorly (opt.f), and above this lie two small anteriorly directed canals that likely transmitted the small ophthalmic arteries, as in *Lawrenciella* (s.oph.a, Fig. 10). In both specimens, the internal carotids (ica, Figs. 7, 10) extend downwards from the optic foramen. Posterior to this, the hypophysial stalk extends ventrally under the optic lobes, as in *Acipenser* and *Lepisosteus*, ending in the bucco-hypophysial canal (bhc, Fig. 10). The full extent of the saccus vasculosus is uncertain in either specimen of *Kentuckia*.

Midbrain.—The mesencephalic region of the endocast is well developed, with the optic lobes over twice the width of the forebrain. Large optic lobes are known in *Mesopoma* and *Lawrenciella*, as well as extant chondrosteans and neopterygians. The lobes are relatively larger and more rounded in MCZ 5226 than in MCZ 8361, and extend dorsal to the more anterior parts of the endocast (opt.l, Figs. 6, 7, 9, 10). The trochlear (IV) nerve pierces the lobe in a slightly more ventral position than in *Mimipiscis*, although the oculomotor (III) nerve bifurcates before entering the orbits in the same way (III, Fig. 10). This bifurcation is not seen in MCZ 8361. The region between the optic lobes is occupied by a large anterior dorsal fontanelle (pin.f, Fig. 9), obscuring any median groove. In MCZ 5226 this extends from the front of the optic lobes to the posterior limit of the cerebellar auricles. This fontanelle has been traversed by a crack in MCZ 8361, and as a result much of the dorsal surface of the portion of the endocast relating to the mid- and hindbrain is obscured. A thin canal extends along the midline behind the fonanelle in MCZ 5226. Comparison with *Mesopoma* and teleosts (Zwehl, 1961; Coates, 1999) indicates that it transmitted the longitudinal dorsal vein (ldv, Fig. 9).

Hindbrain.—The cerebellar region of the endocast is separated from the mesencephalon by a groove. Although this may have housed the middle cerebral vein (Hamel and Poplin, 2008), no supporting ridges are apparent. Dorsally, the cerebellar auricles display a similar morphology in both specimens of *Kentuckia*, extending from the ampulla of the anterior semicircular canal back to the crus commune of the anterior and posterior canals (aur, Figs. 6, 7, 9, 10). Rather than being laterally separated from the endocast, the anterior semicircular canal is set into a deep groove extending along the auricle, producing a ventral auricular lobe that continues towards the utriculus (Figs. 5, 6, 9). This unusual arrangement is seen elsewhere only in *Kansasiella*, where the auricles are so reduced that they only display this ventral lobe. The auricles are relatively larger in MCZ 5226 than in MCZ 8361, standing proud above the rest of the dorsal surface of the endocast.

The layout of the canals in the lateral region of the diencephalon is fairly similar in both specimens of *Kentuckia*. The most medial of the three canals leaves the lateral wall of the cranial cavity and extends laterally and slightly anteriorly to the trigeminofacialis chamber. This carried the profundus (Vprof) nerve. Its position is slightly more ventral in MCZ 5226. Two canals exit medial and ventral to the utriculus. The more dorsal of these is very short, and transmits the trigeminal (V) nerve and lateralis branch of the facial (VIIlat) nerve into the trigeminofacialis chamber (Fig. 8). The more ventral projects laterally to enter the orbit, and carried the facial (VII) nerve. The exit for the abducens (VI) nerve, on the anterior face of the sacculus, is visible only in MCZ 8361 (Fig. 8).

The posterior portion of the rhombencephalon is very poorly known in MCZ 8361, especially dorsally. The sinus superior (s.su) is incompletely resolved in both specimens, but appears to be similar in size to that of *Mimipiscis* and *Lawrenciella*, as is the saccular recess (sac). Only the upper portion of the saccular recess is known in detail, but it appears fairly extensive (sac, Figs. 7, 10), and a canal for the glossopharyngeal (IX) nerve exits the
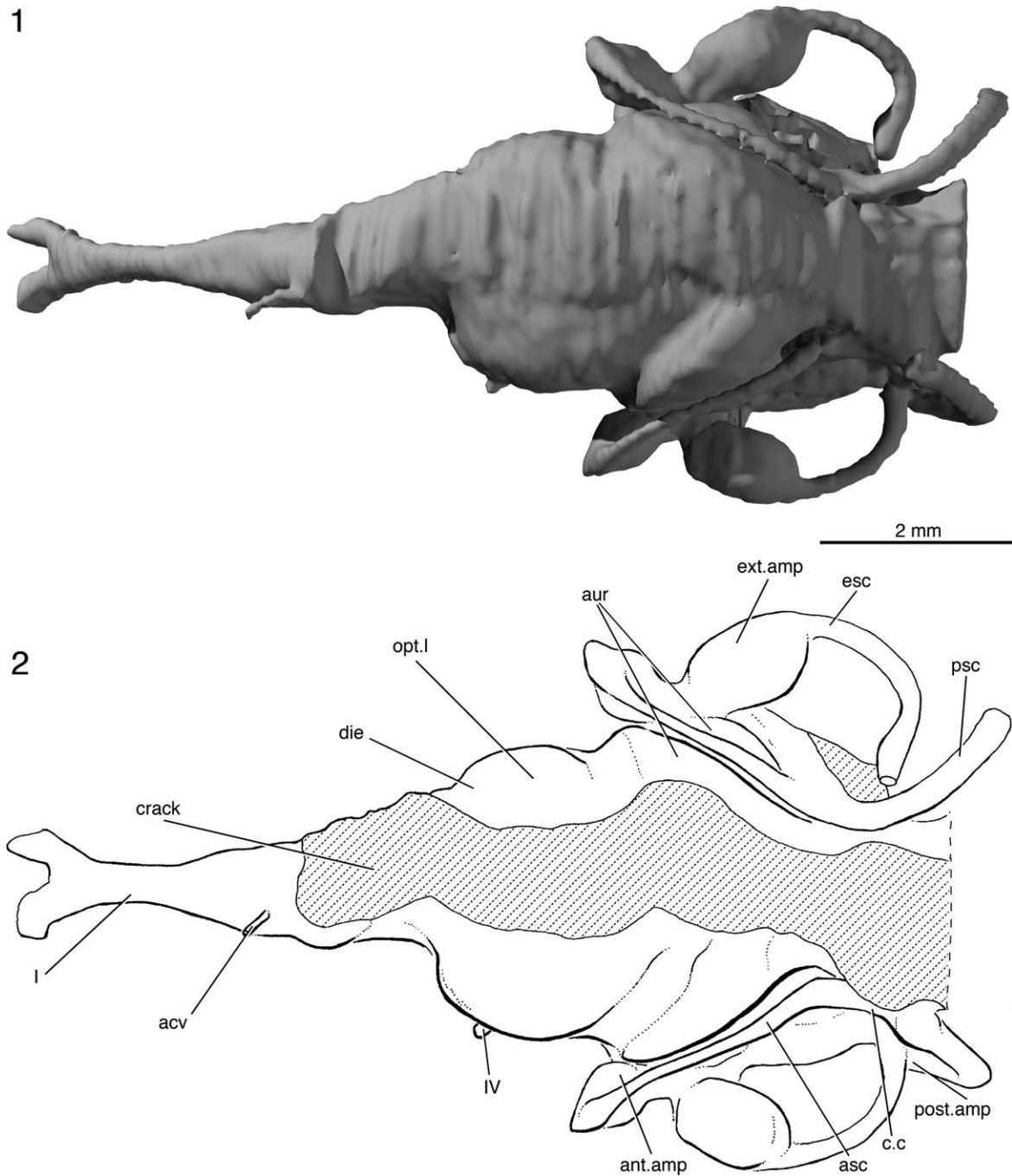
FIGURE 6—Reconstruction of the endocast of *Kentuckia deani*, MCZ 8361, in dorsal view. *1*, three-dimensional rendering of endocast; *2*, interpretive drawing of endocast.

lateral edge of the sacculus in MCZ 8361 (Fig. 8). The opening for the lateral cranial canal is small (l.c.c, Figs. 7, 10), and appears to protrude through the posterior semicircular canal as a "pocket," as in *Lawrenciella*. The region is better resolved in MCZ 5226. As in *Boreosomus* Stensiö 1921 (Nielsen, 1942), *Mesopoma*, *Pteronisculus* (Nielsen, 1942), and *Polypterus*, the hind part of the cerebellum in this specimen of *Kentuckia* displays two lobes divided along the midline, and there is a suggestion that they are further subdivided transversely (c.co, Fig. 9). These lobes are smooth and confluent with the cerebellar auricles, and represent the cerebellar corpus. The endocast narrows to a cylinder behind the posterior dorsal fontanelle.

Labyrinth.—At first glance, the morphology of the semicircular canals in MCZ 8361 and MCZ 5226 appears strikingly different. The canals in MCZ 8361 are very delicate and narrow in comparison to those of MCZ 5226. This, however, appears to be a preservational artifact; CT sections through the specimen reveal that the original bone material is not preserved. Instead, what is preserved is an infilling of the space that would have been occupied in life by the membranous labyrinth, a structure thinner than the osseus labyrinth preserved in MCZ 5226. As mentioned above, the anterior canal is set very closely into the auricle, appearing to divide it into two lobes (aur, Figs. 6, 7, 10). The ampullae of the anterior and external canals in MCZ 5226 are relatively larger than those of *Mimipiscis* and *Lawrenciella*, and
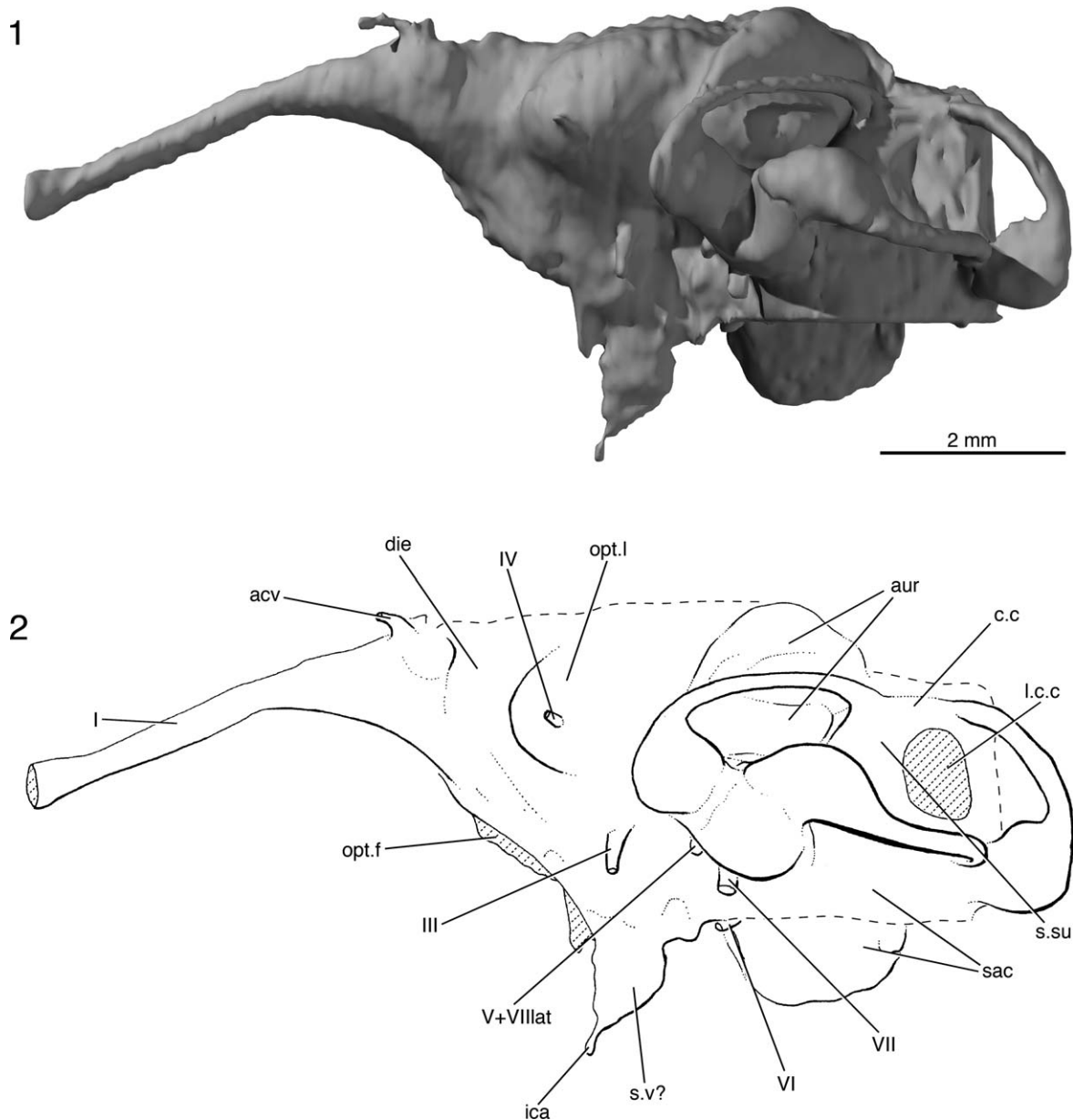
FIGURE 7—Reconstruction of the endocast of *Kentuckia deani*, MCZ 8361, in left lateral view. *1*, three-dimensional rendering of endocast; *2*, interpretive drawing of endocast. The pocket of the lateral cranial canal has been 'cut' to avoid obscuring parts of the labyrinth.

the utriculus is much smaller than in *Mimipisicis*. All three canals in MCZ 8361 and MCZ 5226 are tightly curved and therefore short, as in *Lawrenciella* and *Kansasia*. The sinus superior is positioned below the upper surface of the endocast, and this gives the canals a flattened appearance, quite unlike the condition observed in *Mimipiscis*.

DISCUSSION

Validation of previous interpretations.—The morphological data described in the previous section can be used to test the anatomical descriptions laid out by Gardiner (1984) for *Mimpiscis* and those of Moodie (1915), Rayner (1951) for *Kentuckia*.

The existing description of the endocast of *Mimipiscis* can largely be corroborated, but we are able to add several important features that have not previously been recognized. As part of his description of *Mimipiscis*, Gardiner included a short section on the morphology of the brain cavity, as well as referring to aspects of it elsewhere. He figured the dorsal structure of the endocast (anterior to the pineal

foramen), but much of the morphology is obscured by the extension of the anterior myodome (Gardiner, 1984, figs. 33, 34). A sagittal section through the endocranial cavity was also illustrated (Gardiner, 1984, fig. 26). The description can largely be corroborated, with one or two exceptions in the region of the trigeminofacialis complex. Gardiner referred to the trigeminal (V) nerve and profundus (Vprof) nerve as entering the orbit independently but having a shared root, with the profundus branching from the anterior part of the facial canal. In fact, they appear to leave the cranial cavity through different openings and have entirely separate courses. Consequently, the foramen referred to as "V" (fig. 26) can be reinterpreted as the opening for the root of the profundus nerve. The trigeminal nerve has a separate exit from the cranial cavity, which was misidentified by Gardiner (1984, fig. 26) as the lateralis branch of the facial nerve. The opening for the lateralis branch is not visible in sagittal section, being obscured from view by the ampulla for the anterior semicircular canal.
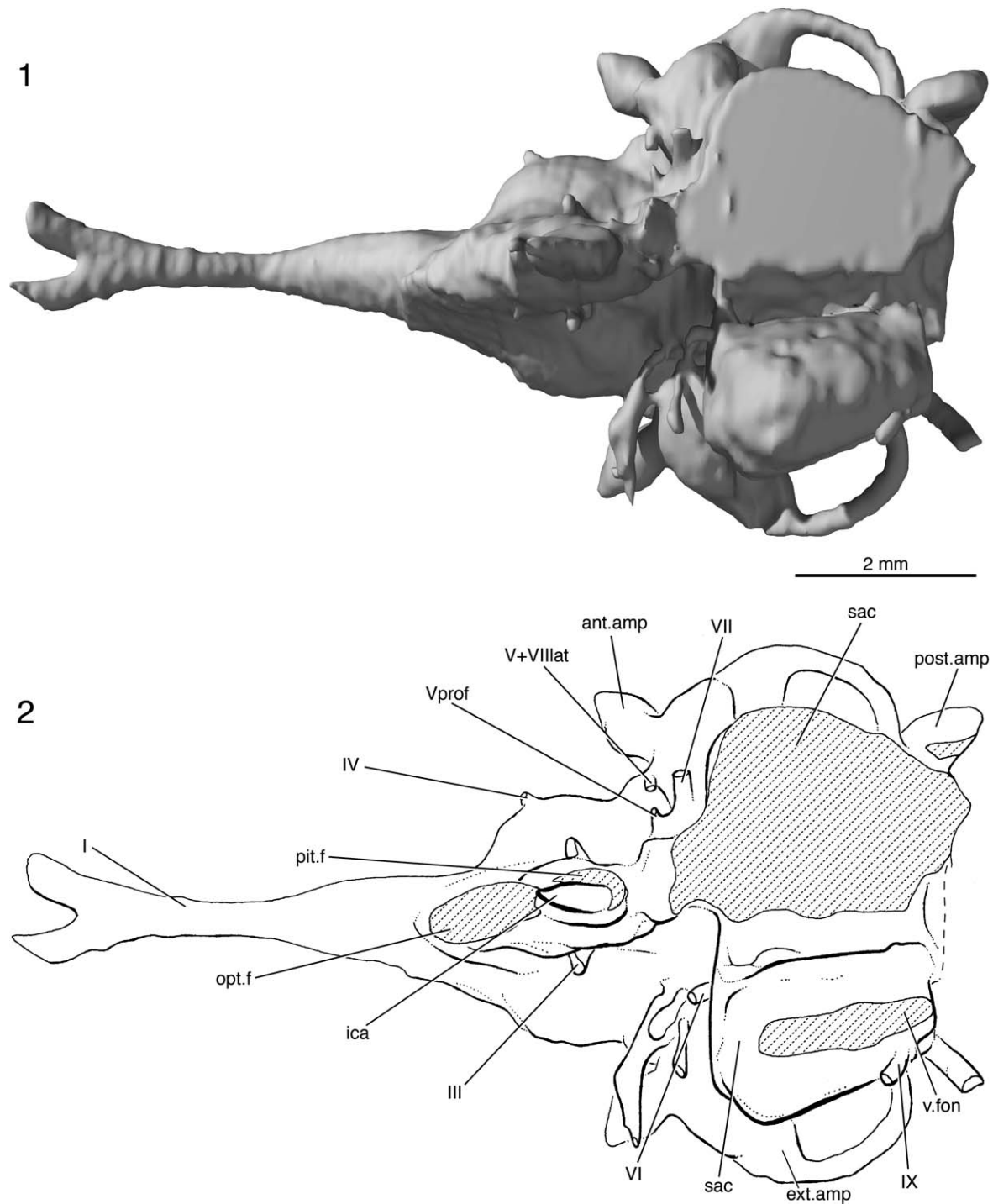
FIGURE *8*—Reconstruction of the endocast of *Kentuckia deani*, MCZ 8361, in ventral view. *1*, three-dimensional rendering of endocast; *2*, interpretive drawing of endocast.

Gardiner's (1984) interpretation of the layout of nerves within the orbit is corroborated by our analysis. The middle cerebral vein enters the orbit via its own foramen in this specimen of *Mimipiscis*, situated dorsally and slightly anteriorly of the common opening for the trigeminal nerve and lateralis branch of the facial nerve.

We are also able to correct some interpretations of the bony labyrinth. Gardiner (1984) described the posterior opening of the exterior semicircular canal as passing through the ampulla of the posterior canal, but it is clear that they enter the cranial cavity

separately. This brings the structure in *Mimispicis* in line with that seen in *Kentuckia*, as well as the Triassic *Boreosomus* and *Pteronisculus* (Nielsen, 1942). A vertical separation between the external semicircular canal and posterior ampulla, with one opening sitting above the other, is evident in placoderms (Goujet, 1984) and chondrichthyans (Schaeffer, 1981; Maisey, 2007), as well as some sarcopterygians (e.g., *Chirodipterus*; Säve-Söderbergh, 1952). The alternative condition is seen in *Kansasiella* (Poplin, 1974) and a number of Triassic actinopterygians (Nielsen, 1942). On a more minor note, the recess for the saccus
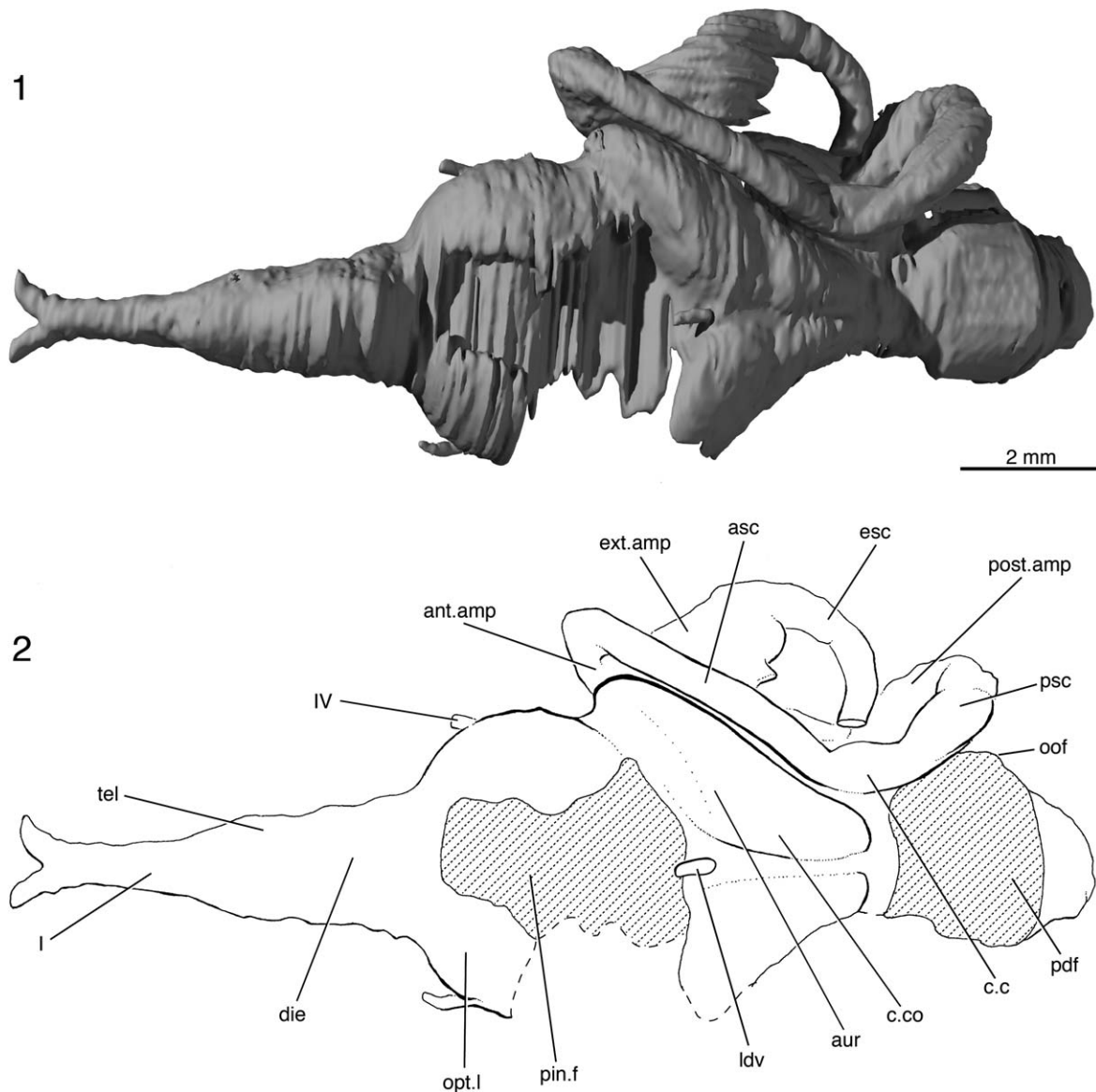
FIGURE 9—Reconstruction of the endocast of *Kentuckia deani*, MCZ 5226, in dorsal view. *1*, three-dimensional rendering of endocast; *2*, interpretive drawing of endocast.

vasculosus is somewhat larger than that figured by Gardiner (1984, fig. 26).

This study is also able to confirm many of Rayner's tentative interpretations concerning the endocranial cavity of *Kentuckia* while revealing new morphological data concerning overall brain structure and proportions. We are also able to test the interpretations made by Moodie (1915) of the lectotype of *Kentuckia*, a natural endocranial cast. The written account of the endocranial cavity provided by Rayner is detailed, but only one figure (1951, fig. 9), a diagrammatic sagittal section through the braincase, provides illustration. While many of the interpretations are correct, the figure as a whole is misleading. The proportions of the braincase are incorrect, and the region behind the orbit needs to be stretched by approximately one third to reflect the true shape. Once the correct proportions are resolved, it becomes clear that the optic lobes are far larger than illustrated, and the arrangement of the utriculus and exits of the semicircular canals resembles that of *Mimipiscis* and other early ray-finned fishes. The root of the abducens (VI) nerve, which Rayner could not locate, emerges from the medial portion of the sacculus and travels forward to exit into the orbit.

Other minor amendments that can be made refer to openings that Rayner could not identify with certainty. The "deep hollow" (Rayner, 1951, fig. 9, "x") found in the loop of the posterior semicircular canal can be confirmed as the lateral cranial canal. A smaller pocket in the loop of the anterior canal is the ventral lobe of the cerebellar auricle, rather than part of the lateral cranial canal network. Segmentation of the complete course of the oculomotor (III) nerve confirms that the tract bifurcates distally to enter the orbit through two separate foramina in at least some specimens of *Kentuckia*, such as MCZ 5226.

As described and illustrated by Rayner, three canals leave the cranial cavity to enter the trigeminofacialis chamber before continuing into the orbit. The external configuration illustrated by Rayner (1951, fig. 8) largely matches that seen in MCZ 5226. The facial (VII) nerve canal (probably also carrying the trigeminal [V] nerve) is described as opening into the orbit from the floor of the trigeminofacialis chamber. This is largely accurate, although the
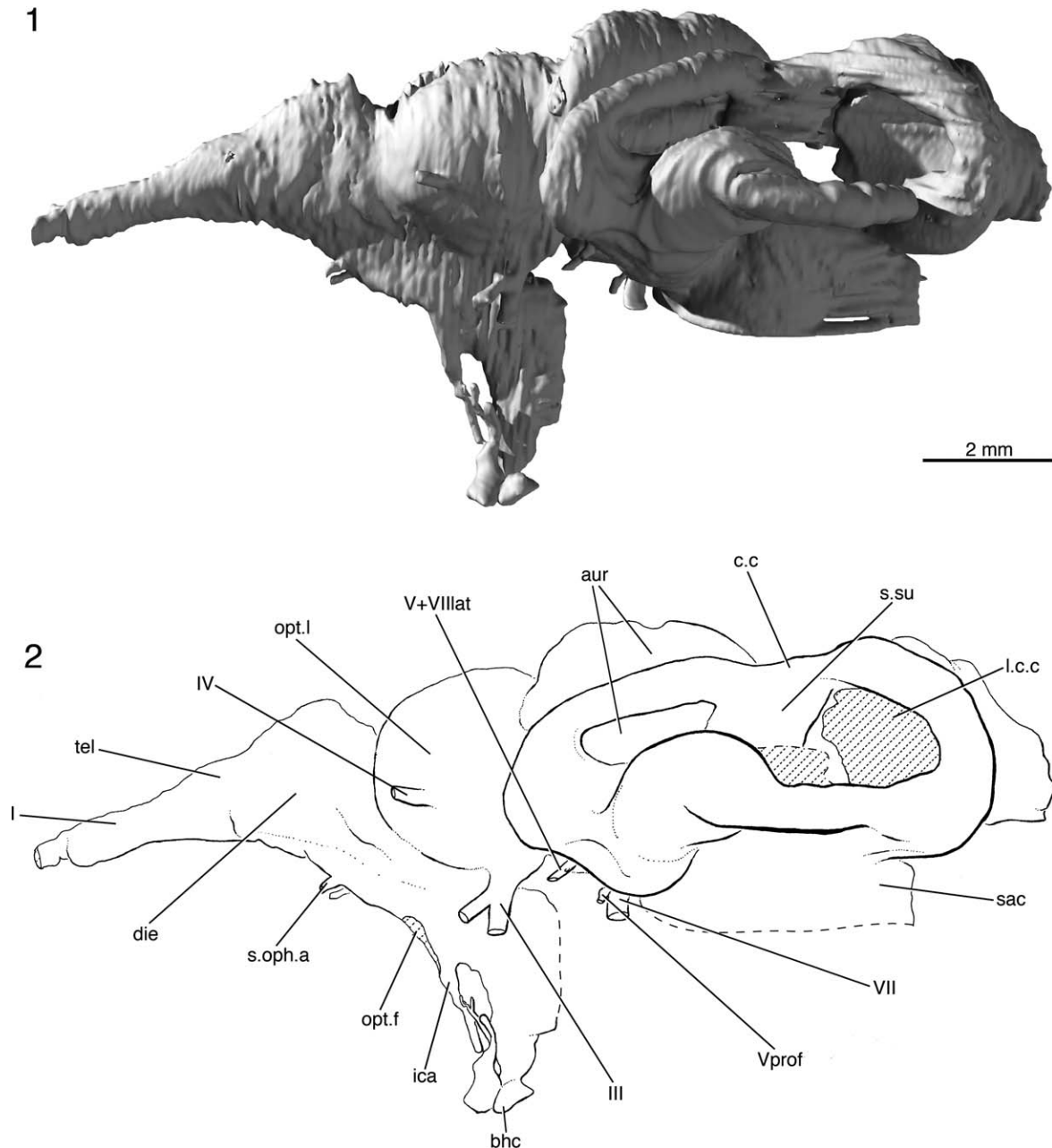
FIGURE 10—Reconstruction of the endocast of *Kentuckia deani*, MCZ 5226, in left lateral view. This image has been flipped horizontally and in fact is of the right side of the endocast. *1*, three-dimensional rendering of endocast; *2*, interpretive drawing of endocast. The pocket of the lateral cranial canal has been "cut" to avoid obscuring parts of the labyrinth.

opening is on the medial wall of the chamber rather than its roof. The profundus nerve (Vprof) enters the orbit via an opening just dorsal to the two oculomotor (III) foramina. Rayner's labeling of this opening in lateral view (1951, fig. 7) is misleading; the opening identified as "Vprof" is in fact a branch of the arterial/venous network. The true position of Vprof is somewhat more ventral, although no corresponding foramen is drawn in Rayner's figure.

The pattern of nerve exits from the cranial cavity proposed by Rayner is more difficult to ratify, particularly as the positioning of these canals differs between MCZ 5226 and MCZ 8361. This variation is even more apparent in sagittal section. Rayner's illustration (1951, fig. 9) identifies three exits: a canal for the facial nerve, leaving from the same region as the anterior ampulla; a slightly more anteriorly-placed canal for the profundus

nerve; and the trigeminal nerve canal more anteriorly still. The relative position of these three nerves largely matches that of MCZ 5662, although the facial nerve exits the cranial cavity more medially than the exit from the ampulla shown by Rayner (1951, fig. 9). This is not the case in MCZ 8361, where the canal for the trigeminal nerve does in fact exit from the region of the anterior ampulla. The facial nerve in MCZ 8361 exits more medially, and the canal for the profundus nerve is situated more anteriorly. Finally, the canal for the glossopharyngeal (IX) nerve exits the cranial cavity of MCZ 8361 considerably more ventrally than indicated by Rayner (1951, fig. 9). This region is not resolved in MCZ 5226, but the exit is assumed to be in a similar position.

The morphology of the lectotype (MCZ 5222) described by Moodie (1915, figs. 3, 4) largely matches that of our virtual
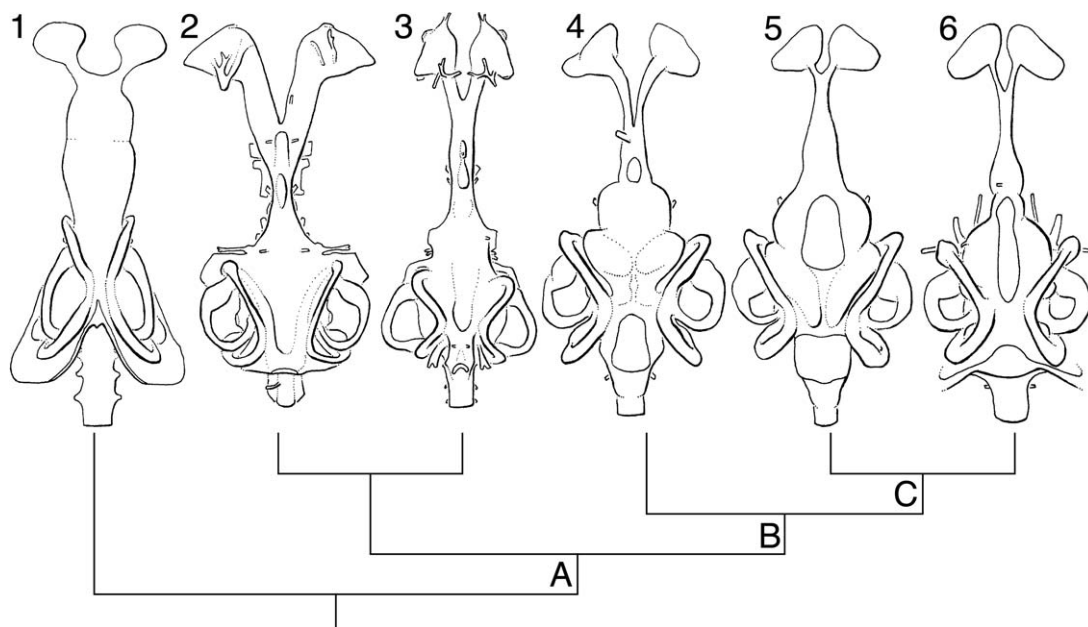
FIGURE *11*—Cladogram showing distribution of potential apomorphies visible in the endocast, with an emphasis on osteichthyans, particularly actinopterygians. Cladogram based on Coates (1999), Hamel and Poplin (2008), and Zhu et al. (2009). Proposed endocast synapomorphies are drawn from this study and others (referenced accordingly). *1*, *Orthacanthus* Agassiz, 1883, modified from Schaeffer, 1981; *2*, *Youngolepis*, modified from Chang, 1982; *3*, *Eusthenopteron*, modified from Jarvik, 1980; *4*, *Mimipiscis*; *5*, *Kentuckia*; *6*, *Lawrenciella*, modified from Hamel and Poplin (2008). Node A: long olfactory tracts (Friedman and Brazeau, 2010); horizontal semicircular canal joins labyrinth level with the ampulla for the posterior semicircular canal (Davis et al., 2012). Node B: lateral cranial canal (Coates, 1999; although see Discussion); cerebral hemispheres formed by evagination of telencephalon (Nieuwenhuys, 1982). Node C: anteriorly directed olfactory tracts (Coates, 1999); olfactory nerves carried in a single tract; optic lobes as wide as cerebellum; crus commune of anterior and posterior semicircular canals ventral to endocranial roof.

endocast models. Despite the fact that many morphological details are obscured in the lectotype, Moodie's description can generally be corroborated, although his 'tuberculum acusticum' is in fact the bilobed cerebellum.

Systematic and evolutionary implications.—As well as representing critical tests of previous morphological interpretations of *Mimipiscis* and *Kentuckia*, the virtual endocasts produced by this study permit more direct comparison with similar reconstructions available for other early gnathostomes (Fig. 11). Although the endocasts of early fossil actinopterygians are thought to faithfully record brain structure (Edinger, 1929; Jerison, 1973; Bjerring, 1971; Coates, 1999), this is not the case for other groups of vertebrates. As a consequence, paleontological comparisons like those below are most accurately framed as being between the anatomy of endocasts rather than brains.

The endocasts of *Mimipiscis* and *Kentuckia* reveal characteristics consistent with previous phylogenetic placements of these genera. Their long olfactory tracts represent an osteichthyan synapomorphy (Friedman and Brazeau, 2010). The presence of a lateral cranial canal is thought to unite these genera with other actinopterans (Coates, 1999), although the discovery of a putative lateral cranial canal in *Meemannia*, *Psarolepis*, and *Ligulalepis* raises the possibility that this feature may be more widely distributed amongst osteichthyans (Zhu et al., 2010). At a finer phylogenetic scale, the endocasts of *Mimipiscis* and *Kentuckia* show some striking differences, especially in terms of overall geometry. The endocast of *Kentuckia* broadly resembles that of stratigraphically younger ray fins from the Pennsylvanian, particularly *Lawrenciella* (Hamel and Poplin, 2008) and *Kansasiella* (Poplin, 1974). All of these Carboniferous taxa are interpreted as branching from more crownward positions on the actinopteran stem than *Mimipiscis* (Coates, 1999; Gardiner et al., 2004). Our new endocast data supports this phylogenetic hypothesis by revealing generalized features shared by

Mimipiscis, sarcopterygians and chondrichthyans, but which show apparently derived conditions in Carboniferous and younger actinopteran ray-finned fishes (Fig. 11). These relate to the morphology of the olfactory tracts, labyrinth, and mesencephalon.

As in sarcopterygians (e.g., Nieuwenhuys et al., 1977, fig. 1; Chang, 1982, figs. 17, 18; Clément and Ahlberg, 2010, fig. 7), the stem osteichthyan *Ligulalepis* (Basden et al., 2000, fig. 1; Basden and Young, 2001, figs. 1, 7), chondrichthyans (Schaeffer, 1981, figs. 14, 15; Maisey, 2005, fig. 27; Pradel, 2010, fig. 30), and placoderms (e.g., Stensiö, 1963b, figs. 26, 27, 29–33, 35), the olfactory canals of *Mimipiscis* are broadly separated along most of their length (Figs. 3, 5). This is opposed to the morphology seen in all other early actinopterygians, where the canal is present as a single midline tube (Fig. 11.5, 11.6, Node C). Related to this, the tracts of *Mimipiscis* are laterally divergent, again more closely resembling the condition in actinopterygian outgroups than that found in other Paleozoic ray fins (Fig. 11.1–11.4, Node C). A further generalized condition apparent in *Mimipiscis* relates to the geometry of the labyrinth region. In previously described ray-finned fish endocasts, the crus commune of the anterior and posterior semicircular canal is typically set into the lateral wall of the cranial cavity (Fig. 11, Node C; e.g., Hamel and Poplin, 2008, figs. 13, 14; Poplin, 1974, fig. 27). This is not the case in *Mimipiscis*; instead, the crus commune sits above the cranial cavity (Figs. 3, 4). This arrangement is seen elsewhere in early members of actinopterygian outgroups (e.g., Chang, 1982, fig. 19; Säve-Söderbergh, 1952, fig. 9), and is developed to such an extent in some Paleozoic chondrichthyans that the crus commune of the left canal almost meets with that of the right canal at the midline (Fig. 11.1; Schaeffer, 1981, fig. 14). Additionally, the general arrangement of the optic lobes in *Mimipiscis* appears to be primitive relative to *Kentuckia* and other Carboniferous actinopterygians. Whereas the optic lobes are conspicuously expanded in the endocasts of these stratigraphically younger ray fins, such

that the optic lobes are the same width as the cerebellum (Fig. 11.5 and 11.6), the endocast of *Mimipiscis* increases gradually in width from the diencephalon to the cerebellum (Fig. 3). This matches the condition in sarcopterygians and chondrichthyans (Fig. 11.1–11.3) (e.g., Chang, 1982, fig. 17; Maisey, 2007, fig. 26), and is presumably the primitive arrangement for crown gnathostomes.

The unusual geometry of the brain seen in *Mimipiscis* reflects the small optic lobes of the genus in comparison to other actinopterygians. Enlargement of the optic lobes in ray fins is generally interpreted as reflecting the strong reliance on vision in this group (Goatley et al., 2010). The absence of large optic lobes in *Mimipiscis* is somewhat surprising, given its proportionally large eyes and presumed reefal ecology (Long and Trinajstic, 2010). An increased dependence on vision appears to have been derived within actinopterygians, based on the relatively small eyes found in the deepest branching members of the group, (e.g., *Cheirolepis* Agassiz, 1843 [Pearson and Westoll, 1979], *Osorioichthys* Casier, 1954 [Taverne, 1997]) and early sarcopterygians, (e.g., *Grossius* Schultze, 1973; *Guiyu* Zhu et al., 2009; *Miguashaia* Schultze, 1973; *Onychodus* Newberry, 1857 [Andrews et al., 2006]; *Osteolepis* Agassiz, 1843; *Porolepis* Woodward, 1891). Assuming that the modest optic lobes of *Mimipiscis* represent a primitive condition rather than a reversal, then enlargement of the eyes in actinopterygians preceded corresponding architectural modifications to the brain. Endocast data for other early ray-finned fishes would provide a critical test of this inference.

CONCLUSION

The study of endocast morphology in early fossil vertebrates has a long scientific history, with the majority of detailed reconstructions available in the literature representing the results of studies conducted several decades ago (online Supplemental Data file 1). We applied CT techniques in order to investigate endocranial anatomy of two phylogenetically significant genera of early ray-finned fishes, *Mimipiscis* and *Kentuckia*. Detailed accounts of the endocranial chamber had been presented for both (Rayner, 1951; Gardiner, 1984), but no endocasts had been produced that would permit more direct comparisons with similar reconstructions available for other early vertebrates. Our virtual endocasts provide a critical test of previous anatomical interpretations of structure in these Paleozoic ray-finned fishes. Apart from some details relating to specific patterns of innervation and proportions, these older accounts are largely accurate. However, our endocasts clearly show new features not apparent in existing descriptions. Key among these are the presence of long, separate olfactory tracts and small optic lobes in *Mimipiscis*. These conditions diverge from those found in other Paleozoic actinopterygians, but agree with those apparent in sarcopterygians, suggesting that they are general features of crown osteichthyans.

Details of the neurocranium in general and its internal structure in particular have great potential in early vertebrate systematics, especially because consistent endoskeletal comparisons can be drawn across groups with radically different dermal skeletons. Despite this promise, relatively few characters pertaining to endocast morphology are incorporated in cladistic analyses (but see Coates, 1999; Friedman, 2007; Friedman et al., 2007; Brazeau, 2009; Zhu et al., 2009; Coates and Friedman, 2010; Davis et al., 2012). In part, this reflects the historical difficulty in obtaining endocast data from fossil specimens, with the consequence that reconstructions are only available for a small number of taxa within each major group of early vertebrates (online Supplemental Data file 1). This problem is clearly illustrated by our contribution, which provides the first endocast models for pre-Pennsylvanian ray-finned fishes. However, the proliferation of tomographic techniques and virtual paleontology, combined with a wealth of excellently preserved neurocrania, provides the means of quickly and efficiently filling these gaps in our understanding of endocranial structure in early vertebrates. As in our analysis, we anticipate that the application of CT scanning to other previously studied taxa will offer a critical test of existing endocast reconstructions (e.g., Gai et al., 2011). The revisions and new discoveries from these classic specimens can be complemented with completely novel endocasts for previously uninvestigated materials. Both will represent important sources of raw morphological data that will provide an important addition to existing character sets for early vertebrates.

ACCESSIBILITY OF SUPPLEMENTAL DATA

Supplemental data deposited in Dryad repository: http://dx.doi.org/10.5061/dryad.6j13r.

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