

Chapter 2

Actinopterygians: The Ray-Finned Fishes —An Explosion of Diversity

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Abstract Living ray-finned fishes number approximately 30,000 species, roughly equal to modern lobe-finned fishes plus tetrapods combined. The fossil record of ray-finned fishes extends to the Early Devonian (ca. 415 Ma), although the oldest taxa for which the morphology of the otic region is known in any great detail are 35 million years younger. Early actinopterygians have consolidated saccular otoliths, open vestibular fontanelles, and a persistent otico-occipital fissure. These general osteichthyan conditions are joined by specializations like the lateral cranial canal, a diverticulum that extends through the loop of the posterior semicircular canal and is thought to be unrelated to hearing. This anatomy persists into early members of the dominant modern radiation of ray-finned fishes, Neopterygii. Neopterygian subclades, including teleosts, show parallel losses of persistent fissures, fragmentation of the endocranium into separate ossification centers, and reduced bony enclosure of the inner ear. Teleosts show remarkable specializations for hearing based on connections between the gas-filled swim bladder and the otic capsule. Cretaceous fossils of clupeomorphs (herrings) and otophysans (catfishes, minnows, characins, and Neotropical knifefishes) document the assembly of the specialized anatomical features associated with hearing in both groups.

Keywords Actinopterygii · Cladistia · Chondrostei · Holostei · Inner ear · Neopterygii · Otolith · Skeletal labyrinth · Teleostei · Weberian apparatus

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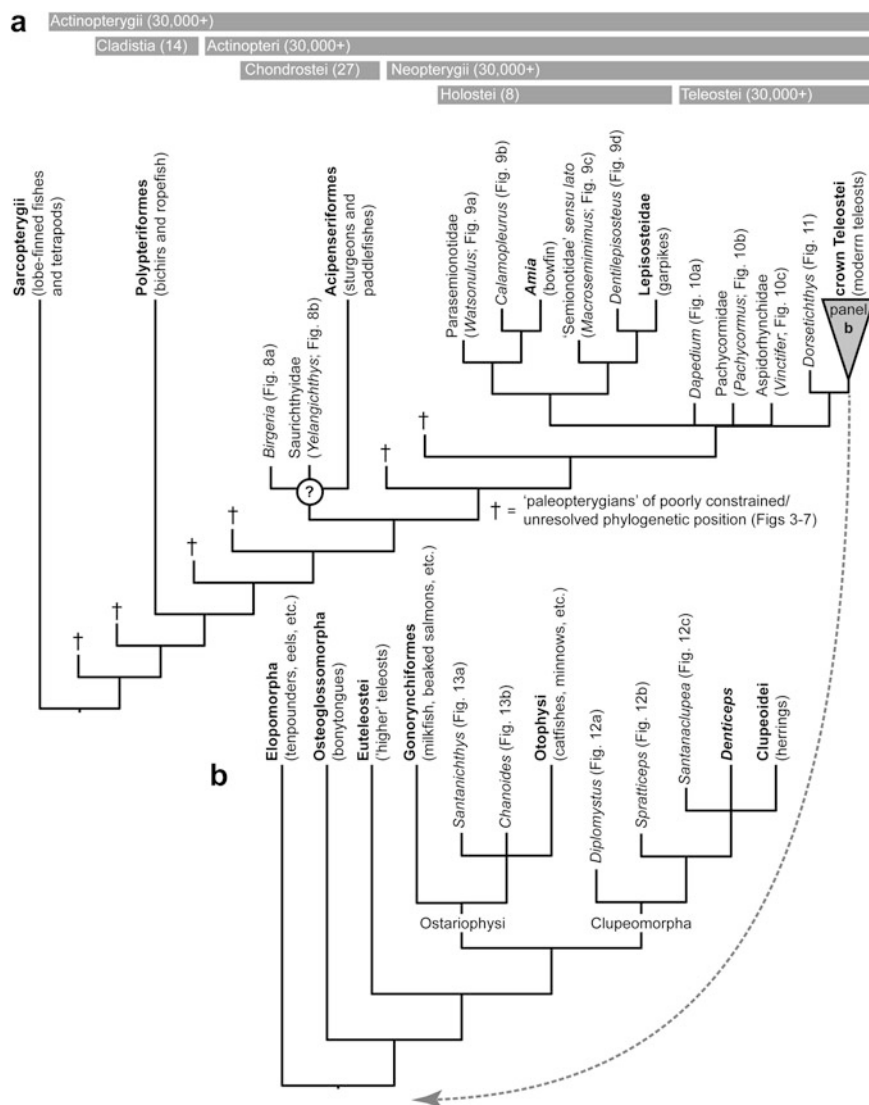
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Abbreviations in Figures

ampa	ampulla of the anterior semicircular canal
ampe	ampulla of external semicircular canal
ampp	ampulla of posterior semicircular canal
asc	anterior semicircular canal
cnX	vagus nerve
df	dorsal fontanelle
esc	external semicircular canal
fb	fossa bridgei
hym	hyomandibula
hymf	hyomandibular facet
lcc	lateral cranial canal
oa	occipital arch
oof	otico-occipital fissure
ot	otolith
pqc	palatoquadrate complex
psc	posterior semicircular canal
sac	sacculus chamber
spc	spiracular canal
vf	vestibular fontanelle
ssu	sinus superior
utr	utricle recess
vf	vestibular fontanelle

2.1 Introduction

Osteichthyans, the bony fishes, comprise two divisions: actinopterygians, or the ray-finned fishes, and sarcopterygians, including the lobe-finned fishes and tetrapods, which represent the other half of this major vertebrate radiation and form the focus of all subsequent chapters. Actinopterygians and sarcopterygians contain roughly equal numbers of living species, so the account given here of ray-finned fishes is necessarily skeletal in its detail relative to that provided for their lobe-finned cousins. The following sections establish the basic context for the overwhelming diversity of actinopterygians, providing broad outlines of skull anatomy in osteichthyans (Sect. 2.1.1) and an overview of paleontological evidence bearing on the very earliest bony fishes. Figure 2.1 shows a basic family tree of actinopterygian groups.



2.1.1 Bony Fish Skull Anatomy: An Overview

Cranial anatomy in early actinopterygians corresponds broadly to that for jawed vertebrates generally (Fig. 2.2) (also see Clack, Chap. 1). The braincase represents the core of the skull with other components of the head suspended from or applied

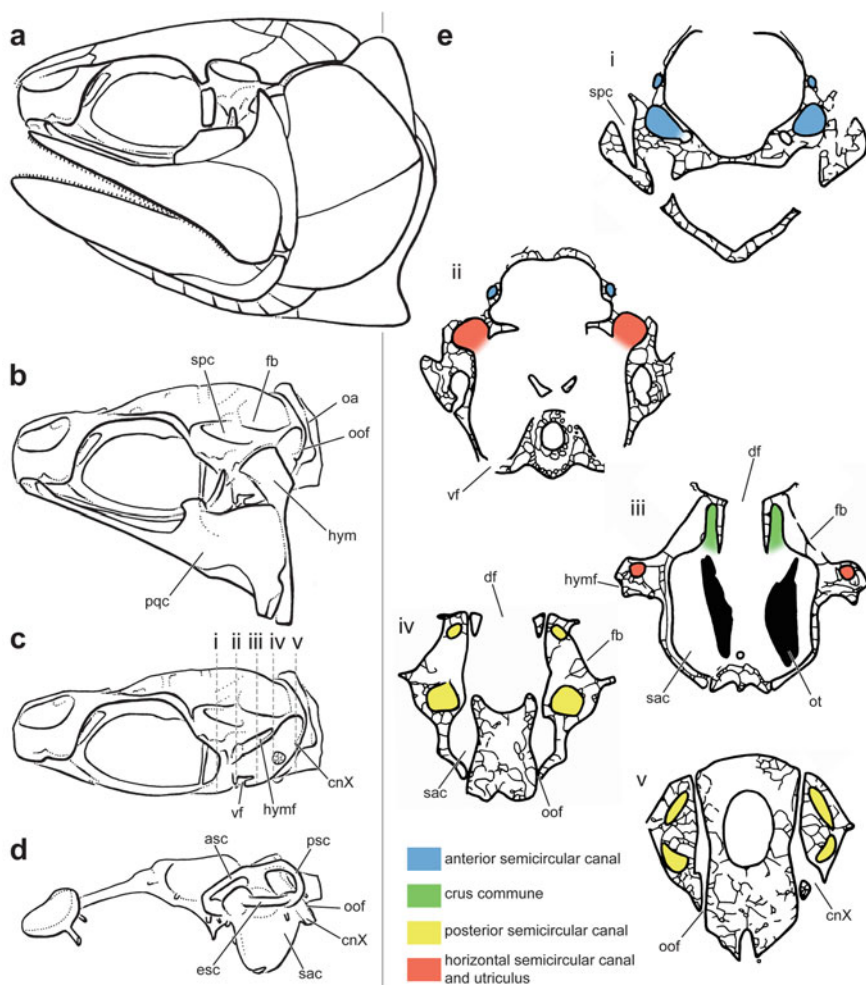


Fig. 2.2 Cranial anatomy in bony fishes, illustrated by the Triassic actinopterygian *Australosomus*. **(a)** Skull showing complete covering of external bones overlying the endoskeleton. **(b)** Skull with external dermal bones, gill arches, and ventral halves of the mandibular and hyoid arches removed. **(c)** Endoskeletal braincase in isolation. **(d)** Cranial endocast (for enlarged version highlighting inner ear, see Fig. 2.7). **(e)** Cross sections through the otic region, with numerals keyed to sections indicated in c. Void spaces corresponding to the skeletal labyrinth are color-coded. (Based on Nielsen 1949)

to it. A series of jointed arches hang beneath the braincase. From anterior to posterior, these are: the mandibular arch, the hyoid arch, and the branchial arches. There is a single pair of mandibular arches, one on each side of the skull, and they represent the primary upper and lower jaws. The upper jaw, which is known as the palatoquadrate, shows many patterns of articulation with the braincase, but the primitive pattern in bony fishes includes a basal articulation beneath the eye and an ethmoid articulation beneath the nasal capsule. The hyoid arch lies behind the mandibular arch and is dominated by two principal segments: the dorsally located hyomandibula, which articulates with the otic region of the braincase, serves an important role in supporting the primary upper jaw, and represents the evolutionary precursor of the tetrapod stapes; and the ventrally located ceratohyal, which is a critical component of suction feeding in many fishes.

Primitively, five gill arches trail the hyoid arch, although this number is reduced in many bony fish lineages. The oral surfaces of the mandibular and gill arches are associated with plate-like dermal bones that often bear teeth. This complex series of arches and the central braincase are then covered to varying degrees by external bones of the skull. It is increasingly clear that this extensive exterior cladding represents the primitive style of jawed-vertebrate skull construction, with the reduction and loss of the outer bony plates typical of cartilaginous fishes representing a specialized arrangement (Zhu et al. 2013).

The braincase arises developmentally from a series of embryonic cartilages that are replaced by bone during ontogeny (see Clack, Chap. 1). Traces of these embryonic precursors persist in the braincases of some extinct ray-finned fishes in the form of persistent fissures between ossifications. Most relevant here are fissures in the posterior half of the braincase, which is divided between the otic and occipital regions. The embryonic otico-occipital fissure between these regions can be completely obliterated, can persist as a cartilaginous band between bones, or can be present as an unfilled gap between ossifications. In many early bony fishes, the persistent fissure intersects a broad, unossified area on the ventrolateral face of the chamber housing the sacculus of the inner ear: the vestibular fontanelle. Anterodorsal to this fontanelle, the otic capsule of bony fishes primitively bears a longitudinal canal for the jugular vein, as well as areas of articulation for the hyoid and gill arches. Some ray-finned and lobe-finned fishes show further modifications to the exterior of the otic region, including partial endoskeletal enclosure of the spiracle (a putatively vestigial gill slit associated with the hyoid arch) and various shallow depressions, or fossae, that lie between the roof of the braincase and the overlying dermal skull roof. The homologies of these fossae are uncertain, leading to the proposal of complex nomenclatural schemes to describe patterns of variation across groups (Bjerring 1984).

When lined with bone, the cranial cavity within the otic region can provide broad outlines of the structure of the inner ear. Positive models of this void space—called an endocast—indicate that the inner ear was almost entirely encased by bone in early osteichthyans. Enclosure of individual components of the inner ear is reduced in living ray-finned fishes in comparison to their earliest relatives, meaning that many major features of inner ear geometry cannot be discerned from cranial endocasts.

2.1.2 *The Earliest Bony Fishes*

Definitive actinopterygians and sarcopterygians are joined by a series of Late Silurian–Early Devonian bony fishes of less secure phylogenetic placement. These “basal osteichthyans” include two Early Devonian (ca. 415–400 Ma; see Clack, Chap. 1 for a geological timescale) forms for which some details of the ear region have been described: *Psarolepis* and “*Ligulalepis*” (enclosed in quotes because the definitive material of the genus is scales with no clear links to relevant cranial material). Current understanding of neurocranial anatomy in these important early taxa is limited, despite their antiquity and clear significance.

Psarolepis (Yu 1998) is known from the earliest Early Devonian of China, and its ear structure is known only from flattened otic capsules. The dorsal surface of the cranial endocavity is visible owing to taphonomic loss of the parachordal region due to the presence of a persistent otico-occipital fissure. Despite the additional exposure of internal anatomy this provides, little can be said of ear structure in *Psarolepis* apart from the presence of three large semicircular canals. “*Ligulalepis*” is potentially more informative with respect to ear morphology in very primitive bony fishes, as it is represented by a single incomplete but uncrushed braincase from Australia that has been subjected to acid preparation (Basden and Young 2001). Like *Psarolepis*, “*Ligulalepis*” bears a complete otico-occipital fissure. Here, too, the parachordal plate is not preserved, revealing the detailed internal surface of the brain cavity and apertures to the semicircular canals. However, no virtual endocast is yet available for the bony labyrinth of this important early osteichthyan, so no detailed comparisons can be made with the arrangement in younger forms.

Joining these early osteichthyans of uncertain placement is *Janusiscus*. Originally interpreted as a species of *Dialipina* (and a ray-finned fish), renewed study using X-ray computed tomography (μ CT) reveals a braincase lacking a basal fissure and vestibular fontanelles. *Janusiscus* is placed as a bony-fish-like member of the gnathostome stem lineage (Giles et al. 2015c). That is, it is more closely related to living jawed vertebrates (the “crown” group) than the next closest living lineage (in this case jawless vertebrates), but does not belong to either bony fishes or cartilaginous fishes, the two surviving lineages of jawed vertebrates. Rather, it branches from the jawed vertebrate tree before the evolutionary divergence between these two familiar groups. Traces of the bony labyrinth are apparent, but not sufficiently well-preserved to make meaningful comparisons with other early gnathostomes.

2.2 The Fossil Record of Actinopterygian Hearing

Knowledge about ear structure in fossil actinopterygians derives principally from two lines of evidence: endocasts of the bony labyrinth and saccular chamber, and saccular otoliths (also known as the sagitta or saccolith). The latter are composed of either of two forms of calcium carbonate, vaterite or aragonite, and are one of the

three pairs of large otoliths or “ear stones” present in most modern ray-finned fishes (a single pair of otoliths characterizes early actinopterygians and sarcopterygians and is likely to be primitive; see Sect. 2.3). These two records are largely non-overlapping in terms of time and phylogeny; a majority of actinopterygian endocasts belong to a modest set of Paleozoic or early Mesozoic non-teleosts that are known in exhaustive detail, while the study of fossil otoliths is almost exclusively limited to latest Mesozoic and Cenozoic teleost remains that are usually found isolated from body fossils. These key lines of anatomical evidence are joined by hard-tissue specializations related to hearing in specific groups, such as the elaborate Weberian system of otophysan teleosts. This overview of actinopterygians will focus principally on aspects of the bony skeleton. The vast otolith record is beyond the scope of this general review, but key aspects are noted below where relevant. More detailed summaries of fossil otoliths can be found in Nolf (2013).

2.3 Devonian Actinopterygians

Despite their dominance in aquatic settings today, ray-finned fishes were neither abundant nor diverse during the Devonian “Age of Fishes” (Friedman 2015). Fragmentary fossils of latest Silurian and Early Devonian age have been aligned with ray-finned fishes in the past (Schultze 2015; see also Sect. 2.1.2), although there is doubt surrounding the veracity of these proposed affinities (Friedman and Brazeau 2010). The earliest taxon reliably identified as an actinopterygian is *Meemannia* (Lu et al. 2016), which is from the same Early Devonian Chinese deposits as *Psarolepis* and was described initially as a lobe-finned fish (Zhu et al. 2006). *Meemannia* is represented by highly incomplete material with partial braincases that permit reconstruction of the dorsal parts of the inner ear. Evidence for the actinopterygian affinity of *Meemannia* includes the presence of a lateral cranial canal, which is a diverticulum that extends from the endocranial cavity through the loop of the posterior semicircular canal (discussed in greater detail for *Mimipiscis* later in this section).

Prior to reinterpretation of *Meemannia*, *Cheirolepis* represented the earliest unequivocal actinopterygian. First appearing in the Middle Devonian (ca. 390 Ma), *Cheirolepis* is represented by hundreds of articulated specimens but details of internal cranial anatomy remain obscure. A badly crushed braincase of the genus reveals a persistent otico-occipital fissure and large vestibular fontanelles like those of some early sarcopterygians (see Clack and Ahlberg, Chap. 3) but no further details of the inner ear (Giles et al. 2015a). The hyomandibula is incompletely known, but it is fused with a splint-shaped dermal ossification known as the dermohyal. This fusion is a common feature among early ray-finned fishes that was lost in later forms. The braincase bears a single articular facet located near the anterior of the otic region, indicating that the hyomandibula showed the single-headed arrangement primitive for jawed vertebrates. The facet appears restricted to the region dorsal of the jugular foramen.

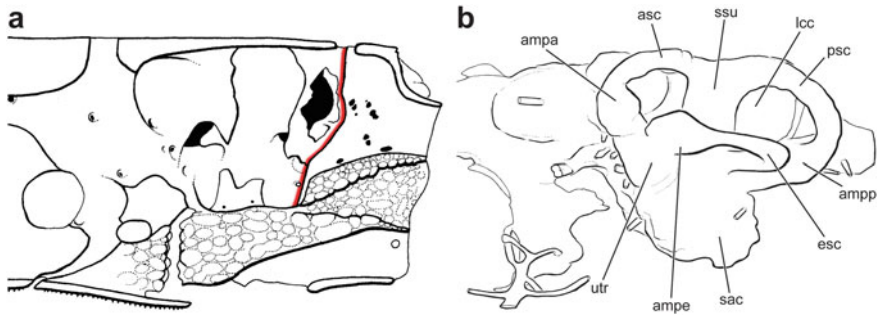


Fig. 2.3 Generalized aspects of otic morphology in actinopterygians, as exemplified by the Late Devonian (Frasnian) *Mimipiscis toombsi*. **(a)** Neurocranium in sagittal section, with anterior to left. Red indicates extent of otico-occipital fissure. **(b)** Endocast highlighting morphology of the inner ear, shown in left-lateral view. Lateral cranial canal sectioned in this image so as to not obscure labyrinth (**a** based on Gardiner 1984; **b** based on Giles and Friedman 2014)

The early Late Devonian (ca. 380 Ma) *Mimipiscis* yields the most detailed information available on ear structure for Devonian ray-finned fishes, and an overview of external structure of the otic capsule and inner details of the bony labyrinth and saccular chamber highlights general conditions of these structures in bony fishes (Fig. 2.3). Exceptionally preserved three-dimensional material of this genus from the Gogo Formation of Western Australia has been extracted from surrounding rock by acid preparation and studied both visually (Gardiner 1984) and through μ CT (Giles and Friedman 2014).

The external surface of the otic capsule bears a small vestibular fontanelle that is intersected by the otico-occipital fissure. Other early actinopterygians and many early sarcopterygians have large vestibular fontanelles, so the condition in *Mimipiscis* might be specialized (Giles et al. 2015a). Apart from the persistent fissure, there are no indications of separate ossification centers. The hyomandibula makes a single articulation with the otic capsule. The articular facet is located near the anterior of the otic region on a transverse wall of the neurocranium that is joined with the postorbital process. The strap-shaped facet is located dorsal to the level of the jugular canal. The hyoid articulation of *Mimipiscis* and other early osteichthyans contrasts strongly with that found in chondrichthyans, where the posteriorly placed articulation lies ventral to the jugular vein. The top of the braincase is tightly applied to the overlying braincase, with no intervening fossae.

As in other early jawed vertebrates (Jarvik 1980), the region occupied by the bony labyrinth is large, representing nearly one-third of skull length. The osseous labyrinth and saccular chamber communicate directly with the rest of the cranial endocavity. This arrangement also characterizes lobe-finned fishes (Jarvik 1980) as well as chondrichthyans (sharks, rays, and ratfishes) (Maisey 2005) and their fossil relatives known as acanthodians (Davis et al. 2012). By contrast, the inner ear is separated from the brain cavity by a cartilaginous or bony wall in placoderms and armoured jawless fishes (Janvier 1996). Absence of this partition seems to be a

specialization of modern jawed vertebrates (Brazeau and Friedman 2014). All three bony semicircular canals bear enlarged ampullae near their anterior (anterior and horizontal canals) or posterior (posterior canal) junctions with the cranial endocavity. Of the three, the anterior canal is the longest. The posterior and anterior bony canals are united at the crus commune and continue into the cranial endocavity as the sinus superior. The horizontal and anterior canals join the endocranial chamber very close to one another in the swollen utricular region. By contrast, the posterior junctions between the horizontal and posterior canals and the endocavity are more broadly separated. As in other bony fishes, the horizontal canal joins the endocranial chamber at the level of the ampulla of the posterior canal (Giles and Friedman 2014). The otic capsules extend far laterally relative to the parachordal plate. The course of the jugular vein extends below—rather than lateral to—the horizontal semicircular canal.

In internal view, the lateral wall of the otic capsule bears a large opening immediately anterior to the otico-occipital fissure. This feature, known as the lateral cranial canal, is unrelated to the bony labyrinth and is interpreted as bearing a hemopoietic organ based on comparisons with modern sturgeons, paddlefish, gars and bowfin (Jarvik 1980). Some have argued for the presence of a lateral cranial canal in basal osteichthyans (Zhu et al. 2010), but these interpretations are problematic (Giles and Friedman 2014) with putative openings to the canal representing the crus commune (Lu et al. 2016).

The saccular chamber extends far below the ventral surface of the chamber for the brain. It is incompletely mineralized posteroventrally, opening to the exterior through the small vestibular fontanelle. The vagus cranial nerve (X) exits from the lateral face of the saccular chamber at roughly the level of the posterior junctions between the horizontal and lateral semicircular canals with the cranial endocavity. A single compact saccular otolith is present but is only known from sectioned skulls; apart from appearing longer than deep, nothing can be said of its morphology and its mineralogy is unknown (Gardiner 1984). The primitive arrangement and composition of actinopterygian—and osteichthyan—otoliths has been the subject of considerable debate (summarized in Coates 1998). However, available evidence from modern and fossil sarcopterygians and early ray-finned fishes suggests that the presence of a single pair of large otoliths is the primitive condition for bony fishes. Modern ray-finned fishes bear three pairs of large otoliths, which is likely a secondary arrangement (Coates 1993).

Outside of *Mimipiscis*, clues about internal ear structure are scant in Devonian ray-finned fishes. Acid-prepared material of the co-occurring *Moythomasia* preserves similar detail of the otic capsules but has not been subject to the same degree of detailed description (Gardiner 1984). Models of the braincase and endocast for *Raynerius* (Giles et al. 2015b) agree with *Mimipiscis* in broad details of the otic region, although there are numerous specific differences elsewhere in the neurocranium. Otoliths in situ are reported for the Middle Devonian *Howqualepis* in association with badly crushed otic capsules (Long 1988) and appear to consist of one large otolith per side. Early–Middle Devonian deposits in the Baltic states, Belarus, and Arctic islands yield isolated otoliths attributed to ray-finned fishes

(Talimaa in Nolf 1985), but these differ in both mineralogy and structure from in situ specimens, leading Coates (1993) to reject placement with actinopterygians.

Cladistia, comprising the modern polypterids *Polypterus* and *Erpetoichthys* (bichirs and reedfish), is traditionally regarded as diverging from other actinopterygians in the Devonian (Patterson 1982). Endocranial structure in the living species differs considerably from that of the earliest ray-finned fishes. Unfortunately, the polypterid fossil record is notoriously thin, with nothing known of the endocranium in extinct members of the group (Friedman 2015).

2.4 “Paleopterygians”

Although the relationships among the principal extant lineages of ray-finned fishes are well-supported by both morphology and molecular data, the placement of Paleozoic and some Mesozoic fossils relative to modern groups remains unclear, as reviewed by Sallan (2014) and Friedman (2015). This assortment includes the “palaeoniscoids” of classical usage: a paraphyletic assemblage of ray-finned fishes recognized on the basis of shared primitive conditions of jaw structure, squamation, and overall body geometry. McCune and Schaeffer (1986) defined the term “Paleopterygii” to encompass the range of fossils that could not be definitively aligned with modern groups, explicitly acknowledging that this assemblage does not constitute a natural group. As this term carries no implication of monophyly, it is applied here as a shorthand reference to early actinopterygians in preference to older names like “palaeoniscoid” that come with considerable historical baggage. Because of uncertainty surrounding relationships, fossil taxa are reviewed in stratigraphic sequence, noting possible affinities with modern taxa where possible.

The oldest post-Devonian actinopterygian for which the otic region is known in any detail is the early Carboniferous (Mississippian) *Kentuckia* (Fig. 2.4a).

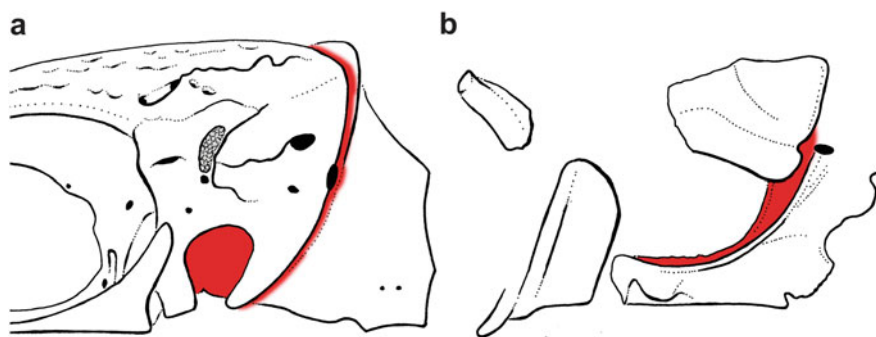


Fig. 2.4 Otic morphology in early Carboniferous (Mississippian) ray-finned fishes. Red indicates extent of otico-occipital fissure and vestibular fontanelles and gray shading defines the region of the hyomandibular facet. (a) Neurocranium of *Kentuckia deani* (Tournaisian-Viséan) shown in left-lateral view. (b) Neurocranium of *Cosmoptychius striatus* (Viséan) shown in left-lateral view (a based on Rayner 1951; b based on Schaeffer 1971)

Represented by three-dimensionally preserved heads from Kentucky, USA, *Kentuckia* (Rayner 1951) served as a key model for primitive ray-finned fish cranial conditions until the discovery and description of Gogo forms like *Mimipiscis* (Schaeffer 1968). Many aspects of the otic region—including the presence of a vestibular fontanelle and a persistent otico-occipital fissure—correspond closely to those found in Devonian taxa. The dorsal surface of the otic region bears a series of irregular depressions thought to be precursors of the paired anterior and posterior fossa bridgei. These depressions create void spaces between the dermal skull roof and the underlying neurocranium. This is unlike the condition in *Mimipiscis*, where the endoskeletal braincase is directly applied to the overlying dermal skull. Dorsal fossae are a prominent feature of many post-Devonian ray-finned fishes.

There are some differences in the endocast of the skeletal labyrinth of *Kentuckia* relative to *Mimipiscis*, the most significant of which is the placement of the crus commune of the anterior and posterior canals ventral to the roof of the endocranial chamber (Giles and Friedman 2014). This is derived relative to the earliest ray-finned fishes and is common to many post-Devonian forms. Information on the otic region is more limited for other early Carboniferous actinopterygians. A juvenile specimen of *Cosmoptychius* bears large vestibular fontanelles and an otico-occipital fissure, but it is unusual among early actinopterygians in having separate paired ossifications of the braincase including paired otic ossifications (Fig. 2.4b) (Schaeffer 1971). Such separate bones are common in stratigraphically younger taxa, especially in smaller individuals before distinct ossification centers become insensibly fused (see Sect. 2.6 and Patterson 1975 for details). No details of the labyrinth are known. A flattened neurocranium of *Woodichthys* from Scotland reveals a persistent otico-occipital fissure and well-developed vestibular fontanelles. This specimen also includes two in situ otoliths, with one each present in the right and left saccular regions. Otoliths are also known in several other specimens, although not in place (Coates 1998). The otoliths are pear shaped, with a flat medial surface and convex lateral surface. Concentric growth rings are present, but there is no central or marginal sulcus. Additional early Carboniferous taxa preserving otoliths include *Melanecta* (Fig. 2.5) (Coates 1998), *Mesopoma* (Coates 1993), *Rhadinichthys* (Moy-Thomas and Bradley Dyne 1938) and possibly *Mansfieldiscus* (Long 1988). Structure of the otoliths is clearest in *Mesopoma* and *Melanecta*. The single pair of large otoliths in *Mesopoma* broadly resembles those of *Woodichthys* in outline, although they bear a clear sulcus. *Melanecta* preserves a pair of large otoliths that differ considerably from these other examples: they are not as elongated, and they bear a prominent ventral rim composed of coalesced, rounded tubercles. More significantly, the two large otoliths of *Melanecta* are joined by three smaller ones in one specimen, suggesting a total of three pairs in the genus (Coates 1998). This complement matches that of extant ray-finned fishes, but is unlike the single pair of other early actinopterygians.

External anatomy of the otic region is known for several late Carboniferous (Pennsylvanian) actinopterygians, including *Amphicentrum* (Bradley Dyne 1939; Fig. 2.6c), *Coccocephalichthys* (Poplin and V  ran 1996), and a natural mould of the skeletal labyrinth is preserved in *Mesopoma* (Coates 1999). From what is

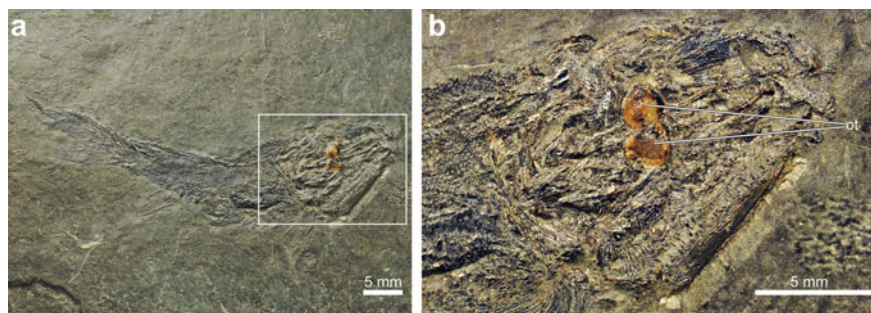


Fig. 2.5 Otolith morphology in early ray-finned fishes, illustrated by in situ examples in the Carboniferous (Serpukhovian) *Melanecta annae* (National Museum of Scotland NMS 1983.33.4). (a) Complete specimen. (b) Close-up of skull, showing large, paired saccular otoliths. (For an interpretive drawing of this same specimen, see Coates 1998)

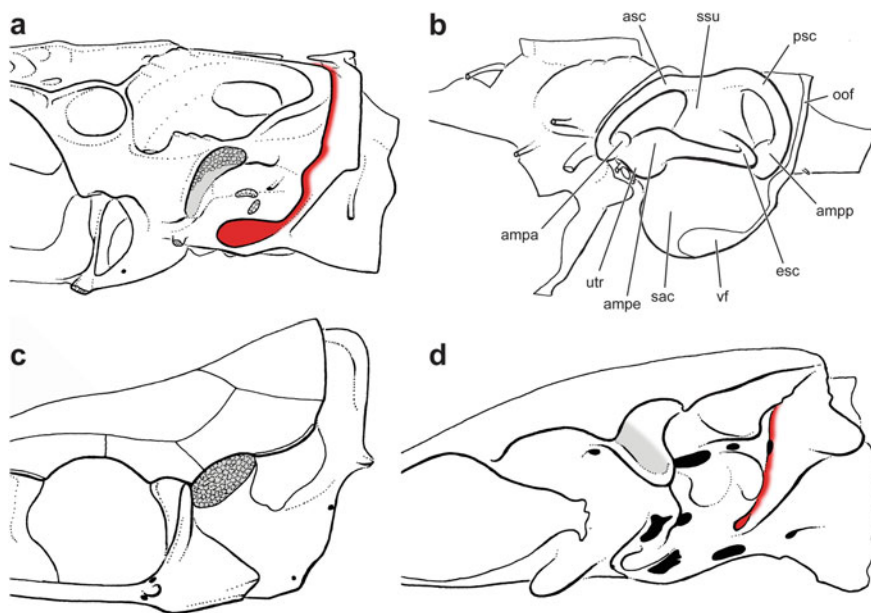


Fig. 2.6 Otic morphology in late Carboniferous (Pennsylvanian) and Permian ray-finned fishes. *Lawrenciella schaefferi* (Kasimovian), (a) neurocranium and (b) cranial endocast shown in left-lateral view. (c) Neurocranium of *Amphicentrum granulosum* (Moscovian) shown in left-lateral view. (d) Neurocranium of *Luederia kempfi* (Artinskian) shown in left-lateral view. Red indicates extent of otico-occipital fissure and vestibular fontanelles, and gray shading defines region of the hyomandibular facet. (a, b based on Hamel and Poplin 2008; c based on Bradley Dyne 1939; d based on Schaeffer and Dalquest 1978)

visible, these taxa have otic capsules broadly similar to those of other early ray-finned fishes, with the exception of the apparent absence of vestibular fontanelles and an otico-occipital fissure in *Amphicentrum*. While anatomical details for these genera are superficial, the otic region of several late Carboniferous actinopterygians are described in exquisite detail. Best known are *Kansasiella* (Poplin 1974) and *Lawrenciella* [Hamel and Poplin (2008); referred to as “palaeoniscid A” and “palaeoniscid B” in Watson (1925) and other older literature], which are represented by three-dimensional crania preserved within concretions collected in Kansas, US (Fig. 2.6a, b). Material of a third taxon (Moodie 1915; “palaeoniscid C” of Rayner 1951) remains incompletely studied. In terms of external anatomy, the otic region is broadly similar in *Kansasiella* and *Lawrenciella*. There is a modest (*Lawrenciella*) or small (*Kansasiella*) vestibular fontanelle that joins a persistent otico-occipital fissure. There are no indications of separate ossification centers. The hyomandibular facet is smaller than in *Mimipiscis* and is located at the level of the jugular canal. Both taxa have well-formed fossa bridgei comprising anterior and posterior depressions. The skeletal labyrinth and its endocast are broadly similar in the two Kansas forms. Well-developed ampullary recesses are associated with each of the semicircular canals, with those of the anterior and horizontal canals in close contact. The posterior end of the horizontal canal joins the endocavity dorsal to the ventral opening for the posterior canal. The dorsal surface of the labyrinth either lies above (*Lawrenciella*) or below (*Kansasiella*) the level of the roof of the endocranial cavity. Despite the excellent preservation of relevant material, no otoliths are known. However, Gottfried (1994) describes *in situ* examples in an unnamed actinopterygian from a different deposit from the late Carboniferous of Kansas.

In contrast to the relative abundance of material from the Carboniferous, Permian deposits yield few informative specimens. This is symptomatic of a poor Permian record of actinopterygians more generally (Friedman and Sallan 2012). *Luederia* (Fig. 2.6d) and *Progyrolepis* are represented by single specimens from the early Permian of Texas, USA. Only a portion of the otic capsule is exposed in *Progyrolepis* (Dunkle 1946), while *Luederia* comprises a complete, three-dimensionally preserved braincase lacking separate ossification centers (Schaeffer and Dalquest 1978). *Luederia* bears an otico-occipital fissure and vestibular fontanelles, although the latter are very small. No details of the inner walls of the otic capsule are known, so anatomy of the skeletal labyrinth remains uncertain. These early Permian remains are joined by late Permian material of *Palaeoniscum*, which radiographs reveal to have a pair of large otoliths (Haubold and Schaumburg 1985).

Rocks of Triassic age yield a variety of actinopterygians with well-preserved crania that have been subjected to very detailed study. The best known examples derive from Early Triassic deposits in Greenland, Spitzbergen, and Madagascar, which provide broadly similar faunas, including a range of “paleopterygians” as well as taxa branching close to or within the modern neopterygian radiation. This latter group comprises the vast majority of post-Paleozoic actinopterygian fossils and is dealt with in the following sections. Because of the great number of Mesozoic taxa for which detailed information on the otic region is available,

accounts are necessarily abbreviated with references provided for more complete descriptions.

The otic morphology of some Triassic actinopterygians is broadly similar to that of Paleozoic forms, bearing well-developed vestibular fontanelles in conjunction with an otico-occipital fissure but lacking separate ossification centers (Figs. 2.2, 2.7).

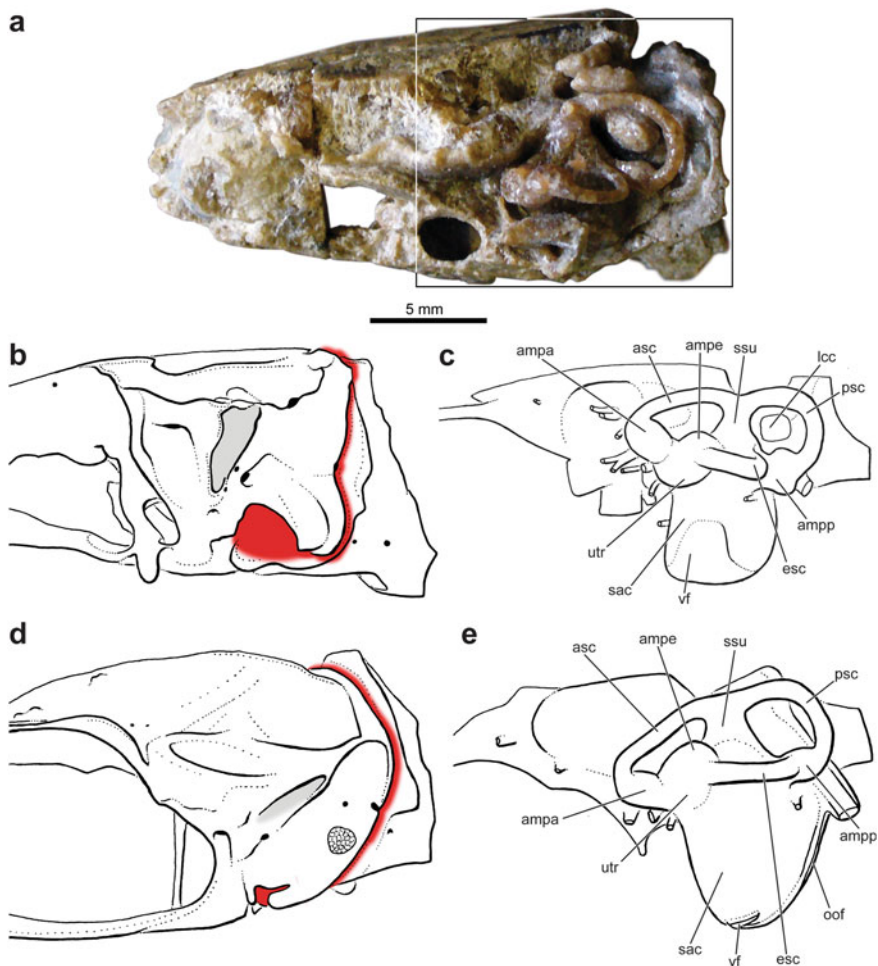


Fig. 2.7 Otic morphology in Triassic ray-finned fishes. *Red* indicates extent of otico-occipital fissure and vestibular fontanelles and *gray* shading defines region of the hyomandibular facet. (a–c) *Pteronisculus stensioei* (Induan). (a) Mechanically prepared fossil specimen showing natural endocast of skeletal labyrinth, reversed to match orientation of other figures (anterior semicircular canal missing; University Museum of Zoology, Cambridge UMZC GN.851). (b) Neurocranium. (c) Cranial endocast shown in left-lateral view. (d, e) *Australosomus kochi* (Induan). (d) Neurocranium. (e) Cranial endocast shown in left-lateral view. (a, b based on Nielsen 1942; d, e based on Nielsen 1949)

Examples include *Pteronisculus* (Nielsen 1942; referred to as *Glaucolepis* in older accounts) and *Australosomus* (Nielsen 1949), where the otico-occipital fissure sometimes extends anterior to the level of the vestibular fontanelle and joins the ventral fissure, thus completely separating the parachordal region from the otic capsules. Internal details of the otic region are known in great detail from both serial sectioning (e.g., Nielsen 1942) and natural endocasts (e.g., Coates 1999).

2.5 Chondrosteans

Many Triassic actinopterygians deviate from the conservative pattern seen in stratigraphically older taxa (Fig. 2.8). The braincase of *Birgeria* comprises several ossification centers with two sets of paired otic ossifications contributing to the postorbital process and the lateral wall of the otic capsule (Fig. 2.8a) (Nielsen 1949). The latter bones carry the posterior and anterior semicircular canals but lie dorsal to the horizontal canal. No detailed model of the labyrinth or associated structures is available for *Birgeria*. *Saurichthys* and other saurichthyids have monolithic endocrania lacking not only separate ossification centers but also vestibular fontanelles or a persistent otico-occipital fissure (Fig. 2.8b) (Stensiö 1925). *Perleidus* shows a similar degree of consolidation of the endocranium (Stensiö 1932), although separate ossification centers can be distinguished in small individuals (Patterson 1975). Despite these striking differences in the degree of neurocranial consolidation, *Saurichthys* and *Birgeria* are sometimes considered closely related to one another as adjacent branches on the stem of Chondrostei (paddlefishes and sturgeons; but see Coates 1999). Unambiguous members of this group lack extensive neurocranial ossification, so nothing can be said of otic capsule morphology in fossil members, some of which are otherwise exceptionally preserved (Grande and Hilton 2006).

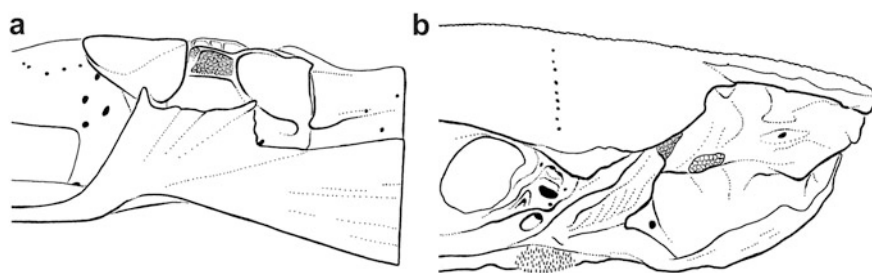


Fig. 2.8 Otic morphology in anatomically specialized Triassic ray-finned fishes often associated with chondrosteans. Gray shading defines region of the hyomandibular facet. **(a)** Neurocranium of *Birgeria groenlandica* (Induan), shown in left-lateral view. **(b)** Neurocranium of *Yelangichthys macrocephalus* (Anisian), a close relative of *Saurichthys*, shown in left-lateral view. **(a)** based on Nielsen 1949; **b** based on Wu et al. 2013)

2.6 Holosteans

Modern holosteans comprise roughly half a dozen species of Ginglymodi (garpikes; Grande 2010) and a single species of Halecomorphi (bowfin; Grande and Bemis 1998). Together they are the living sister lineage of teleosts and along with them comprise crown group Neopterygii. The limited richness of modern holosteans is complemented by restricted environmental and geographic distribution. However, fossil examples show substantially higher levels of taxonomic diversity and morphological disparity, particularly in the Mesozoic.

2.6.1 *Parasemionotids*

The earliest unequivocal members of Holostei are also the earliest definitive neopterygians, and they belong to an assemblage known as parasemionotids. The anatomy of the otic region is known in varying detail for this Early Triassic group, with the best information available for *Watsonulus* (Fig. 2.9a) (Olsen 1984) and

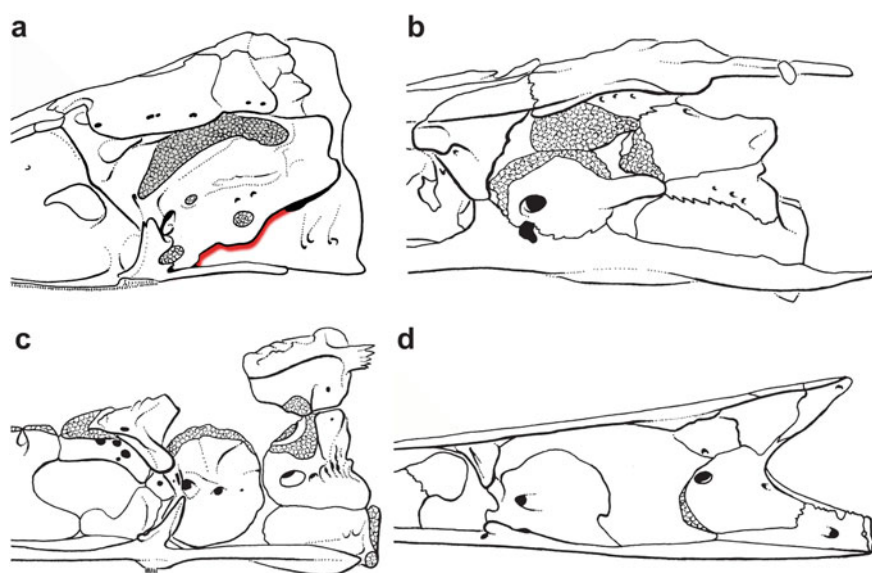


Fig. 2.9 Otic morphology in Mesozoic holosteans. Red indicates extent of otico-occipital fissure, which is sutural in *Watsonulus*. (a) Neurocranium of *Watsonulus eugnathoides* (Early Triassic: Induan) shown in left-lateral view. (b) Neurocranium of *Calamopleurus cylindricus* (Early Cretaceous: Aptian-Albian) shown in left-lateral view. (c) Neurocranium of *Macrosemimimus toombsi* (Late Jurassic: Kimmeridgian-Tithonian) shown in left-lateral view. (d) Neurocranium of *Dentilepisosteus laevis* (Early Cretaceous: Aptian-Albian) shown in left-lateral view (a based on Olsen 1984; b based on Maisey 1999; c based on Patterson 1975 where the specimen is identified as *Lepidotes*; d based on Wenz and Brito 1996 where the specimen is identified as *Obaichthys*)

Ospia (Stensiö 1932). Separate ossification centers of the otic region are visible to a varying extent among parasemionotids with some specimens showing completely co-ossified endocrania and others bearing distinct bones. However, most—if not all—parasemionotids bear vestibular fontanelles and persistent otico-occipital fissures, although the degree of development of both is variable. Rudimentary reconstructions of the skeletal labyrinth are given for *Watsonulus* and *Devillersia* by Beltan (1968), for *Ospia* by Stensiö (1932), and for an unnamed form by Giles et al. (2016), but they show no particularly striking features relative to derived Paleozoic actinopterygians like *Kansasiella* and *Lawrenciella*. The relationships of parasemionotids to other neopterygians have been controversial (Olsen 1984), and their monophyly has not been corroborated. However, there is broad consensus that *Watsonulus* is an early diverging member of the halecomorph stem, and thus a relative of the extant bowfin *Amia* and a crown-group holostean (Grande and Bemis 1998).

2.6.2 Halecomorphs

Ossified endocrania are known for a great variety of halecomorphs, and the most detailed examples are known from the Jurassic and Cretaceous. These include several examples referred to *Caturus* (reviewed in Patterson 1975), *Osteorachis* (Gardiner 1960), and *Ionoscopus* (Maisey 1999) from the Jurassic, and *Macrepistius* (Schaeffer 1971) and *Calamopleurus* (Fig. 2.9b) (Maisey 1991, 1999) from the Cretaceous. These taxa all lack a persistent otico-occipital fissure and vestibular fontanelles, and separate ossification centers of the otic region are clearly delimited, with a few exceptions (Gardiner 1960; Rayner 1948). In *Calamopleurus*, the ossifications of the otic region are separated by broad, cartilage-filled gaps, anticipating the arrangement in the modern *Amia* (Grande and Bemis 1998). Anatomy of the skeletal labyrinth and associated structures has been reconstructed for *Caturus* (Aldinger 1932; Rayner 1948) and to a lesser degree for *Ionoscopus* and *Calamopleurus* (Maisey 1999). The braincase is more completely mineralized in *Caturus*, with the semicircular canals lying completely within bone. By contrast, portions of some or all of the canals were cartilage-enclosed in the two Cretaceous forms. The structure of the saccular chamber is unknown in *Caturus* (its extent is inferred by Maisey 1999), but in *Ionoscopus* and *Calamopleurus* this feature is relatively shallow relative to the height of the skeletal labyrinth. These latter two taxa also show a clearly delimited utricular recess. The lateral cranial canal is complete rather than blind ended in both *Caturus* and *Ionoscopus*, joining the endocavity anterior and posterior to the sinus superior. The canal is absent in *Calamopleurus*, as in *Amia*.

2.6.3 *Ginglymodians*

The other major division of Holostei is Ginglymodi, the only living representatives of which are two genera of garpike. Fossil members of this clade include two other major assemblages in addition to gars: macrosemiids, which are a clade, and “semionotids” *sensu lato*, which are a grade. Both appear limited to the Mesozoic, although the Permian *Acentrophorus* is often interpreted as a “semionotid.” Features of the otic region are known for only a handful of forms in each group. The inner surface of the neurocranium in a flattened specimen of *Macrosemius* (Bartram 1977) provides the most detailed information for macrosemiids. These are slender-bodied fishes with a long-based, high dorsal fin; to draw a modern parallel, macrosemiids can be crudely described as goby-like in their overall body proportions. The otic capsule comprises a series of separate ossifications that are tightly sutured with one another. A vestibular fontanelle is absent. Although the lateral surface of the saccular chamber is preserved, openings to the skeletal labyrinth are not apparent (Bartram 1977). The “semionotids” are broadly carp-like in overall form, although obviously not closely related to that group of modern teleosts. Among “semionotids,” the otic region is best shown in material historically deposited in *Lepidotes*, a problematic wastebin taxon (Lopez-Arbarello 2012). Some relevant specimens seem correctly assigned to that genus (e.g., *L. semiseratus* in Rayner 1948), but others have been distributed to the newer taxa *Macrosemimimus* (*L. toombsi* in Patterson 1975) and *Scheenstia* (*L. mantelli* in Gardiner 1960). Otic structure is most exhaustively described in *Macrosemimimus* (Patterson 1975), but this seems largely representative of the other forms (Fig. 2.9c). There are separate ossification centers, many of which are broadly separated by cartilage. Vestibular fontanelles and an otico-occipital fissure are absent. Reduced ossification prohibits any detailed reconstruction of the inner ear. Other “semionotids” preserving portions of the otic region include *Semionotus* (Olsen and McCune 1991) and *Araripelepidotes* (Wenz and Brito 1996), although morphology is less clear in these examples due to crushing or other distortion.

External anatomy of the otic region is known for fossil representatives of both living gar genera, as well as several extinct genera (Fig. 2.9d) (Grande 2010). As in “semionotids,” there are separate ossification centers separated by substantial cartilage-filled gaps, but vestibular fontanelles and otico-occipital fissures are absent.

2.7 Teleosts

Numbering almost half of all living vertebrate species, the taxonomic richness and morphological diversity of living teleosts is staggering. The modern variety of teleosts is complemented by a rich fossil record. An exhaustive treatment of otic morphology in fossil teleosts is beyond the scope of this contribution, which instead

focuses on a few key examples: early members of the extended teleost branch of the tree of life, paleontological evidence of special innovations related to hearing in some teleost groups, and a broad overview of the otolith-based fossil record.

2.7.1 Stem Teleosts

A number of fossil fish groups have been aligned with teleosts but clearly fall outside of the modern radiation. Several Mesozoic lineages are universally accepted to branch from the teleost stem, but the placement of several others is strongly debated: Pycnodontiformes, Pachycormiformes, Aspidorhynchiformes, and Dapediidae (Fig. 2.10). These controversial groups will be reviewed first, with the acknowledgement that future study might export them to other branches of neopterygian phylogeny or outside the modern radiation entirely (e.g., Poyato-Ariza 2015).

The Jurassic dapediid *Dapedium* provides the most detailed information on the otic region in this group (Fig. 2.10a). The braincase is fully mineralized with

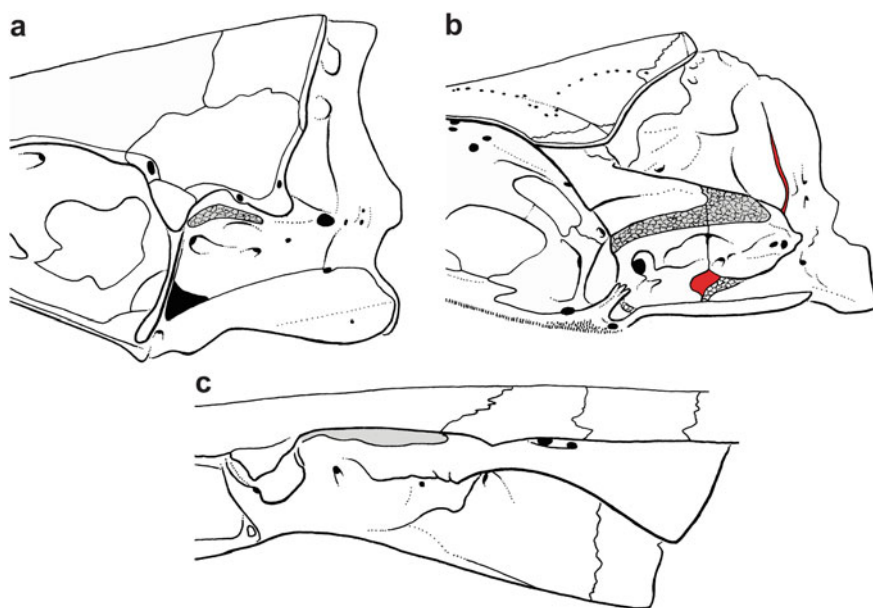


Fig. 2.10 Otic morphology in Mesozoic neopterygian groups associated with the teleost stem. *Red* indicates extent of otico-occipital fissure and vestibular fontanelles and *gray* shading defines the region of the hyomandibular facet. (a) Neurocranium of *Pachycormus* sp. (Early Jurassic: Toarcian), shown in left-lateral view. (b) Neurocranium of *Dapedium* sp. (Early Jurassic: Sinemurian), shown in left-lateral view. (c) Neurocranium of *Vincitifer comptoni* (Early Cretaceous: Aptian-Albian) shown in left-lateral view. (a, b based on Patterson 1975; c based on Maisey 1991)

separate ossification centers lacking (Patterson 1975). Both the otico-occipital fissure and vestibular fontanelles are absent. The morphology of the inner ear has recently been described based on μ CT (Giles et al. 2016), but was previously known only from apertures to the skeletal labyrinth and saccular chamber visible on the inner wall of an incomplete braincase (Rayner 1948).

Only external morphology of the otic capsules is known for pycnodontiforms and aspidorhynchiforms. *Mesturus* preserves the most informative neurocranial material among pycnodontiforms (Nursall 1999). Sutures are apparent between different ossification centers but are incomplete, and the full margins between bones cannot be traced. A short otico-occipital fissure is reported, and there is a large, apparently unossified region of the ventrolateral wall of the otic capsule above the dorsal margin of the parasphenoid. Positionally, this corresponds to the vestibular fontanelle but has not been interpreted as such. The only other pycnodontiform in which the otic region is known in any detail is the Cretaceous *Neoprosclerites*, where ossification is greatly reduced relative to *Mesturus* (Nursall and Maisey 1991).

Aspidorhynchiforms are superficially needlefish-like or gar-like fishes restricted to the Jurassic and Cretaceous. The endocranium is best represented in acid-prepared specimens of the Early Cretaceous *Vinctifer* but only from external details (Fig. 2.10c) (Maisey 1991). The braincase is also known from acid-prepared material of the closely related *Richmondichthys*, and it agrees with that of *Vinctifer* in structure (Bartholomai 2004). Separate ossification centers are present and are tightly sutured with one another. There is no otico-occipital fissure or vestibular fontanelle. The braincase attributed to “*Aspidorhynchus*” in the literature (e.g., Rayner 1948) is not, in fact, an aspidorynchiform but rather a halecomorph holostean (Patterson 1975).

Pachycormiforms are a Jurassic–Mesozoic group that includes a series of tuna-like and swordfish-like forms, as well as large-bodied suspension feeders ecologically analogous to baleen whales. Otic capsules are known in several genera, including *Bonnerichthys* (Friedman et al. 2010), but mechanically and acid-prepared material of the early representative *Pachycormus* reveals the most detailed information (Patterson 1975; Fig. 2.10a). Separate ossification centers are present, and occur in conjunction with small, comma-shaped vestibular fontanelles and persistent otico-occipital fissures that become increasingly closed in larger specimens. Some features of the skeletal labyrinth are noted by Patterson (1975) and Mainwaring (1978), but the overall geometry of the inner ear is unknown. In contrast to three-dimensionally preserved material available for *Pachycormus*, known endocrania of other pachycormiforms are heavily compressed and are not described in detail.

A series of lineages of unambiguous teleostean affinity join these putative members of the teleost total group (Fig. 2.11). These include grades like “pholidophoriforms” and “leptolepids” *sensu lato*, as well as well-characterized monophyletic groups like Ichthyodectiformes. The Early Jurassic *Dorsetichthys bechei* (called *Pholidophorus bechei* in older accounts) represents the archetypal “pholidophorid,” and its otic region is known in considerable detail on the basis of both

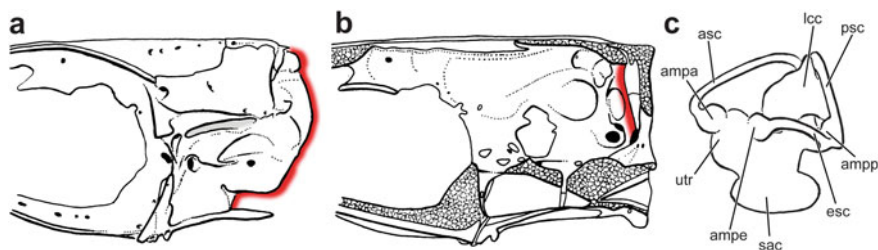


Fig. 2.11 Otic morphology of early teleosts as exemplified by the Early Jurassic (Sinemurian) *Dorsetichthys bechei*. (a) Neurocranium shown in left-lateral view, occipital arch removed. (b) Neurocranium in sagittal section, with anterior to left. (c) Endocast of inner ear and lateral cranial canal shown in left-lateral view. (Figures based on Patterson 1975)

mechanically (Rayner 1948) and acid-prepared (Patterson 1975) material, which has recently been examined via μ CT scanning (Giles et al. 2016). A vestibular fontanelle and otico-occipital fissure are present. The latter is lined with perichondral bone dorsal to the level of the vestibular fontanelle. Separate ossification centers are present in small individuals, but individual bones are fused in larger specimens. The semicircular canals and their ampullae are largely encased within bone with the exception of the sinus superior, which is unenclosed medially. The posterior canal is almost transverse in its orientation, and both it and the horizontal canal are substantially shorter than the anterior canal. The posterior end of the horizontal canal joins the ampulla of the posterior canal, and the ampullae of the anterior and horizontal semicircular canals are broadly separated (Fig. 2.11c). As in holosteans, a lateral cranial canal extends through the loops of the anterior and posterior canals, flanking the sinus superior laterally. The utricular recess is particularly well developed and is separated from the endocranial cavity by a constriction. Similarly, the bean-shaped saccular chamber is set off from the remainder of the bony inner ear by a constriction. A Middle Jurassic “*Pholidophorus*” described by Patterson (1975) is broadly similar to *Dorsetichthys*, but the labyrinth cavity is less fully enclosed by bone. The anterior canal lay within the cranial cavity, the posterior and horizontal canals were partially enclosed by cartilage, and the utricular recess is less clearly demarcated. Giles et al. (2016) present a virtual endocast of this specimen.

“Leptolepids” like *Leptolepis coryphaenoides* and “*Leptolepis*” *dubia* lack both otico-occipital fissures and vestibular fontanelles (Patterson 1975). Sutures between separate bones may be present, or the otic region can be represented by a single, continuous ossification. Internally, there appears to be a reduced correspondence between endocavities and the soft-tissue features they would have contained. This stands in contrast to less crownward members of the teleost stem, early holosteans, and Paleozoic ray-fins, but anticipates the morphology of crown-group teleosts. The anterior canal and sinus superior lay completely within the endocranial cavity. Additionally, the bar separating the anterior and posterior opening of the lateral cranial canal is lost, resulting in a simple diverticulum, and the utricular recess is not differentiated from the remainder of the cranial endocavity. However, the

posterior and horizontal canals are completely enclosed by bone, matching the condition in living teleosts and attributed by Patterson (1975) to changes in ossification pattern associated with loss of the otico-occipital fissure. Little has been described of the endocranial chamber in taxa crownward of “leptolepids.” Dunkle (1940) provided a diagrammatic reconstruction of the semicircular canals in the pachyrhizodontid *Notelops*, based on serial sectioning of a three-dimensionally preserved specimen.

2.7.2 *Crown Teleosts I: Innovations in Hearing*

The fossil record of crown teleosts is exceptionally rich in articulated body fossils. In spite of this—or perhaps because of it—there are few accounts presenting detailed descriptions of either internal or external anatomy of the otic region of the braincase, especially when considering the amount of available material. In the light of this descriptive bias and the overwhelming variety of fossil forms, focus will be placed here on paleontological evidence with a bearing on remarkable innovations for hearing found within teleosts. There are a variety of anatomical strategies for enhanced auditory capability in fishes (Braun and Grande 2008) but most are tied to direct or indirect linkages between the swim bladder and otic region (Popper and Coombs 1982). At least some of these modifications are apparent in hard tissues and thus have the potential to be detected in fossil material. The discussion here will review the most concrete examples of these specializations in fossils, noting other groups bearing similar features but for which clear evidence in fossil members is not available.

Modifications for hearing in teleosts are most readily apparent in a clade variously termed Ostarioclupeomorpha or Otocephala. This is a remarkably diverse teleost group, including species as morphologically and ecologically divergent as minnows, catfishes, electric eels, and anchovies. Alepocephaliforms (slickheads and tubeshoulders), an unusual radiation of deep-sea species, represent an unexpected addition to Otocephala arising from molecular studies (Ishiguro et al. 2003). Specifically, many clupeomorphs and ostariophysans show elaborate linkages between the swim bladder and ear, either through direct connections or an elaborate relay of highly modified bones. Otocephalans share a series of modifications that might pre-adapt them to such otophysic connections, most notably, posterior extension of the labyrinth and placement of the saccular and lagenar otoliths in a posteriomedian position (Braun and Grande 2008). Like many deep-sea species, alepocephaliforms lack a swim bladder, but existing accounts of their anatomy do not indicate whether they share other modifications of the otic region common to clupeomorphs and ostariophysans (e.g., Gosline 1969).

Clupeomorpha, or herrings, is the sister lineage of all remaining otocephalans. Extant clupeomorphs show a variety of remarkable specializations of the otic region generally, and acousticolateralis system specifically, that provide key evidence for the monophyly of the group as a whole or its constituent clades. These include the

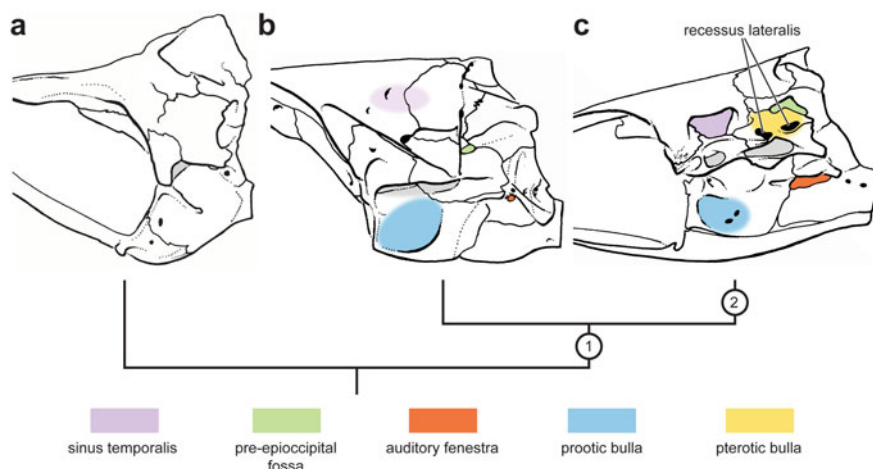


Fig. 2.12 Modifications of clupeomorph skull anatomy associated with elaborations of the acousticolateralis system. Gray shading indicates position of hyomandibular facet(s). **(a)** Neurocranium of *Diplomystus* sp. (Late Cretaceous: Cenomanian) shown in left-lateral view. **(b)** Neurocranium of *Spratticeps gaultinus* (Early Cretaceous: Albian) shown in left-lateral view. **(c)** Neurocranium of *Santanaclupea silvasantosi* (Early Cretaceous: Aptian-Albian) shown in left-lateral view. Transformations at *node 1*: development of rudimentary sinus temporalis (remains covered by skull roof), appearance of prootic bulla and auditory fenestra that indicate invasion of otic region by diverticulum of swim bladder, origin of pre-epioccipital fossa. Transformations at *node 2*: exposure of sinus temporalis and origin of pterotic bulla. **(a)** based on Forey 2004; **b** based on Patterson 1970; **c** based on Maisey 1993)

sinus temporalis, a sac-like enlargement of the supraorbital sensory canal housed within a fenestration in the temporal region of the skull; the recessus lateralis, a bone-enclosed chamber within the temporal region communicating with the multiple branches of the cranial lateral-line system; the pre-epioccipital fossa (called a pre-epiotic fossa in older literature), a canal of uncertain function that opens through a foramen between the parietal, pterotic and epioccipital; prootic and pterotic bullae, swellings of those bones marking diverticulae of the swim bladder that invade the braincase via the auditory foramen (for more details, see de Dario 2004). Clupeomorphs also have a rich and well-studied fossil record (e.g., Grande 1985) that helps to document the origin of many of these innovations (Fig. 2.12).

Ellimmichthyiformes, represented by the single family Paraclupeidae, are a Cretaceous–Paleogene clade of primitive clupeomorphs known from a range of marine and freshwater settings. Braincase anatomy is most clearly illustrated by a three-dimensionally preserved, acid-prepared example of *Diplomystus* from early Late Cretaceous marine deposits of the UK (Fig. 2.12a) (Forey 2004). This genus shows none of the auditory specializations associated with modern clupeomorphs (Clupeiformes). Any kind of connections between the ear and swim bladder, if present, must have been simple and external.

A series of well-preserved late Early Cretaceous fossils provide the important evidence for the stepwise acquisition of sensory modifications characteristic of modern herrings: *Spratticeps* from the UK (Patterson 1970), and the Brazilian *Pseudoellimma* (de Figueiredo 2009) and *Santanaclopea* (Maisey 1993). *Spratticeps* is known only from isolated braincases, but these show well-developed prootic bullae that indicate the development of an internal swim-bladder inner-ear connection, a rudimentary pre-epioccipital fossa, and an incipient sinus temporalis that remains covered by the roof of the posttemporal fossa (Fig. 2.12b). *Pseudoellimma* seems more closely related to modern clupeiforms than *Spratticeps* and bears evidence of a recessus lateralis. With the additional presence of a pterotic bulla and fully exposed temporal fenestra, *Santanaclopea* shows an essentially complete suite of modern clupeiform auditory specializations (Fig. 2.12c).

Ostariophysans include two divisions: Anotoptysi, which includes the milkfish, beaked salmons, and shellears; and Otophysi, which includes minnows and allies, catfishes, characins and allies, and Neotropical knifefishes. Anotoptysans show many of the features interpreted as potential preadaptations foreshadowing the more elaborate auditory systems of otophysans (Rosen and Greenwood 1970), but many of these pertain to large scale (e.g., swim bladder structure; Grande and de Pinna 2004) or small scale (e.g., cellular orientation in the lagenar epithelium; Popper and Platt 1983) aspects of soft tissue anatomy that cannot be detected in fossils.

Otophysans famously bear the so-called Weberian apparatus: a series of specialized bones, derived from various components of the anterior axial column, some of which transmit vibrations from the swim bladder to the skull (Weber 1820). These ossicles include, from anterior to posterior (with possible precursors, as identified by comparative and developmental studies, indicated in parentheses): the claustrum, a small ossicle that bears no connection to other Weberian ossicles and thus is not part of the vibration-transmitting chain (homologized with the accessory neural arch of other clupeocephalans); the scaphium, which lies immediately dorsal to the first vertebral centrum (arises developmentally from the first basidorsal in many taxa, but apparently a composite structure in others); the intercalarium, which lies above the second vertebral centrum (derived from the second neural arch) and bears an anterolateral process called the manubrium; and the tripus, a variously triradiate bone that extends ventrolaterally from the third vertebral centrum (formed by the pleural rib and parapophysis of the third vertebra). Joining these is the os suspensorium, the modified pleural rib of the fourth vertebra. This structure is considered a component of the Weberian apparatus by some and shows varying degrees of modification across modern otophysans (Grande and de Pinna 2004). The presence of Weberian ossicles is associated with further modifications of the anterior vertebral column, including the foreshortening of centra that is readily apparent in fossil material.

As a complicated morphological system, the Weberian apparatus has attracted considerable attention from comparative anatomists attempting to document its evolutionary assembly (e.g., Chardon and Vanderwall 1997). Paleontological evidence bearing on the origin of this complex morphological system has been the subject of some controversy. Because of their position at the anterior of the

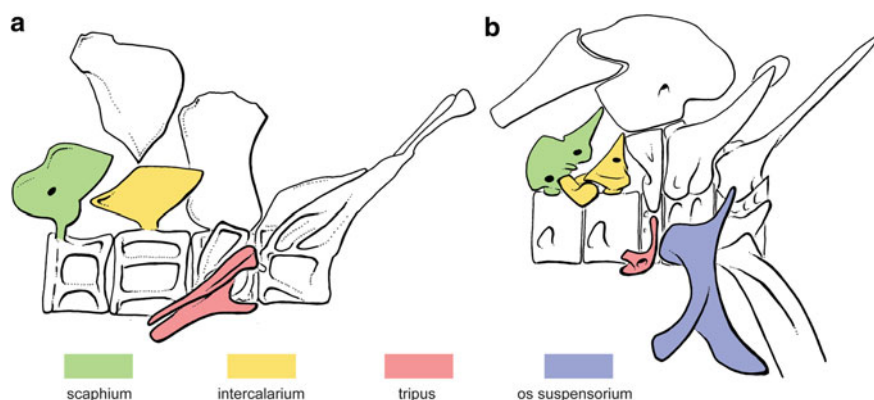


Fig. 2.13 Examples of the Weberian apparatus in stem otophysans help to document the stepwise assembly of this complex auditory system. **(a)** Weberian apparatus of *Santanichthys diasii* (Late Cretaceous: Aptian-Albian) shown in left-lateral view. **(b)** Weberian apparatus of *Chanoides macropoma* (Eocene: Ypresian) shown in left-lateral view. **(a)** based on Filleul and Maisey 2004; **b** based on Patterson 1984)

vertebral column, the Weberian ossicles are often overlapped or otherwise disrupted by bones of the skull, opercular series, and shoulder girdle in fossil material. Specimens that are clearly aligned with individual otophysan orders show uncontroversial Weberian ossicles or other associated vertebral modifications closely comparable with those of modern species. Clear examples are present in Characiformes (e.g., Weiss et al. 2014), Siluriformes (e.g., Grande and Lundberg 1988), and Cypriniformes (e.g., Grande et al. 1982). Fossil Gymnotiformes are rare and existing material is too poorly preserved to show the ossicles (e.g., Albert and Fink 2007).

A variety of fossil fishes have been nominated as particularly relevant to understanding the origin of the Weberian apparatus: the Early Cretaceous *Santanichthys* (Fig. 2.13a) (Filleul and Maisey 2004), the Late Cretaceous *Lusitanichthys* (Gayet 1981) and *Clupavus* (Taverne 1995), and the Eocene *Chanoides* (Fig. 2.13b) (Patterson 1984). Cretaceous material previously assigned to *Chanoides* has now been placed in *Nardonoides*, an *incertae sedis* ostariophysan (Mayrincik et al. 2015). Arguments for a Weberian apparatus in the gonorynchiform *Ramallichthys* (Gayet 1986) and the attendant complexities implied for the evolution of this elaborate anatomical system have been comprehensively rejected in detailed rebuttals by Fink et al. (1984) and Grande and Grande (2008). Some of these remaining fossils were initially associated with specific extant otophysan lineages (e.g., *Santanichthys* with characiforms) (Filleul and Maisey 2004), thus suggesting that some features characteristic of the modern Weberian apparatus evolved multiple times. However, more extensive analyses suggest that all fall outside of crown Otophysi and thus do not reject a monophyletic origin of the Weberian apparatus (Grande and de Pinna 2004).

Features of the Weberian apparatus are preserved to varying degrees in these stem otophysans (reviewed in detail by Diogo 2009). Material of *Lusitanichthys* and *Clupavus* is flattened, but both *Santanichthys* and *Chanoides* are known from acid-prepared material that permits detailed description and attempted reconstruction of the Weberian apparatus. In particular, the individual ossicles preserved in these taxa appear to be more primitive than those of crown otophysans. The claustrum is unknown in either. The scaphium and intercalarium of *Chanoides* bear foramina for ventral and dorsal nerve roots, a primitive feature of neural arches not commonly found in these Weberian ossicles among extant otophysans. In addition, the intercalaria of both *Chanoides* and *Santanichthys* lack co-ossified manubria (although a small sesamoid ossification representing this feature is present in *Chanoides*), again, showing a primitive neural-arch-like condition relative to the derived intercalarium morphology of crown otophysans. The claustrum is not preserved in either genus but both genera show unusual morphologies of the tripus. The particularly primitive tripus of *Santanichthys* comprises a separate rib and parapophysis. By contrast, the tripus of *Chanoides* appears to be a single bone, but it is substantially smaller than the equivalent ossification in either *Santanichthys* or modern otophysans. The os suspensorium is unknown in *Santanichthys*; however, in *Chanoides* the os suspensorium is a compound structure formed from the rib and parapophysis of the fourth vertebra. As in modern species, the anatomy of the os suspensorium appears variable among primitive otophysans.

Outside of Otocephala, modifications to the skeleton potentially associated with hearing enhancement are found in a variety of teleost groups and include extracranial bullae in megalopids (tarpons), otic bullae in mormyrids (elephant-fishes), holocentrids (squirrelfishes), and cichlids, and suprabranchial chambers in anabantoids (labyrinth fishes) (Braun and Grande 2008). Laterally directed openings associated with bulla-like otic swellings are found in a variety of fossil non-percomorph acanthomorphs, including the polymixiid *Homonotichthys* and the “beryciforms” *Hoplopteryx*, *Caproberyx* (Patterson 1964), and *Holocentrites* (Dunkle and Olsen 1959). However, a similar arrangement is found in modern species with no connection between the otic capsule and swim bladder. Such a connection is present in some living holocentroids, but is marked by very distinctive modifications to the bony structure of the otic capsule not apparent in these fossils (Nelson 1955).

2.7.3 Crown Teleosts II: The Otolith Fossil Record

No morphological account of auditory capsules in fossil actinopterygians would be complete without mention of the rich archive of isolated otoliths. The density of the Cenozoic teleost otolith fossil record has drawn comparisons to the tooth record of mammals (Patterson 1977), but there is an important distinction: teleost otoliths are rarely associated with additional skeletal remains (there are, however, noteworthy exceptions: Nolf 1985). Much of this appears to reflect taphonomic bias against

otoliths in depositional settings conducive to the preservation of fish skeletons (Nolf 1985, 2013). As a consequence, fossil otoliths are typically identified through comparison with reference collections of otoliths from modern species. This approach has clear limitations, with taxonomic identifications becoming more difficult in progressively older sediments to the degree that reliable interpretations of Mesozoic otoliths are very difficult. The literature surrounding fossil otoliths is vast, but owing to the isolated nature of these remains, largely separate from that from the body fossil record. However, computed tomography might have the potential to reveal otoliths in a broader range of fish body fossils than are known at present, representing a means of beginning to unify these parallel records of actinopterygian biodiversity (cf. Friedman et al. 2015).

2.8 Summary

1. Excepting specializations of the two groups, internal anatomy of the skull—and the apparatus of hearing—in early ray-finned fishes is broadly comparable between early fossil lobe-finned fishes and ray-finned fishes. Details of otic anatomy are only hazily known in the most ancient osteichthyans. There is substantially more information available for younger fossils that can be clearly aligned with one of the two branches of the bony fish tree.
2. Fossil evidence bearing on the evolution of ear structure in ray-finned fishes stems largely from endocasts of the inner ear and isolated saccular otoliths. These archives are largely non-overlapping both stratigraphically and phylogenetically.
3. Known from exceptionally well-preserved and acid-prepared material, the Late Devonian *Mimipiscis* provides the most detailed model for the primitive geometry of the actinopterygian inner ear.
4. External and internal anatomy of the otic region is known in a variety of Carboniferous and Permian actinopterygians classically identified as “palaeoniscoids” (a taxonomic wastebin of anatomically generalized ray-finned fishes), with the most detailed information available for the Early Triassic based on studies using destructive physical tomography. These taxa generally retain morphologies broadly similar to those of the earliest ray-finned fishes, including the presence of an otico-occipital fissure and vestibular fontanelles and the absence of separate ossification centers.
5. Anatomy of the otic region and inner ear in extinct relatives of chondrosteans (sturgeons and paddlefishes) is limited to highly specialized early Mesozoic forms whose affinities to modern lineages are not well established.
6. Fossil holosteans—members of the group containing garpikes and the bowfin—show a variety of otic morphologies. The most ancient examples lack separate ossification centers but bear a persistent otico-occipital fissure and vestibular fontanelles. Later examples in both the garpike and bowfin lineages show separate ossification centers. In both cases, reduction of the mineralized walls of

the endocranial cavity severely reduces the detail with which the inner ear can be reconstructed in fossils.

7. A series of highly specialized Mesozoic groups have been aligned with teleosts. Details of otic anatomy in these lineages are limited almost exclusively to external features, which vary considerably among the groups.
8. Otic structure in early undisputed members of the teleost clade is broadly similar to that of early holosteans in retention of an otico-occipital fissure and vestibular fontanelles, absence of separate ossification centers, and tight enclosure of the inner ear by bone. These features are lost in more crownward members of the teleost stem lineage.
9. Cretaceous fossils deliver clear evidence for the stepwise origin of hearing specializations in clupeomorphs and ostariophysans.

Compliance with Ethics Requirements Matt Friedman and Sam Giles have declared that they had no conflicts of interest.

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