



General palaeontology

Labyrinth morphology and the evolution of low-frequency phonoreception in elasmobranchs

Morphologie du labyrinthe et évolution de la phonoréception à basse fréquence chez les élasmobranches

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ABSTRACT

Labyrinth morphology in extant elasmobranchs (neoselachians: sharks, skates and rays) and several extinct chondrichthyans ranging in age from Pliocene to Devonian is investigated using high-resolution computed tomography (CT scanning) and digital reconstitution techniques. The elasmobranch labyrinth is highly specialized toward low-frequency semi-directional sound detection (LFSDP), optimally around 100 Hz. Several features associated with LFSDP in neoselachians also occur in Mesozoic hybodonts (e.g., *Egertonodus*, *Tribodus*) and in some incertae sedis extinct sharks (*Acronemus*, *Tristychius*), but are absent in osteichthyans, extant and fossil holocephalans, and certain Paleozoic chondrichthyans (ctenacanths, symmoriiforms, *Pucapampella*). Thus, LFSDP is regarded as an evolutionary novelty of elasmobranchs that arose some time after their divergence from chimaeroids. The suite of characters associated with LFSDP was probably acquired progressively, some characters being more widely distributed among fossil chondrichthyans than others. LFSDP evolved only within chondrichthyans whose otico-occipital fissure became secondarily closed during ontogeny.

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R É S U M É

Les morphologies du labyrinthe d'élasmobranches actuels (néosélaciens : requins et raies) et de plusieurs genres de chondrichthyens fossiles, datés du Dévonien au Pliocène, ont été étudiées par la tomographie à haute résolution assistée par ordinateur (CT scan) et les techniques de reconstitutions digitales. Le labyrinthe des élasmobranches est hautement spécialisé pour la détection des sons semi-directionnels à basse fréquence (LFSDP), autour d'une valeur de 100 Hz. Plusieurs caractères anatomiques associés à la LFSDP des néosélaciens sont également présents chez les hybodontes mésozoïques (par exemple, *Egertonodus* et *Tribodus*) et chez quelques requins fossiles incertae sedis (*Acronemus*, *Tristychius*), mais absents chez les ostéichthyens, les holocéphales fossiles et actuels, ainsi que chez certains chondrichthyens paléozoïques (cténacanthés, symmoriiformes, *Pucapampella*). Ainsi, la LFSDP est ici considérée comme une caractéristique nouvelle des élasmobranches, apparue peu de temps après leur divergence avec les chiméroïdes. La série de caractères

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associée avec la LFSDP a probablement été acquise progressivement, certains caractères étant plus largement distribués parmi les chondrichthyens fossiles que d'autres. La LFSDP n'est présente que chez les chondrichthyens dont la fissure otico-occipitale est secondairement close au cours de l'ontogénie.

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1. Introduction

The mechanosensory components of the craniate inner ear are located inside a closed system of delicate fluid-filled tubes (semicircular canals) and vestibular chambers (sacculus, utriculus, lagena) that collectively form the membranous labyrinth. This structure is enclosed by the otic capsule, within a perichondrally- or periosteally-lined space known as the skeletal labyrinth (Torrey, 1962). The space is filled with perilymphatic fluid, which acts as a cushion for the membranous labyrinth suspended from the walls of the skeletal labyrinth by scattered strings of connective tissue. Whereas features of the membranous labyrinth are not normally preserved in fossils, the skeletal labyrinth (or its endocast) is often well preserved although its morphology may be obscured by the surrounding hard tissues. While the skeletal labyrinth may not correspond exactly to the size and shape of the membranous labyrinth it enclosed, its morphology is nevertheless open to comparison in extinct and extant craniates (Maisey, 2001a).

In order to study the skeletal labyrinth in fossils, previously the only recourse was destructive sampling by serial grinding or sectioning techniques (Jarvik, 1942; Romer, 1937; Stensiö, 1927). The advent of computerized tomography provided an important non-invasive procedure with which to investigate fossils (Rowe et al., 1997), a technique now improved by Synchrotron scanning (Pradel et al., 2009a, 2009b). Computerized tomography has proven to be particularly valuable in providing comparative data concerning skeletal labyrinth morphology in extant and extinct chondrichthyans (Lane, 2010b; Maisey, 2001a, 2004a, 2004b, 2005, 2007).

It is well known that the inner ear of gnathostomes is an important organ of mechanoreception, helping maintain equilibrium, motion and balance (Jollie, 1962; Retzius, 1881; Torrey, 1962). In some fishes (e.g., ostariophysans), parts of the inner ear may also be specialized to form a pressure-to-displacement transducer for low-frequency phonoreception (mainly below 1000 Hz; higher frequencies are poorly transmitted through the aqueous medium). Sound waves spread much more rapidly through water (1500 m/s) than through air (330 m/s), but those which result from alternating compression and rarefaction of water molecules (pressure waves) decay slowly with distance in a frequency-dependent manner (i.e., low-frequency pressure waves travel much farther than do high-frequency ones, even across an entire ocean); thus, the source of such far-field sound waves may be so distant as to be of little value in prey detection. However, kinetic (displacement) sound waves decay very rapidly (proportional to the square of the distance from the sound source) regardless of the sound's frequency, and therefore predominate close to the sound source.

Extant elasmobranchs are known to use sound detection to identify and locate stressed or injured prey, although the inner ear apparently lacks pressure-to-displacement transducers comparable to those found in ostariophysans or tetrapods. The inner ear of extant elasmobranchs is nevertheless highly specialized toward low-frequency semi-directional phonoreception (LFSDP) (Corwin, 1977; Maisey, 2001a) and is capable of detecting the kinetic component of a sound wave (Banner, 1967; Bleckman and Hoffman, 1999; Corwin, 1981a; Myrberg et al., 1972). This phonoreceptor system is ideally suited for detecting near-field displacement sound waves and comprises two distinct components. One of these is otolithic (involving the saccular macula) and is probably non-directional or directionally ambiguous in sensitivity, while the other involves the non-otolithic macula neglecta and is probably semi-directional in sensitivity (optimally forward-based). The non-otolithic component appears to depend on preferred transmission of near-field kinetic sound waves via a well-defined path which passes through the perilymphatic fenestra, along the posterior canal duct, and across the macula neglecta. The two-component (otolithic plus non-otolithic) system provides limited directional resolution of the sound source (Corwin, 1981b), and behavioral experiments suggest that the elasmobranch phonoreceptor system can determine whether the sound source is left or right, in front or "not in front", and above or "not above" (Corwin, 1977; Fänge, 1982; Tester et al., 1972). The combination of forward-based (macular) and symmetrical (otolithic) sensitivity may therefore help resolve directional ambiguity in low-frequency signal source. By contrast, the high-impedance ear of humans is incapable of resolving directionality at such low frequencies.

Semi-directional phonoreception in extant elasmobranchs involves a physical pathway for the transmission of near-field kinetic sound waves that does not exist in chimaeroids and osteichthyans. The evolution of this pathway seems to have involved numerous modifications of the basic gnathostome inner ear arrangement; a preliminary investigation of the elasmobranch inner ear (Maisey, 2001a) identified 16 potentially apomorphic features of the extant elasmobranch labyrinth and otico-occipital region associated with LFSDP, including: isolation of the posterior semicircular canal from the other canals, the posterior semicircular canal describes an almost complete circuit, separation of the saccular and utricular regions, the posterior canal has only a single connection with the vestibular region, the sensory crista neglecta is isolated and elaborated, an extensive medial wall to otic capsule is present, perilymphatic fenestrae are present, a crus is present distally between anterior and external (horizontal) semicircular canals, the external semicircular canal has an out-of-plane orientation, anterior and external canals share

a common opening into the vestibular region, exogenous sand grains are present within the endolymphatic ducts and sacculus, an endolymphatic (parietal) fossa is present, the embryonic metotic fissure closes secondarily to form a glossopharyngeal canal, lateral otic processes are present, the anterior ampulla is located between or in front of the postorbital process, and the occipital block is wedged anteriorly between the otic capsules.

The labyrinth of chimaeroids lacks many of these features and is not adapted toward LFSDP, but may nevertheless be independently specialized in lacking a lagenar chamber (Maisey, 2001a). No apomorphic features of the labyrinth have been recognized that would unite all osteichthyans. Instead, it appears that the labyrinth of extant bony fishes represents a highly conserved morphological pattern that was retained by early chondrichthyans and from which the extant elasmobranch one may have evolved. Apomorphic characters of the labyrinth are nevertheless recognized within certain groups of osteichthyans, including closure of the endolymphatic ducts in many actinopterygians, phonoreceptors associated with the otic capsule (including the Weberian apparatus of ostariophysans and the air-bladder diverticulum of clupeomorphs), the vaterite otoliths of actinopterygians and monocrySTALLINE otoliths of dipnoans and tetrapods, the basilar papilla associated with the lagenar chamber of anurans, and features associated with the high-impedance ear in tetrapods (e.g., cochlea, middle and outer ear).

Modification of the elasmobranch inner ear toward phonoreception is associated with several specializations of the skeletal labyrinth that are potentially observable in fossils (Maisey, 2001a). Initial observations revealed that not all extinct shark-like chondrichthyans possessed these features (Maisey, 2004b), suggesting that LFSDP evolved comparatively late in chondrichthyan history. In order to determine the wider distribution of features associated with LFSDP in living and extinct chondrichthyans, skeletal labyrinth morphology has been examined in several fossil chondrichthyans by computerized tomography and 3-D imaging techniques. Most of the features of interest listed above were investigated, except for “soft” ones that are unavailable in fossil material (e.g., sensory maculae and crista neglecta, membranous coverings of the perilymphatic fenestrae, and parts of the endolymphatic ducts, vestibular walls and semicircular canals). The results of this survey are presented here, along with some observations and comments about the possible phylogenetic and evolutionary history of phonoreception in elasmobranchs.

2. Materials and methods

Notorynchus cepedianus (Péron). Extant; provenance unknown, but probably San Francisco Bay. Uncatalogued, California Academy of Sciences; wax-impregnated braincase probably used as a partial basis of original description (Daniel, 1934; Maisey, 2004a). Scanned by R. Ketcham and M. Colbert 12 March 1999. RLS, 420 kV, 1.8 mA, no filter, air wedge, 130% offset, gain 8, integration time 32 ms, slice thickness 0.25 mm, S.O.D. 730 mm, 1000 views, 2

rays averaged per view, 1 sample per view, interslice spacing 0.25 mm, field of reconstruction 95 mm, reconstruction offset 400, reconstruction scale 1450. 8-bit export parameters: level 2047, width 4095.

Undetermined carcharhinid shark ear region. Lower Pliocene; Goose Creek Limestone, South Carolina, PV 4173 Charleston Museum, South Carolina. Isolated three-dimensional otic capsule from a large individual. Scanned by R. Ketcham and M. Colbert 13 December 1999. RLS, 150 kV, 0.16 mA, no filter, glass wedge, 160% offset, slice thickness 4 lines (= 0.23 mm), S.O.D. 101 mm, 3000 views, 3 samples per view, interslice spacing 3 lines (=0.1726 mm), field of reconstruction 49 mm, reconstruction offset 1400, reconstruction scale 37. Scanned in three-slice mode. Identification of the specimen to generic level is problematic, but carcharhinid affinity is suggested by comparison with extant elasmobranch braincases.

Tribodus limae (Brito & Ferreira). Lower Cretaceous (Aptian-Albian); Santana Formation, Chapada do Araripe, Brazil, AMNH 13958, complete three-dimensional braincase associated with well preserved jaw and hyoid arch elements (Lane, 2010a, 2010b). Scanned by R. Ketcham and M. Colbert 16 March 1999. 8-bit and 16-bit: RLS, 420 kV, 1.8 mA, 2 brass filters, air wedge, 160% offset, gain of 4, integration time 128 ms, slice thickness 0.25 mm, source object distance 630 mm, 2000 views, 4 rays per view, 1 sample per view, scan position 141 mm, interslice spacing 0.25, field of reconstruction 94 mm, reconstruction offset 400, reconstruction scale 500. 8-bit export parameters: 2400/1000.

Egertonodus basanus (Egerton). Lower Cretaceous (Valanginian); Ashdown Sand, Cooden, nr. Pevensey Sussex, England, BMNH P.60010, isolated, three-dimensional but slightly crushed braincase in ironstone (Lane, 2010a, 2010b; Maisey, 1983). Scanned by R. Ketcham and M. Colbert 26–27 January 2001. 16-bit: RLS, 420 kV, 4.7 mA, on brass filter, empty mount wedge, offset 130%, gain 4, integration time 64 ms, slice thickness 0.25 mm, S.O.D. 595 mm, 1000 views, 5 rays averaged per view, 1 sample per view, interslice spacing 0.25 mm, field of reconstruction 77 mm, reconstruction offset 630, reconstruction scale 448. Detector running average width 5 pixels (skip 1).

Acronemus tuberculatus (Bassani). Middle Triassic (Anisian-Ladinian); Besano Formation, Monte San Giorgio, northern Italy, T/I 1289, Paleontological Institute, University of Zurich, incomplete but three-dimensional otico-occipital region of braincase associated with other remains (Rieppel, 1982). Scanned by M. Colbert 23 October 2008. 16-bit: 1024 × 1024 16-bit TIFF images. II, 210 kV, 0.15 mA, intensity control off, high-power mode, no filter, empty container wedge, no offset, slice thickness 1 line (= 0.07293 mm), S.O.D. 209 mm, 1400 views, 3 samples per view, interslice spacing 1 line (= 0.07293 mm), field of reconstruction 66 mm (maximum field of view 69.53 mm), reconstruction offset 7700, reconstruction scale 3100. Acquired with 31 slices per rotation and 25 slices per set. Ring-removal processing done by Amira Abdul-Hafiz based on correction of raw sinogram data using the IDL routine “RK.SinoRingProcSimul” with parameter “bestof5=11.” Reconstructed with beam-hardening coefficients [0,0.8,

0.05, 0.05]. Deleted the first six duplicate slices of each rotation. Total final slices = 1125.

Cladodoides wildungensis (Jaekel), Upper Devonian (Frasnian); Wildungen, Germany, P 2468, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, isolated three-dimensional braincase (probably from a ctenacanth shark) preserved in a carbonate matrix (Gross, 1937; Maisey, 2001c, 2005; Schaeffer, 1981). Scanned by R. Ketcham and M. Colbert 17 December 1999. Original scanned Images 180 kV, 0.133 mA, no filter, glass wedge, 160% offset, slice thickness 5 lines (= 0.262 mm), S.O.D. 92 mm, 2400 views, 2 samples per view, interslice spacing 4 line (= 0.2096 mm), field of reconstruction 43.2 mm, reconstruction offset 750, reconstruction scale 33. Scanned in three-slice mode.

Cobelodus sp., Mississippian (Chesterian); Fayetteville Shale, Fayetteville, Arkansas, FMNH PF13242, Field Museum, Chicago, isolated three-dimensional symmoriiform/stethacanthid braincase preserved in a pyritic nodule, giving excellent density contrast with the prismatic calcification (Maisey, 2007). Scanned by R. Ketcham and M. Colbert 6 March 1999. P250D, 420 kV, 1.8 mA, 2 brass plate filters (1/8 inch total), translate-rotate, integration time 16 ms, slice thickness 0.25 mm, S.O.D. 752 mm, 1 ray averaged per view, 1 sample per view, oversampling ratio 2.0, interslice spacing 0.25 mm, field of reconstruction 56.5 mm, reconstruction offset 450, reconstruction scale 120. 8-bit export parameters: level 2047, width 4095.

Pucapampella sp., Middle Devonian (Upper Eifelian-Givetian); Belén, western Bolivia, AMNH FF19631, isolated braincase lacking parachordal-occipital cartilage, mechanically prepared from phosphatic concretion (Maisey, 2001b). Scanned by R. Ketcham and M. Colbert 3 March 1999. 120 kV, 0.2 mA, no filter, air wedge, 160% offset, slice thickness 0.174, S.O.D. 38 mm, 1800 views, 2 samples per view, interslice spacing 0.174 mm, field of reconstruction 38 mm, reconstruction offset 550, reconstruction scale 33. Sample scanned in overlapped three-slice mode, discarding third of each set of 3 slices. 8-bit export parameters: level 2047, width 4095.

Pucapampella sp., Middle Devonian (Upper Eifelian-Givetian); Padilla, Bolivia, Le Grand Smith collection, American Museum of Natural History; associated parachordal-occipital cartilage and otic region in concretion. Specimen scanned by M. Colbert 2 April 2004. 180 kV, 0.133 mA, no filter, air wedge, no offset, slice thickness 2 lines (= 0.0905 mm), S.O.D. 132 mm, 1600 views, 2 samples per view, interslice spacing 2 lines (= 0.0905 mm), field of reconstruction 41 mm (maximum field of view 43.25688 mm), reconstruction offset 4120, reconstruction scale 855. Acquired with 15 slices per rotation. Ring-removal processing done by Rachel Racicot based on correction of raw sinogram data using IDL routine "RK.SinoRingProcSimul" with parameters "binwidth=21, bestof5=11". Reconstructed with beam-hardening coefficients: 0.0, 0.9, 0.05. Rotation correction processing done by R. Racicot using IDL routine "DoRotationCorrection". Total slices = 270.

Pucapampella sp., Lower Devonian (Upper Emsian); Gydo Formation, South Africa, GSB 0499, 0497A&B,

Museum of the Council for Geosciences, Transvaal Museum, Pretoria, articulated braincase and associated elements of visceral skeleton (Maisey and Anderson, 2001). Scanned by R. Ketcham and M. Colbert 13 December 1999. 150 kV, 0.16 mA, no filter, glass wedge, 160% offset, slice thickness 4 lines (= 0.23 mm), S.O.D. 101 mm, 3000 views, 3 samples per view, interslice spacing 3 lines (= 0.1726 mm), field of reconstruction 49 mm, reconstruction offset 1400, reconstruction scale 37. Scanned in three-slice mode.

Doliodus problematicus (Woodward), Lower Devonian (Emsian); Campbellton Formation, Atholville, New Brunswick, Canada, NBMG 10127-1A, New Brunswick Museum, part of an articulated specimen containing the head skeleton (Maisey et al., 2009). Scanned by M. Colbert 6 June 2007. 200 kV, 0.13 mA, no filter, empty container wedge, no offset, slice thickness 1 line (= 0.0817 mm), S.O.D. 235 mm, 2200 views, 2 samples per view, interslice spacing 1 line (= 0.0817 mm), field of reconstruction 75 mm (maximum field of view 77.91953 mm), reconstruction offset 5000, reconstruction scale 4000. Acquired with 31 slices per rotation and 25 slices per set. Streak- and ring-removal processing done by Jessie Maisano based on correction of raw sinogram data using IDL routines "RK.SinoDeStreak" with default parameters, and "RK.SinoRingProcSimul" with parameters "binwidth=21, bestof5=11." Reconstructed with beam-hardening coefficients [0,0.75, 0.1, 0.05]. Deleted last six duplicate slices of each rotation, and first 10 blank slices. Total final slices = 1190.

Additional un-scanned material examined includes: Permian xenacanth braincases AMNH 7928, 7930, 7246, 7247, 7254, casts of MCZ 12872 and UCLAVP 3155; horizontally slabbed Mississippian ctenacanth braincase AMNH 2140 referred to *Tamiobatis* sp. (Schaeffer, 1981); and two uncatalogued silicone cranial endocasts of *Squalus acanthias* (Maisey, 2004b; Schaeffer, 1981). An attempt was made to scan a Permian xenacanth braincase, but the material lacked sufficient contrast to yield useful information.

The scans were analysed using Imaris[®] and Mimics[®] software. Imaris[®] images of *Tribodus* and *Egertonodus* were produced by J.A.L. at the American Museum of Natural History, New York, as part of her Ph.D. thesis at The City University of New York. Other reconstitutions in Imaris[®] and Mimics[®] were produced by J.G.M. at the Muséum national d'Histoire naturelle, Paris, and the American Museum of Natural History. While both Imaris[®] and Mimics[®] software create highly detailed three-dimensional reconstitutions of the scanned braincases, each program utilizes different analytical protocols that produce subtly different results (Fig. 1). Imaris[®] renderings utilized in this study were mostly generated using contours plotted manually on each slice, from which a geodesic surface was automatically computed and smoothed. Alternatively, surface and/or volume renderings can be generated automatically using this software. Mimics[®] utilizes different threshold values to fill in regions of interest on each slice, then computes a three-dimensional volume based on the stack of selected areas. Images and movie files of the reconstitutions can be captured in both programs. One advantageous feature of Imaris[®] is the ability to save objects as inventor files that

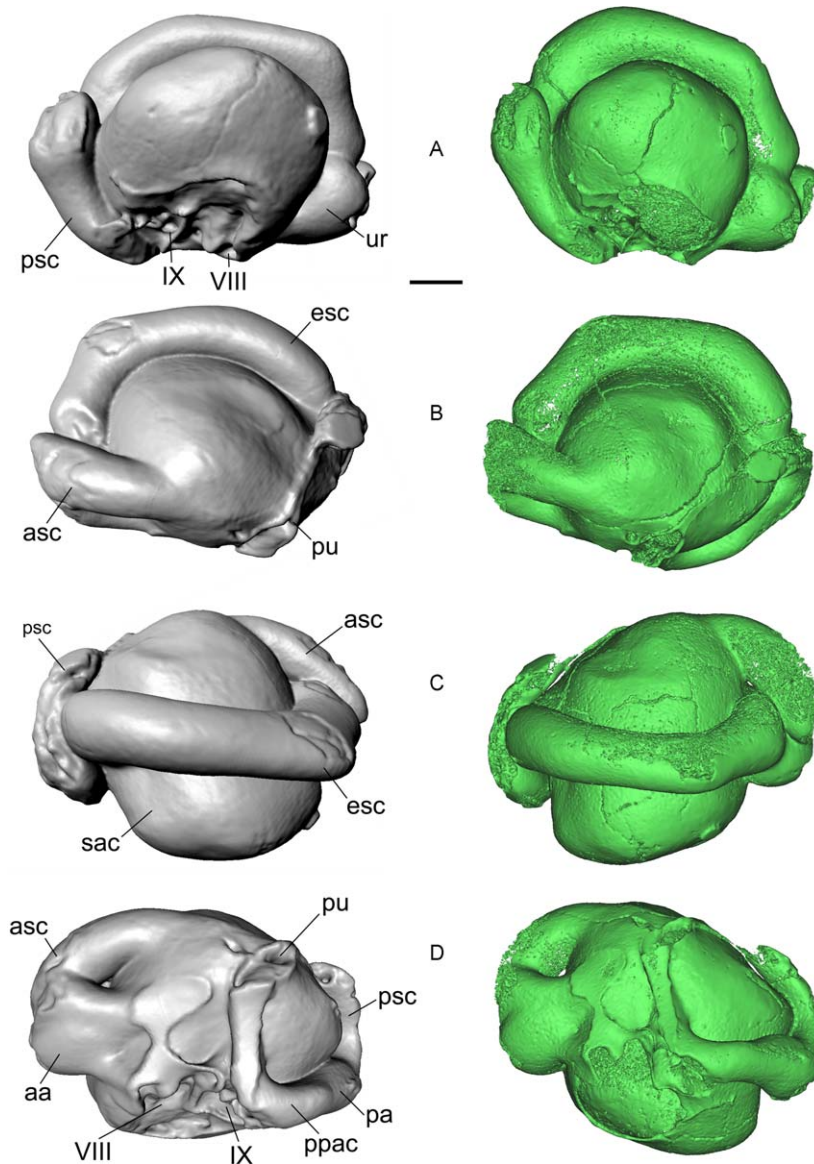


Fig. 1. Reconstitutions of fossilized otic region from an unnamed Lower Pliocene carcharhinid shark PV 4173, Charleston Museum, made from the same CT scan (see Materials and methods), using Imaris® (left) and Mimics® (right) software. Views may differ slightly depending on orientation. A. Ventral view. B. Dorsal view. C. Lateral view. D. Medial view. Scale bar = 10 mm. aa: anterior ampulla; asc: anterior semicircular canal; esc: external semicircular canal; pa: posterior ampulla; ppac: posterior pre-ampullary canal; psc: posterior semicircular canal; pu: "posterior utriculus"; ur: utricular recess; VIII: opening for octaval (acousticovestibular) nerve; IX: passage for glossopharyngeal nerve.

Fig. 1. Reconstitutions de la région otique d'un requin carcharhinidé du Pliocène inférieur PV 4173, Charleston Museum, réalisées à partir d'acquisitions par CT scan (voir Materials and methods) avec les logiciels Imaris® (à gauche) et Mimics® (à droite). Les vues diffèrent sensiblement en fonction de leur orientation. A. Vue ventrale. B. Vue dorsale. C. Vue latérale. D. Vue médiale. Barre d'échelle = 10 mm. aa: ampulla antérieure; esc: canal semicirculaire externe; pa: ampulla postérieure; ppac: canal préampullaire postérieur; psc: canal semicirculaire postérieur; pu: « utricule postérieur »; ur: *recessus* utriculaire; VIII: entrée du nerf acoustico-vestibulaire; IX: passage pour le nerf glossopharyngien.

can be subsequently imported and combined with others (even from different specimens), reoriented and re-scaled, and saved in new configurations without leaving the program. However, thresholding in Mimics® provided more detailed reconstitutions than contour plotting, and proved to be a faster method under most circumstances. In both cases, accuracy and speed were both improved by use of a Wacom® tablet and stylus to define structures and regions of interest.

3. Analysis of character distribution

3.1. Isolation of posterior canal from other semicircular canals

In extant elasmobranchs, the anterior and external semicircular canals are connected together, but the posterior canal forms an essentially separate circuit which is connected only to the vestibular region near the crista

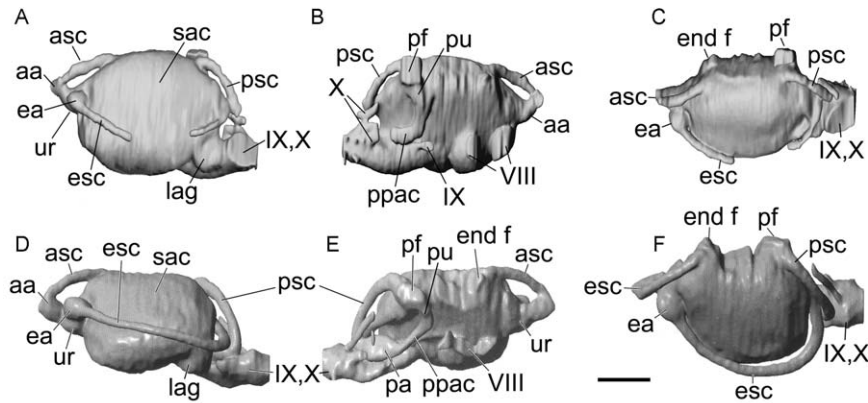


Fig. 2. Imaris[®]-based reconstructions of the skeletal labyrinth in two Early Cretaceous hybodont sharks. A–C. *Egertonodus* BM(NH) P.60010. D–F. *Tribodus* AMNH 13958. A, D. Lateral view. B, E. Medial view. C, F. Dorsal view (Lane, 2010b). Breaks in posterior and external canals in *Egertonodus* are artefacts of preservation. Note complete isolation of the posterior canal, which has an extensive ascending pre-ampullary ramus expanding dorsally to form a “posterior utriculus” (presumably housing the macula neglecta opposite the perilymphatic fenestra), and separate anterior and external connections with the utricular recess. Scale bar = 10 mm. aa: anterior ampulla; asc: anterior semicircular canal; ea: external ampulla; end f: endolymphatic fossa (line shows position of endolymphatic duct); esc: external semicircular canal; lag: lagenar chamber; pa: posterior ampulla; pf: perilymphatic fenestra; ppac: posterior pre-ampullary canal; psc: posterior semicircular canal; pu: “posterior utriculus”; sac: sacculus; ur: utricular recess; VIII: opening for octaval (acousticovestibular) nerve; IX: glossopharyngeal canal; IX,X: glossopharyngeal-vagal canal; X: separate passage for vagal nerve.

Fig. 2. Reconstitutions sous Imaris[®] du squelette labyrinthique chez deux requins hybodontes du Crétacé inférieur. A–C. *Egertonodus* BM(NH) P.60010. D–F. *Tribodus* AMNH 13958. A, D. Vue latérale. B, E. Vue médiale. C, F. Vue dorsale (Lane, 2010b). L’absence de canaux postérieur et externe complets chez *Egertonodus* est due à des artefacts de préservation. Noter l’isolement du canal postérieur, qui présente un rameau préampullaire ascendant, développé dorsalement pour former un « utricule postérieur » (supposé contenir la *macula neglecta*, à l’opposé de la fenêtre périlymphatique), et les connexions antérieure et externe séparées du *recessus* utriculaire. Barre d’échelle = 10 mm. aa : ampulla antérieure ; asc : canal semicirculaire antérieur ; ea : ampulla externe ; end f : fosse endolymphatique (le trait montre la position du conduit endolymphatique) ; esc : canal semicirculaire externe ; lag : chambre de la *lagena* ; pa : ampulla postérieure ; pf : fenêtre périlymphatique ; ppac : canal préampullaire postérieur ; psc : canal semicirculaire postérieur ; pu : « utricule postérieur » ; sac : chambre sacculaire ; ur : *recessus* utriculaire ; VIII : entrée du nerf acoustico-vestibulaire ; IX : canal glossopharyngien ; IX,X : canal glossopharyngien-vague ; X : passage séparé pour le nerf vague.

neglecta close to the base of the endolymphatic duct (de Beer, 1931, 1937; Retzius, 1881). A crus commune is therefore absent in extant elasmobranchs. The crus is also absent in the Pliocene otic region PV 4173 (Fig. 1) and in the two Early Cretaceous hybodont sharks scanned (*Tribodus*, *Egertonodus*); in all these forms, the posterior semicircular canal was found to be isolated as in extant elasmobranchs (Fig. 2). Data are unavailable for other Mesozoic and Paleozoic hybodonts, but it is possible that the posterior canal was isolated in most or even all of them. The anterior and posterior semicircular canals in the incertae sedis Triassic shark *Acronemus* (T/I 1289) appear to be widely separated, although the specimen investigated was too poorly preserved to provide many details of its skeletal labyrinth (Fig. 3). The phylogenetic relationships of *Acronemus* are uncertain; it has been classified as a ctenacanthiform on the basis of possibly plesiomorphic features of its fin spines (Rieppel, 1982), but presence of an isolated posterior semicircular canal supports a relationship with hybodonts and/or neoselachians. The anterior and posterior semicircular canals in *Tristychius* are said to be connected by a crus commune located below a laterally-directed branch of the dorsal otic ridge on the surface of the braincase (Dick, 1978). Whether the anterior and posterior canals actually meet within this ridge is unclear, but if this interpretation is correct the presence of a crus would represent an important difference from extant elasmobranchs and hybodonts, suggesting that *Tristychius* may be more distantly related to them than is *Acronemus*.

Unlike in extant elasmobranchs, there is a descending crus commune connecting the anterior and posterior canals in extant chimaeroids, osteichthyans, lampreys, as well as in *Acanthodes*, osteostracans, and galeaspids (Davis and Coates, 2009; Janvier, 1996; Maisey, 2001a; Miles, 1973). The semicircular canal arrangement in placoderms is apparently different from that seen in osteichthyans and has in the past been compared to that of elasmobranchs (Stensiö, 1950, 1963), although there are important differences between the placoderm and elasmobranch skeletal labyrinth, and the placoderm posterior canal was probably never completely isolated from the others (Maisey, 2005). Among extinct chondrichthyans, a crus commune connecting the anterior and posterior semicircular canals has been identified in *Pucapampella*, *Doliodus*, *Cladodoides*, and symmoriiforms including “*Cobelodus*” (Maisey, 2001b, 2005, 2007; Maisey and Anderson, 2001; Maisey et al., 2009). These early chondrichthyans therefore resemble osteichthyans, *Acanthodes*, and chimaeroids in retaining the crus commune (Figs. 4 and 5). Iniopterygian labyrinth morphology is probably specialized in having the anterior and posterior canals somewhat flattened in the horizontal plane (Pradel et al., 2009a), but a crus commune nevertheless seems to be present. It has been suggested that the anterior and external canals were united in Permian xenacanth, and that the xenacanth posterior canal was circular (and by inference isolated) as in extant elasmobranchs (Schaeffer, 1981). However the xenacanth endocast suggests that a crus commune was

present although it does not reveal a pre-ampullary canal (see next section). Interpretation of a neoselachian-like arrangement of the posterior canal in xenacanth therefore seems doubtful, especially in view of other primitive features in the skeletal labyrinth shared by xenacanth and *Cladodoides* (Maisey, 2005). The semicircular canal arrangement has not yet been determined in the enigmatic Devonian gnathostome *Ramirosuarezia* (Pradel et al., 2009b).

3.2. Posterior semicircular canal describes almost complete circuit

In extant elasmobranchs, there is an elongated extension of the posterior semicircular canal anterior to the ampulla (de Beer, 1931; Retzius, 1881; Schaeffer, 1981), termed the posterior pre-ampullary canal (Maisey, 2001a). The semicircular canal curves dorsally to complete its circuit and reach the perilymphatic fenestra. An identical arrangement has been found in the Pliocene carcharhinid otic region, as well as in the hybodonts *Tribodus* and *Egertonodus* (Lane, 2010b; Maisey, 2004b, 2005) (Figs. 1 and 2). The posterior canal in *Acronemus* also appears to have an ascending pre-ampullary ramus (Fig. 3), although it is incompletely preserved in the material investigated.

A short posterior pre-ampullary canal is present in extant chimaeroids and *Acipenser*, but extends anteriorly only as far as the utricular chamber. There is no ascending ramus like that seen in extant elasmobranchs; instead, the crus commune extends downward to meet the utricular chamber, and perilymphatic openings are absent. A pre-ampullary canal is absent in other osteichthyans, as well as in galeaspid and osteostracans, but it is unknown whether one was present in *Acanthodes*. In placoderms, however, the posterior canal may form an almost complete circuit and there is a well-developed posterior pre-ampullary canal, which has been interpreted as forming a neoselachian-like “posterior utriculus” (e.g., *Jagorina*, *Tapinosteus*, *Kujdanowiaspis*) (Stensiö, 1969). This similarity to extant elasmobranchs has been credited with considerable phylogenetic importance, supposedly supporting the view that placoderms and elasmobranchs are closely related (e.g., as elasmobranchiomorphs) (Stensiö, 1963, 1969). However, it is important to note that at the time that proposal was made no information was available concerning labyrinth morphology in early chondrichthyans; instead, it was assumed that they possessed the extant elasmobranch condition. A posterior pre-ampullary canal has not been recognized in Permian xenacanth. There may be a short pre-ampullary canal in *Cladodoides*, but there is no evidence of one in symmoriiforms (Maisey, 2005, 2007). The labyrinth in all the specimens of *Pucapampella* examined to date have failed to reveal details of the posterior semicircular canal below its ampulla, and the ampullae remain unknown in *Doliodus*. However, the skeletal labyrinths of both *Pucapampella* and *Doliodus* include a crus commune, showing that the posterior canal was not isolated (Fig. 5).

3.3. Separation of saccular and utricular regions

In extant elasmobranchs, this feature is related to isolation of the posterior semicircular canal, which is connected via the posterior pre-ampullary canal to the “posterior utriculus” containing the sensory crista neglecta (de Beer, 1931, 1937; Maisey, 2001a, Retzius, 1881; Torrey, 1962). The “posterior utriculus” in *Notorynchus* forms an inflated chamber in the dorsal part of the posterior pre-ampullary canal, containing both the crista neglecta and a connection with the sacculus (see next section), and is therefore probably homologous with the posterior part of the utricular chamber in osteichthyans where the macula neglecta is also located. The elasmobranch “anterior utriculus” includes the entrance of the combined anterior and external semicircular canals, like the anterior part of the utriculus in other gnathostomes. The posterior pre-ampullary canal has been considered part of a “posterior utriculus” in chimaeroids and placoderms (Norris, 1929; Stensiö, 1963). The posterior pre-ampullary canal lacks an inflated utricular chamber in these forms, but in chimaeroids the crista neglecta lies within the corresponding part of the posterior pre-ampullary canal, and perhaps this was also the case in placoderms. Additionally, the posterior pre-ampullary canal in some extant elasmobranchs (e.g., *Torpedo*) is not inflated into a distinct “posterior utriculus” around the crista, and the crista is located within the posterior canal duct instead of the posterior pre-ampullary canal (Maisey, 2001a).

In the Pliocene otic region (PV 4173; Fig. 1), the posterior pre-ampullary canal broadens dorsally, presumably forming an inflated chamber which was clearly separated from the sacculus by cartilage, although its outer wall is broken and its original size is uncertain. In the hybodonts *Tribodus* and *Egertonodus*, the dorsal part of the posterior pre-ampullary canal widens just below the perilymphatic fenestra (Fig. 2), suggesting the presence of an inflated “posterior utriculus” as in many extant sharks. The corresponding region of the *Acronemus* braincase was poorly resolved in the CT scan and its morphology could not be deduced. There is no evidence of an inflated pre-ampullary region in the xenacanth endocast, nor in endocasts of *Cladodoides* and “*Cobelodus*” sp. (Maisey, 2005, 2007; Schaeffer, 1981). This region is unknown in *Pucapampella* or *Doliodus*, but other features of the labyrinth resemble those of osteichthyans (in which a “posterior utriculus” is absent). Among gnathostomes, therefore, an inflated “posterior utriculus” within the posterior pre-ampullary canal is known at present only in neoselachians and hybodonts.

3.4. Posterior canal has single connection with vestibular region

The posterior semicircular canal in extant elasmobranchs has a single opening into the vestibular region (posterior utriculo-sacculus opening). The posterior canal duct which extends from this opening is one of the most obvious morphological features of the elasmobranch non-otolithic phonoreceptor (Bleckman and Hoffman, 1999; Corwin, 1978, 1981a). In chimaeroids and osteichthyans, however, there are two openings; the canal opens into

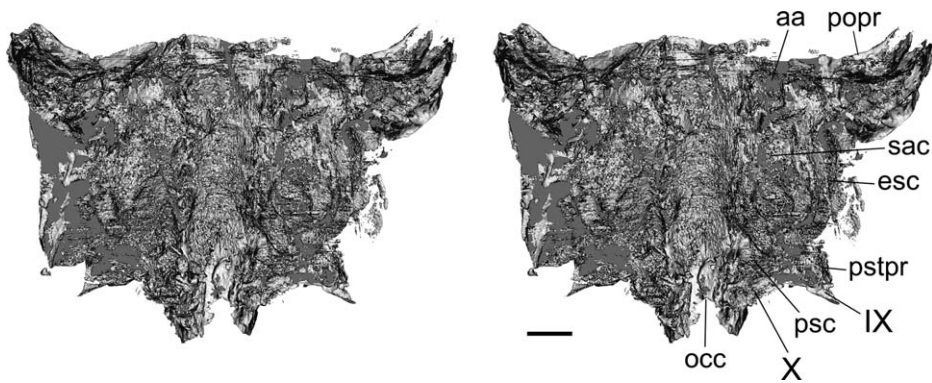


Fig. 3. Mimics®-based reconstitution of the otico-occipital region in the Middle Triassic shark *Acronemus* T/l 1289 (stereopair images in dorsal view). Note anterior and posterior canals apparently separated by a space, presence of a medial capsular wall, glossopharyngeal canal terminating in post-otic process, external canal lying in a single plane, and anterior ampulla located level with postorbital process. Scale bar = 10 mm. aa: anterior ampulla; esc: external semicircular canal; occ: occipital cotyle; popr: postorbital process; psc: posterior semicircular canal; pstpr: post-otic process; sac: saccular chamber; IX: glossopharyngeal canal; X: vagal canal.

Fig. 3. Reconstitution sous Mimics® de la région otico-occipitale du requin du Trias moyen *Acronemus* T/l 1289 (images stéréo-paires, en vue dorsale). Noter les canaux antérieur et postérieur apparemment séparés par un espace, la présence d'un mur capsulaire médian, le canal glossopharyngien se terminant dans le processus post-otique, le canal externe se situant dans un seul plan, et l'ampulla antérieure située au niveau du processus postorbitaire. Barre d'échelle = 10 mm. aa: ampulla antérieure; esc: canal semicirculaire externe; occ: cotyle occipital; popr: processus postorbitaire; psc: canal semicirculaire postérieur; pstpr: processus post-otique; sac: chambre sacculaire; IX: canal du nerf glossopharyngien; X: canal du nerf vague.

the vestibular chamber ventrally and also shares a dorsal connection with the anterior canal. There is a single posterior utriculo-saccular opening in the Pliocene carcharhinid otic region PV 4173 (Fig. 1), and a single connection is also evident in *Tribodus* and *Egertonodus* (Fig. 2), but the arrangement in *Acronemus* is unknown. By contrast, in *Cladodoides*, “*Cobelodus*” sp., *Pucapampella*, and *Doliodus*, confluence of the anterior and posterior canals of the skeletal labyrinth resembles the osteichthyan arrangement, suggesting that the posterior canal had separate connections to the vestibular region dorsally and ventrally (Fig. 4). The nature of this connection in xenacanth has not yet been established.

Despite the fact that the skeletal labyrinth of placoderms has been interpreted after an extant elasmobranch paradigm (Stensiö, 1950, 1963, 1969), none of the placoderm labyrinth endocasts described so far has revealed whether the posterior canal had one or two openings into the vestibular region; moreover, the manner in which the semicircular canals are connected to the vestibular region is different (see below). We are thus reluctant to accept earlier interpretations of the placoderm posterior canal configuration based solely on an extant elasmobranch model.

3.5. Isolation and elaboration of sensory crista neglecta

In holocephalans and osteichthyans, the crista neglecta is located in the posterior part of the large utricular chamber, behind the utricular macula and the openings for the anterior and external ampullae. By contrast, in elasmobranchs, the crista neglecta is located adjacent to the posterior utriculo-saccular opening of the posterior semicircular canal, usually within the “posterior utriculus”. In batoids, the crista is either associated with the saccular end of the posterior canal duct or is located within the duct (Corwin, 1989; Retzius, 1881). The crista neglecta

is considerably larger in extant elasmobranchs than in most other craniates, but nevertheless displays a wide range of size and complexity (Corwin, 1978). The sensory crista is not preserved in fossils, so its former position and extent can only be inferred from other features of the labyrinth. It may well have been located close to the posterior utriculo-saccular opening in *Tribodus* and *Egertonodus*, but in Paleozoic chondrichthyans such as *Cladodoides* and “*Cobelodus*” it could have been located in the posterior part of the utriculus, as in extant osteichthyans and chimaeroids.

The crista neglecta in extant elasmobranchs varies in size and complexity, offering a potentially informative source of new phylogenetic data for extant elasmobranchs once a sufficient taxon sample has been investigated. For example, the macula in *Mustelus*, *Ginglymostoma*, *Carcharhinus*, *Negaprion*, and *Notorynchus* is divided into two sensory fields, located on opposite sides of the posterior canal duct (anteriorly and posteriorly) and separated by a longitudinal area lacking sensory hair cells; the posterior area is considerably larger than the anterior one (Corwin, 1978, 1981a, 1981b). By contrast, in *Torpedo* and *Myliobatis* there is a single macula with a central area lacking hair cells, potentially representing an important distinction between extant sharks and batoids. It is unknown whether the single sensory area in batoids is homologous with both or only one of the areas in sharks, but it corresponds topographically to the posterior area. In *Carcharhinus*, *Negaprion*, and *Notorynchus*, macular sensory hair cells are directed toward the perilymphatic fenestra in the anterior field and away from it in the posterior field, but in *Mustelus* and *Ginglymostoma* some of the cells are misaligned. Hair cells in the macula of batoids tend to be aligned medially and laterally. These limited observations suggest that there may be functionally-related phylogenetic patterns in macular structure and sensory hair cell orientation among extant elasmobranchs that would merit further investigation.

3.6. Extensive medial wall to otic capsule

An extensive medial capsular wall is present in extant elasmobranchs, almost completely separating the endocranial and labyrinth spaces apart from foramina for the acoustic and glossopharyngeal nerves. By contrast, the medial wall of the otic capsule is membranous in extant holocephalans, actinopterygians and dipnoans (de Beer, 1937; Romer, 1937). Among extant gnathostomes, therefore, only elasmobranchs have a chondrified medial capsular wall. A medial capsular wall is nevertheless well developed in placoderms, osteostracans, and galeaspids. In extant adult lampreys, the posterior part of the medial capsular wall is chondrified anterior to the acoustic nerve and fuses to the cartilaginous lateral wall of the cranial cavity (Jarvik, 1977), but the wall is unchondrified in hagfishes.

The medial capsular wall is fully developed in the Pliocene otic region PV 4173 (Fig. 1) and in both of the hybodont sharks investigated here (*Tribodus*, *Egertonodus*; Fig. 2) as well as in *Acronemus* (Fig. 3), but it is only partially chondrified in xenacanth (*Schaeffer*, 1981) and is mostly unchondrified in earlier chondrichthyans (Fig. 4); e.g., *Cladodoidea*, *symmoriiforms*, *Pucapampella*, *Doliodus*. Within chondrichthyans, therefore, the presence of a chondrified medial capsular wall completely separating the saccular chamber from the endocranial space appears to be restricted to neoselachians, hybodonts, and the incertae sedis taxon *Acronemus*, although the condition in *Tristychius* and Paleozoic hybodonts (e.g., *Hamiltonichthys*, *Onychoselache*) needs further investigation. Collectively, these findings suggest that a medial capsular wall was primitively present in gnathostomes but was lost in the common ancestors of osteichthyans and chondrichthyans, only to be re-acquired within chondrichthyans after the divergence of elasmobranchs and chimaeroids but before the divergence of hybodonts and neoselachians.

3.7. Perilymphatic fenestrae

The perilymphatic fenestrae or fenestrae vestibuli are paired openings in the dorso-medial capsular wall in extant elasmobranchs that expose small sections of the posterior semicircular canal (Howes, 1883; de Beer, 1931, 1937; Holmgren, 1940, 1941). During ontogeny, their position is defined in part by the margins of the taenia medialis forming the floor of the endolymphatic (parietal) fossa (see below). Each of the fenestrae lies medial to a posterior utriculo-saccular opening and is therefore located directly opposite the crista neglecta. The perilymphatic fenestrae act as a sound-transmitting device into the non-otolithic component of the phonoreceptor system (Corwin, 1977; Fay et al., 1974; Tester et al., 1972) and are closed by a specialized membrane in some elasmobranchs (Norris, 1929).

The perilymphatic fenestrae are usually visible on the dorsal surface of an extant elasmobranch braincase as paired openings just behind the endolymphatic fenestrae. Similar openings have been identified in some fossils (Brito and Seret, 1996) and were probably present in many if not all extinct neoselachians. Cartilage is not preserved adjacent to the expected position of the perilymphatic fenestra in the Pliocene otic region PV 4173, but the fenestrae may

be represented by expanded areas above each posterior canal in CT reconstitutions of the labyrinth in *Tribodus* and *Egertonodus* (Fig. 2). Perilymphatic fenestrae seem to be present in *Acronemus* although these were not readily observed in the reconstitution. Vestibular fenestrae are said to be present in *Tristychius* (Dick, 1978). Perilymphatic fenestrae were not observed in any of the scanned Paleozoic sharks investigated here and are absent in extant chimaeroids, osteichthyans, lampreys and hagfishes. They have also not been found in placoderms, *Ramiro Suarezia*, or fossil agnathans. Collectively, these findings suggest that perilymphatic fenestrae have a very restricted occurrence within craniates, and their presence is interpreted here as a potential synapomorphy of neoselachians, hybodonts, *Acronemus*, and *Tristychius*.

3.8. Crus distally between anterior and external semicircular canals

In the membranous labyrinth of extant elasmobranchs, the distal (i.e. non-ampullary) end of the external semicircular canal meets the descending distal part of the anterior canal, forming a crus that meets the anterior utricular region. Unfortunately, this union is located deep within the vestibular chamber and is consequently not evident in endocasts of the skeletal labyrinth (Maisey, 2004b; Schaeffer, 1981). The labyrinth in some placoderms is said to possess an elasmobranch-like crus between the anterior and external semicircular canals (Goujet, 1984; Stensiö, 1963), although these are situated superficial to the sacculus rather than deep within it as in extant elasmobranchs. Furthermore, the connection between the anterior and external semicircular canals in some placoderms (e.g., *Tapinosteus*, *Macropetalichthys*) was located dorsal to the loop of the posterior canal instead of ventral to it as in elasmobranchs (Stensiö, 1969). In others (e.g., *Kujdanowiaspis*, *Dicksonosteus*), the external semicircular canal apparently met the posterior one, and the combined canal then continued forward to meet the anterior canal (Goujet, 1984; Stensiö, 1969). The labyrinth of *Jagorina* has been restored using an extant elasmobranch paradigm (Stensiö, 1950), but its endocast could just as readily have included a crus commune. Thus the posterior semicircular canal in placoderms was probably not isolated as in extant elasmobranchs, and in some forms a crus commune may have been present. While some placoderms may have possessed a crus between the external and anterior semicircular canals, the arrangement apparently differed from that found in extant elasmobranchs and therefore provides less morphological support for a phylogenetic relationship than was previously supposed. There is also no evidence to suggest that the odd semicircular canal arrangement in placoderms was associated with an elasmobranch-like semi-directional phonoreceptor system.

3.9. Out-of-plane orientation of external semicircular canal

In lateral view, the external canal of extant elasmobranchs passes posteriorly from its ampulla within the lateral wall of the sacculus, then curves upwards posteri-

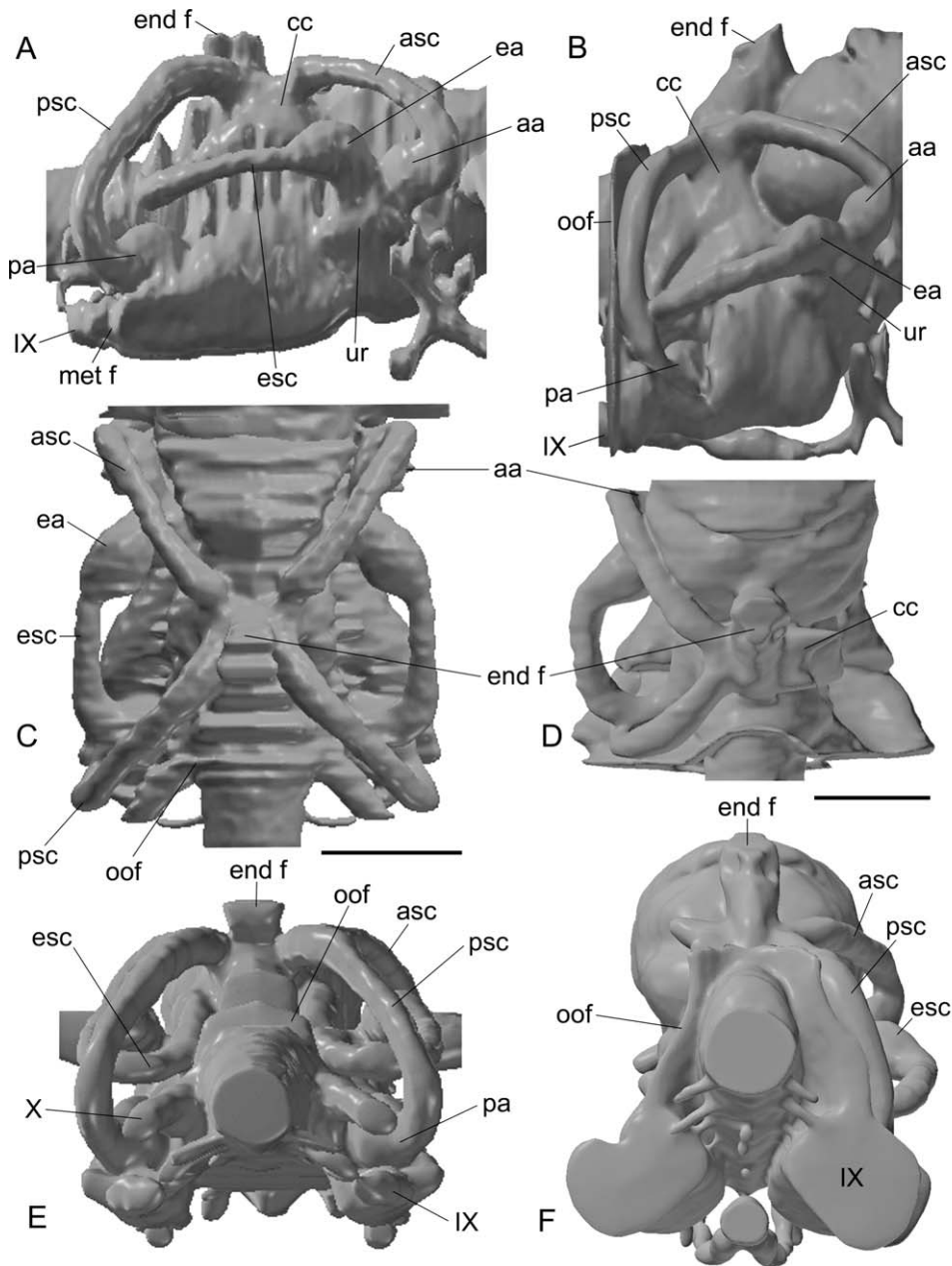


Fig. 4. Imaris®-based reconstructions of the skeletal labyrinth and cranial endocast in *Cladodoides* (A, C, E) and in a Late Mississippian symmoriiform “*Cobelodus*” FMNH PF13242 (B, D, F) (Maisey, 2005, 2007). A, B. Right lateral view (anterior to right). C, D. Dorsal view (anterior to top). E, F. Posterior view. Note confluence between labyrinth and cranial cavity (indicating absence of chondrified medial capsular wall), presence of crus commune dorsally between anterior and posterior semicircular canals, narrow but well-defined endolymphatic fossa separated from the persistent otico-occipital fissure by a posterior tectum, and a well-defined glossopharyngeal canal within the metotic fissure. Scale bars = 10 mm. aa: anterior ampulla; asc: anterior semicircular canal; cc: crus commune; ea: external ampulla; end f: endolymphatic fossa; esc: external semicircular canal; met f: metotic fissure; pa: posterior ampulla; psc: posterior semicircular canal; oof: otico-occipital fissure; ur: recessus utriculaire; IX: expansion in metotic fissure for glossopharyngeal nerve; X: expansion in otico-occipital fissure for vagal nerve.

Fig. 4. Reconstitutions sous Imaris® du squelette labyrinthique et du moulage endocrânien de *Cladodoides* (A, C, E) et du symmoriiforme du Mississippien supérieur « *Cobelodus* » sp. FMNH PF13242 (B, D, F) (Maisey, 2005, 2007). A, B. Vue latérale droite. C, D. Vue dorsale. E, F. Vue postérieure. Noter la confluence entre le labyrinthe et la cavité crânienne (indiquant l'absence de mur capsulaire médian chondrifié); la présence d'une *crus commune* située dorsalement entre les canaux semicirculaires antérieur et postérieur; la fosse endolymphatique, étroite mais bien définie, séparée de la fissure otico-occipitale par un tectum postérieur; et un canal glossopharyngien clairement visible au sein de la fissure métotique. Barres d'échelle = 10 mm. aa: ampulla antérieure; asc: canal semicirculaire antérieur; cc: *crus commune*; ea: ampulla externe; end f: fosse endolymphatique; esc: canal semicirculaire externe; met f: fissure métotique; pa: ampulla postérieure; psc: canal semicirculaire postérieur; ur: *recessus utriculaire*; IX: expansion de la fissure métotique pour le nerf glossopharyngien; X: expansion de la fissure otico-occipitale pour le nerf vague.

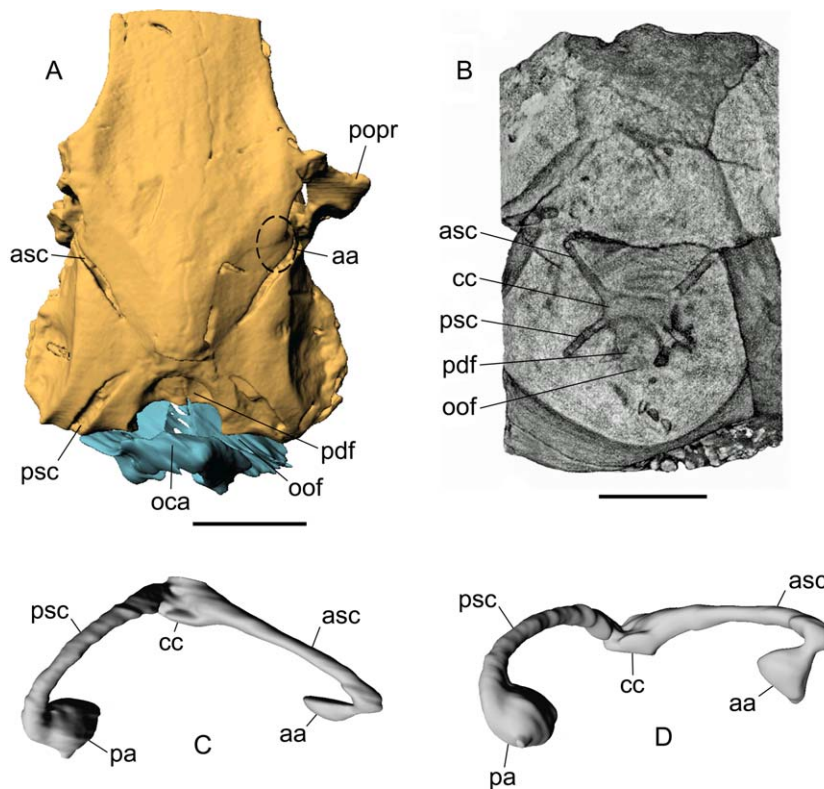


Fig. 5. Features of the skeletal labyrinth in *Pucapampella*. A. Combination (dorsal view) of two Imaris[®] reconstructions (braincase AMNH FF19631, plus occipital arch from uncatalogued AMNH specimen from Le Grand Smith collection). Note crus commune, posterior dorsal fontanelle lacking posterior tectum, lack of perilymphatic fenestrae leading to posterior canal, and position of anterior ampulla behind postorbital process (dashed oval shape). B. Horizontal CT scan section of GSB 0497A. Note crus commune, posterior dorsal fontanelle, otico-occipital fissure. C, D. Imaris[®] reconstructions of anterior and posterior semicircular canals in Le Grand Smith specimen. C. Lateral view. D. Dorsal view. Scale bars for A, B = 10 mm. No scale for C, D. aa: anterior ampulla (or its location in A); asc: anterior semicircular canal; cc: crus commune; oca: occipital arch; oof: otico-occipital fissure; pdf: posterior dorsal fontanelle; popr: postorbital process; pa: posterior ampulla; psc: posterior semicircular canal.

Fig. 5. Caractères anatomiques du squelette labyrinthique chez *Pucapampella*. A. Combinaison de deux reconstructions sous Imaris[®], en vue dorsale, de la boîte crânienne AMNH FF19631 et de l'arche occipitale d'un spécimen non catalogué de la collection Le Grand Smith, AMNH. Noter la *crus commune*; la fontanelle dorsale postérieure sans tectum postérieur; l'absence de fenêtre périlymphatique menant au canal postérieur et la position de l'ampulla antérieure derrière le processus postorbitaire (ovale en pointillés). B. Section horizontale acquise par CT scan du spécimen GSB 0497A. Noter la *crus commune*; la fontanelle dorsale postérieure; la fissure otico-occipitale. C, D. Reconstitutions sous Imaris[®] des canaux semicirculaires antérieur et postérieur du spécimen Le Grand Smith. C. Vue latérale. D. Vue dorsale. Barres d'échelle pour A, B = 10 mm. Pas à l'échelle pour C, D. aa: ampulla antérieure (ou sa position en A); asc: canal semicirculaire antérieur; cc: *crus commune*; oca: arc occipital; oof: fissure otico-occipitale; pdf: fontanelle dorsale postérieure; popr: processus postorbitaire; pa: ampulla postérieure; psc: canal semicirculaire postérieur.

only as it approaches the anterior canal (Maisey, 2001a). The inner and outer parts of the canal do not therefore lie in the same plane. This feature can also be observed in the Pliocene otic region PV 4173 and in the skeletal labyrinths of *Tribodus* and *Egertonodus* (Figs. 1 and 2). However, in *Acronemus*, *Cladodoides*, *symmoriiforms*, *Doliodus* and *Pucapampella*, the external canal lies almost entirely within a plane passing through the mid-region of the saccular region, as in osteichthyans (Maisey, 2005, 2007). In extant chimaeroids, the canal may climb slightly out of the mid-saccular plane. In some placoderms, the external canal passes around the sacculus much as in osteichthyans, although its distal end may be slightly elevated where it passes over the saccular chamber (it does not pass deeper within the chamber as in extant elasmobranchs). The external semicircular canal in *symmoriiform* sharks has an unusual anterodorsal inclination with respect to the vertebral axis (Maisey, 2007), but this affects the

entire canal and not merely its distal part. These observations suggest that out-of-plane orientation of the external canal may unite neoselachians and hybodonts (and perhaps chimaeroids), but would exclude *Acronemus* and many earlier chondrichthyans. From its rather disjunct distribution, this feature is probably unrelated to LFSDP in elasmobranchs.

3.10. Anterior and external canals share a common opening into vestibular region

In extant elasmobranchs, the membranous anterior and external canals share a single anterior utriculo-saccular opening (Torrey, 1962), whereas in osteichthyans and holoccephalans these canals open separately into the utriculus. The scan of the Pliocene otic region PV 4173 reveals that the anterior and external ampullae make contact before entering the utricular recess and share an opening into the

utricular recess (which is connected to the saccular chamber dorsally via a single opening; Fig. 6). In *Notorynchus*, the chambers of the anterior and external ampullae meet above the utricular recess and their openings are confluent, with a single opening into the utricular recess and sacculus (Fig. 7). In endocasts of *Tribodus*, *Egertonodus*, *Cladodoides*, symmoriforms, the anterior and external ampullary chambers lie close together but probably opened separately into the utricular recess, although there is still a single utricular entrance into the sacculus (Figs. 2 and 4). The arrangement was probably similar in *Pucapampella*, but has not yet been determined in *Acronemus* and *Doliodus*.

In placoderms, the anterior and external ampullae are widely separated and clearly have separate connections with the utriculus; in *Jagorina* the ampullae lie on opposite sides of a small, indistinct utricular recess, and in other placoderms (e.g., *Kujdanowiaspis*, *Tapinosteus*) the anterior ampulla is separated from the utricular recess by a pre-ampullary extension of the anterior canal (Stensiö, 1950, 1969). No placoderm is known in which the anterior and external ampullae meet as in elasmobranchs. Pre-ampullary extensions of the anterior and external canals are present in some batoids (e.g., *Torpedo*) but these typically unite before entering the utricular recess via a single opening (Maisey, 2001a), unlike in placoderms. Such pre-ampullary canals are absent in the fossil chondrichthyans examined here. A common utricular opening for the anterior and external ampullae may therefore be an apomorphic character of neoselachians, although its distribution needs further investigation.

3.11. Exogenous sand grains of endolymphatic ducts and sacculus

Instead of solid otoliths, extant chondrichthyans possess an otolithic mass within the saccular chamber, consisting primarily of endogenous crystalline calcium carbonate otoconia bound together by an organic matrix (Mulligan and Gauldie, 1989). Additional exogenous grains of sand (quartz, feldspar) and ferruginous material (magnetite, hematite) are sometimes present within the otolithic mass of elasmobranchs (Fänge, 1982; Norris, 1929; Stewart, 1906) although it is still unknown whether these also occur in chimaeroids. Exogenous sand grains may have been present within the otic labyrinth of osteostracans, acanthodians, and putative fossil chondrichthyans from the Early Devonian of Canada (Sahney and Wilson, 2001), suggesting a widespread distribution among early vertebrates including many forms which probably lacked an elasmobranch-like phonoreceptor. It is unlikely that exogenous sand grains play a role in LFSDP of elasmobranchs, and are instead probably related to the inner ear's mechanosensory function (Hanson et al., 1990). Mechanoreception using assimilated exogenous sand grains is most parsimoniously interpreted as a primitive feature of gnathostomes that has been conserved by elasmobranchs. Although exogenous sand grains were not recognized in scans of the fossil chondrichthyans investigated, they may have been present originally and either were lost or simply not detected.

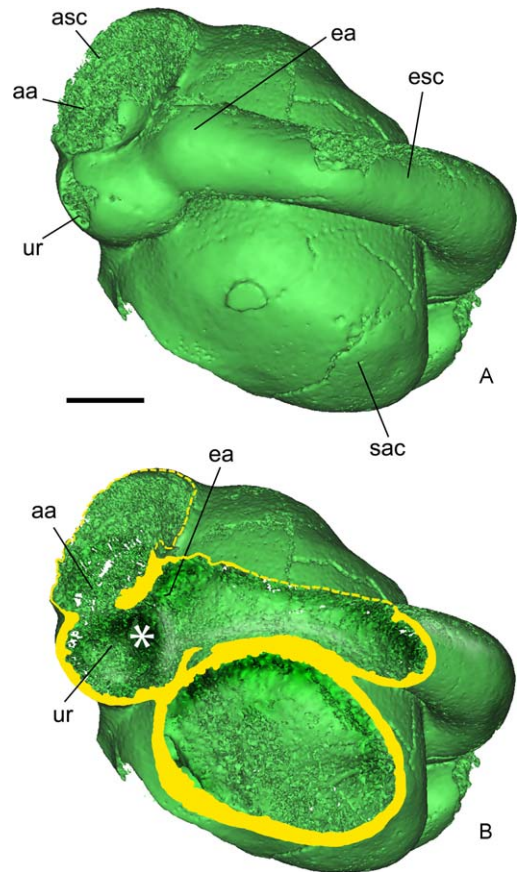


Fig. 6. Mimics® reconstitution of Pliocene carcharhinid otic region, Charleston Museum PV 4173. Lateral views showing complete capsule (A) and with clipping plane (B) through anterior and external ampullae and utricular recess (slice also clips the saccular chamber). Note confluence of anterior and external ampullae above the recess. Scale bar = 10 mm. aa: anterior ampulla; asc: anterior semicircular canal; ea: external ampulla; esc: external semicircular canal; sac: saccular chamber; ur: utricular recess; *: internal opening of utricular recess.

Fig. 6. Reconstitutions sous Mimics® de la région otique d'un requin carcharhinidé pliocène, Charleston Museum PV 4173. Vues latérales montrant la capsule complète (A) et avec un plan de coupe (« clipping tool » de Mimics®) à travers les ampullae antérieure et externe et le recessus utriculaire (la coupe passe également par la chambre sacculaire). Notez la confluence des ampullae antérieure et externe au-dessus du recessus. Barre d'échelle = 10 mm. aa: ampulla antérieure; asc: canal semicirculaire antérieur; ea: ampulla externe; esc: canal semicirculaire externe; sac: chambre sacculaire; ur: recessus utriculaire; *: ouverture interne du recessus utriculaire.

3.12. Endolymphatic (parietal) fossa

The endolymphatic fossa in extant elasmobranchs is a depression in the cranial roof between the otic capsules, filled with a gelatinous subcutaneous fluid with an acoustic impedance matching that of sea water (Corwin, 1989). The fossa is associated with paired perilymphatic fenestrae (see above), plus small paired muscles connected with the endolymphatic ducts. During ontogeny, the anterior margin of the fossa is defined by the embryonic tectum synoticum and it becomes floored by cartilage derived from the embryonic taenia medialis, which extends between the otic capsules and represents either a posterior extension of

the synotic tectum or an independent bridge of cartilage (de Beer, 1931; Holmgren, 1940). The embryonic otico-occipital fissure (a space between the otic capsules and occipital arch) becomes closed during ontogeny, leaving the posterior dorsal fontanelle open as the parietal fossa. However, closure of the fossa posteriorly in extant elasmobranchs is brought about in various ways, for example by direct fusion of the occipital pilae to the otic capsules (e.g., *Squalus*), or by posterior extension of the synotic tectum (which forms the floor of the fossa; e.g., *Heterodontus*). Thus, the posterior tectum behind the fossa can originate either from cartilage of the otic region or from the occipital arch.

Many extinct chondrichthyans are known to have the parietal fossa completely surrounded by cartilage as in neoselachians (Maisey, 1983; Maisey et al., 2004), but a chondrified floor to the fossa is known only in neoselachians, hybodonts and a few incertae sedis taxa such as *Acronemus* and *Tristychius*. This floor helps define discrete perilymphatic openings, and thus contributes to the channeling of sound waves into the posterior canal duct. The otico-occipital fissure is closed in all these forms, suggesting that there may be a developmental and/or functional correlation between closure of the fissure and the formation of a chondrified floor to the fossa between the otic capsules in elasmobranchs. The posterior tectum and the floor of the fossa in hybodonts and *Acronemus* probably included cartilage derived from the synotic tectum, the taenia medialis, and/or the occipital arch. There is no direct evidence that the fossa in hybodonts or *A. tuberculatus* contained impedance-matching gel or muscles closing the endolymphatic ducts, although this seems a reasonable assumption since other neoselachian-like features are evident in their labyrinths. Where the floor of the fossa is unchondrified, the otico-occipital fissure is typically persistent whether the fossa is closed by a cartilaginous tectum posteriorly (e.g., xenacanth, *Tamiobatis*, symmoriiforms, *Cladodoides*) (Maisey, 2005; Schaeffer, 1981) or is confluent with the otico-occipital fissure (e.g., *Pucapampella*) (Maisey, 2001b; Maisey and Anderson, 2001). It is unlikely that the posterior tectum in early chondrichthyans was derived ontogenetically from the synotic tectum farther anteriorly because the intervening floor of the fossa is unchondrified. It seems equally implausible that the occipital arch made a contribution to the posterior tectum in forms where the two were separated by the otico-occipital fissure. It is therefore concluded that the posterior tectum in Paleozoic chondrichthyans probably represents a separate embryonic taenia tecti medialis situated at the posterior end of the fossa.

An endolymphatic fossa is said to be absent in extant chimaeroids (Schaeffer, 1981), but there is an unpaired “endolymphatic duct” in the corresponding position, housing the paired endolymphatic canals and their associated sacs (de Beer and Moy-Thomas, 1935; Jollie, 1962). A small unpaired endolymphatic opening has also been found in extinct holocephalimorphs (e.g., *Squaloraja*, *Debeerius*, iniopterygians) (de Beer and Moy-Thomas, 1935; Grogan and Lund, 2000; Pradel et al., 2009b). This small canal is probably homologous with the much larger fossa of extant elasmobranchs although it lacks a chondrified floor in holo-

cephalans. The ontogeny of the otic region in chimaeroids is poorly known, but there is no otico-occipital fissure in the adult; the arch is already fused to the otic region in a 6-month *Chimaera* embryo, but is not at all evident in a 60 mm *Callorynchus* (de Beer and Moy-Thomas, 1935). It is concluded that an endolymphatic fossa is primitively present in crown-group chondrichthyans and became secondarily reduced early in holocephalan evolution (for a discussion of its possible homology with the osteichthyan posterior dorsal fontanelle, see reference Maisey (2005)). The endolymphatic fossa in symmoriiforms is also comparatively small and lacks a chondrified floor (Maisey, 2007), and probably housed both endolymphatic ducts. Presence of this small median opening is therefore a potential synapomorphy of holocephalans and symmoriiforms.

A posterior dorsal fontanelle may have been present in *Acanthodes*, although its interpretation as forming a neoselachian-like endolymphatic fossa is considered highly speculative (Maisey, 2005). Endolymphatic ducts were present in placoderms, and in *Brindabellaspis* these follow a tortuous path reminiscent of the ducts in elasmobranchs, with expanded upper parts that have been interpreted as forming an endolymphatic fossa (Young, 1980), although that interpretation has been questioned and it is doubtful whether any placoderm possessed a posterior dorsal fontanelle comparable to that of osteichthyans or chondrichthyans (Maisey, 2001a). There is no evidence of a fontanelle or endolymphatic foramina in *Ramirosuarezia* (Pradel et al., 2009b). The posterior dorsal fontanelle is therefore considered a plesiomorphic feature of crown-group gnathostomes associated with paired endolymphatic ducts and primitively continuous with the otico-occipital fissure. Since there is no evidence of a persistent otico-occipital fissure in placoderms, osteostracans or galeaspid, this feature may also represent another apomorphic feature of crown-group gnathostomes (possibly related to the evolution of the posterior dorsal fontanelle). Isolation of the fontanelle from the otico-occipital fissure apparently occurred early in chondrichthyan evolution, prior to closure of the fissure and the development of a continuous cartilaginous floor by the taenia medialis.

3.13. Embryonic metotic fissure forms glossopharyngeal canal

In extant elasmobranchs, the parachordals are expanded laterally below the otic capsules, forming the hypotic lamina (de Beer, 1931). The presence of this lamina has been regarded as an apomorphic character uniting non-holocephalan chondrichthyans, despite the apparent presence of an expanded parachordal plate in some placoderms (Schaeffer, 1981). However, the lamina may be secondarily absent in chimaeroids if holocephalans are derived from shark-like chondrichthyans (Coates and Sequeira, 2001; Ginter, 2005) (see Discussion below).

The metotic fissure represents a ventrolateral continuation of the otico-occipital fissure, and forms a transient embryonic space between the floor of the otic capsule and the hypotic lamina (a lateral extension of the parachordal cartilage in extant elasmobranchs). The fissure closes during ontogeny apart from the glossopharyngeal canal, which

passes below the otic capsule and opens posteroventrally in extant elasmobranchs, hybodonts, *Acronemus* and *Tristychius*. A persistent metotic fissure has been documented in numerous Paleozoic chondrichthyans (e.g., xenacanth, *Tamiobatis*, *Cladodoides*, symmoriiforms, *Pucapampella*) and one may also be present in *Doliodus* and *Antarctilamna* (Maisey, 2001b, 2001c, 2004b, 2005, 2007; Maisey and Anderson, 2001; Maisey et al., 2009; Schaeffer, 1981). In all these sharks, however, the glossopharyngeal nerve probably passed through the metotic fissure between the otic capsule and a hypotic lamina, and the course of the nerve is sometimes marked by a local widening of the fissure in a similar position to the glossopharyngeal canal in extant elasmobranchs (e.g., *Cladodoides*, “*Cobelodus*”; Fig. 4). It could therefore be argued these forms possess both a persistent metotic fissure and a glossopharyngeal canal.

Closure of the metotic and otico-occipital fissures in the common ancestors of neoselachians and hybodonts probably represents an important precursor state for the evolution of LFSDP, since the medial wall of the posterior semicircular canal (forming part of the non-otolithic phonoreceptor component in elasmobranchs) also forms the outer surface of the otico-occipital fissure both in extant elasmobranchs prior to its closure and in Paleozoic sharks with a persistent fissure. Chimaeroids are thought to lack an expanded hypotic lamina because their glossopharyngeal foramen is situated ventrally as in osteichthyans (de Beer, 1937). The positions of the vagal and glossopharyngeal foramina in *Ramirosuarezia* resemble those of chimaeroids (Jollie, 1962; Pradel et al., 2009b), suggesting that it also lacked a hypotic lamina. A metotic fissure is present in some early actinopterygians (Gardiner, 1984) and may be a primitive feature of crown-group gnathostomes. Persistent metotic and otico-occipital fissures are typically absent in placoderms. No vertebrate is known with a persistent metotic fissure and a closed otico-occipital one.

3.14. Lateral otic process

This large paired process represents an extension of the posterolateral wall of the otic capsule and encloses the outer loop of the posterior semicircular canal in xenacanth, *Tamiobatis*, and *Ctenacanthus* from the Cleveland Shale (Schaeffer, 1981). The lateral walls of the otic capsules are broken in the only known braincase of *Cladodoides*, exposing the loops of the posterior semicircular canals (Fig. 8D). Consequently, the lateral otic processes are missing in the specimen and their original extent can only be surmised (Maisey, 2005). Lateral otic processes are absent in symmoriiform sharks (Fig. 8E) and in *Ramirosuarezia* (Maisey, 2007; Pradel et al., 2009a). Chimaeroids and osteichthyans also lack such a process, and the placoderm posterior postorbital process is probably not homologous with the lateral otic process of sharks (Schaeffer, 1981). However, in a three-dimensional iniopterygian braincase, the posterior semicircular canal appears to bulge into the base of a small process on the posterolateral wall of the otic capsule (Pradel et al., 2009a), although it apparently did not articulate with a hyomandibula as in xenacanth or *Tamiobatis*.

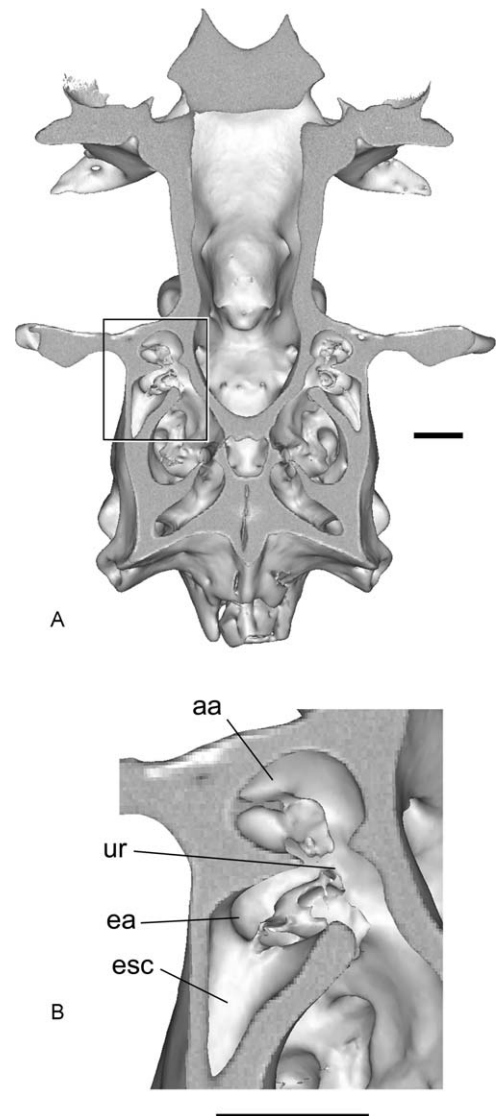


Fig. 7. Mimics® reconstructions showing the confluence of the anterior and external ampullae in *Notorynchus*. A. Entire braincase, dorsal view with horizontal clipping plane through ampullae above utricular recess. B. Detail showing confluence of ampullae in roof of recess. Scale bars = 10 mm. aa: anterior ampulla; ea: external ampulla; esc: external semicircular canal; ur: utricular recess.

Fig. 7. Reconstitutions sous Mimics® montrant la confluence des ampullae antérieure et externe chez *Notorynchus*. A. Boîte crânienne complète, en vue dorsale avec un plan de coupe horizontal à travers les ampullae au-dessus du recessus utriculaire. B. Détail montrant la confluence des ampullae au niveau du toit du recessus. Barre d'échelle = 10 mm. aa: ampulla antérieure; ea: ampulla externe; esc: canal semicirculaire externe; ur: recessus utriculaire.

It has been suggested that a lateral otic process occurs in many extant and fossil elasmobranchs (Coates and Sequeira, 2001; Maisey, 2001a; Schaeffer, 1981), although the process as originally defined (Schaeffer, 1981) is absent in neoselachians, hybodonts, and certain other chondrichthyans (Maisey, 2005). Neoselachians possess a post-otic process (Fig. 8A: pstpr) containing the glossopharyngeal canal (Holmgren, 1941). A similar process is

present in *Acronemus* (Fig. 3). By contrast, the glossopharyngeal nerve in xenacanth and *Tamiobatis* apparently passed mesial and ventral to the lateral otic process rather than through it. The supposed lateral otic process of *Egertonodus* (Maisey, 1983) is probably not homologous with either the lateral otic process of Paleozoic sharks or the post-otic process of neoselachians, since it does not contain either the posterior semicircular canal or the glossopharyngeal canal. The posterior semicircular canal is not enclosed by a process in symmoriiforms, *Pucapampella*, *Doliodus*, neoselachians, hybodonts, or *Acronemus*. The “otic process” of *Tristychius* has been compared with the lateral otic process of *Tamiobatis* and xenacanth (Dick, 1978), although it did not form part of the hyomandibular articulation (which is apparently located farther anteriorly) and it resembles the neoselachian post-otic process in being located immediately above the glossopharyngeal foramen.

3.15. Anterior ampulla located between (or in front of) postorbital process

The location of the postorbital arcade on the side walls of the braincase in extant elasmobranchs seems to be highly constrained ontogenetically (Holmgren, 1940), but its position is slightly more variable in extinct chondrichthyans (Maisey, 2005). The arcade is positioned entirely anterior to the otic labyrinth in *Cladodoides*, xenacanth, *Tamiobatis* sp., symmoriiforms, *Doliodus*, and *Pucapampella* (Figs. 5A and 8D, E), whereas in hybodonts and neoselachians the postorbital arcade or process is positioned farther posteriorly, either lateral to the anterior ampulla (e.g., *Notorynchus*; Fig. 8A) or just behind the ampulla (e.g., *Tribodus*, *Egertonodus*; Fig. 8B, C). The anterior ampulla is located medial to the postorbital arcade in *Acronemus*, providing additional support to the hypothesis that it is phylogenetically related to hybodonts and/or neoselachians. The anterior part of the otic capsule is located level with the postorbital wall in iniopterygians (Pradel et al., 2009a), but the capsule in extant chimaeroids is located entirely behind the postorbital wall (Jollie, 1962). The ampulla is positioned behind the level of the postorbital wall in early osteichthyans (e.g., *Kansasiella*) and in *Latimeria* (Millot and Anthony, 1958; Poplin, 1974), and this arrangement has been considered primitive for crown-group gnathostomes (Maisey, 2001a). The arrangement in hybodonts and neoselachians has been interpreted as a derived condition (Maisey, 2005), resulting from a posterior shift in the attachment point of the primary postorbital process formed in the posterior part of the embryonic supraorbital cartilage (Holmgren, 1940). Nevertheless, in *Kujdanowiaspis* the anterior ampulla is located medial to the anterior postorbital process as in neoselachians and hybodonts (Stensiö, 1969), possibly offering some evidence of homology between this process and the postorbital process of elasmobranchs. The position of the anterior ampulla in *Ramirosuarezia* is unknown and there is no obvious postorbital process although there is a slight bulge in the anterolateral surface of the otic capsule (Pradel et al., 2009b).

It is unlikely that the relative positions of the anterior ampulla and postorbital arcade had any bearing on the

evolution of phonoreception in elasmobranchs (which primarily involves the posterior part of the otic region).

3.16. Occipital block wedged between otic capsules posteriorly

The occipital region is located behind the otic capsules in osteostracans, placoderms, and *Acanthodes* (Janvier, 1996), and this may be the primitive gnathostome condition (Schaeffer, 1981). In extant elasmobranchs, however, the occipital arch extends anteriorly during ontogeny, ultimately becoming wedged between the posterior parts of the otic capsules (Johnels, 1948). The extant elasmobranch arrangement can also be observed in Mesozoic hybodonts, as well as in *Acronemus* and *Tristychius*. Even in those Paleozoic chondrichthyans whose occipital region extends a considerable distance posteriorly (e.g., xenacanth, *Tamiobatis*, *Ctenacanthus*, *Cladodoides*), the anterior part of the occipital arch is wedged between the otic capsules (Maisey, 2001c, 2005, 2007; Schaeffer, 1981). The occipital arch also extends a short distance between the otic capsules in Paleozoic symmoriiform sharks and *Cladoseleche* (Maisey, 2007). However, the occipital arch in *Pucapampella* and *Doliodus* does not intrude at all (Maisey and Anderson, 2001; Maisey et al., 2009). Much of the occipital arch in chimaeroids is situated anteriorly (between the posterior parts of the otic capsules), apart from paired lateral extensions forming an articulation with the synarcual (Jollie, 1962). The arch in iniopterygians intrudes slightly between the capsules (Pradel et al., 2009a) but the condition is uncertain in *Ramirosuarezia* (Pradel et al., 2009b).

Based on these observations, wedging of the occipital region between the otic capsules seems to represent a synapomorphy of a large clade of chondrichthyan fishes including neoselachians, holocephalans, hybodonts, *Acronemus*, *Tristychius*, xenacanth, and Paleozoic *Ctenacanthus*-like cladodont sharks (i.e., crown-group chondrichthyans plus many stem chondrichthyans), and excludes only a few early chondrichthyans such as *Doliodus* and *Pucapampella*.

4. Results

Among the features investigated here, only one appears to be restricted to extant neoselachians within chondrichthyans (including fossils), namely a shared opening for the anterior and external semicircular canals into the vestibular region). Two other characters (isolation and elaboration of the crista neglecta; distal crus present between anterior and external semicircular canals) could be observed in extant elasmobranchs but not in fossils, and are therefore phylogenetically uninformative.

Several apomorphic characters of the otic region are shared by neoselachians and hybodonts (posterior semicircular canal isolated, canal forms a complete circuit, chondrified medial capsular wall, perilymphatic fenestrae, out-of-plane orientation of external semicircular canal, glossopharyngeal canal, postorbital arcade lateral to anterior ampulla). All but one of these features has also been observed in *Acronemus* (its external semicircular canal

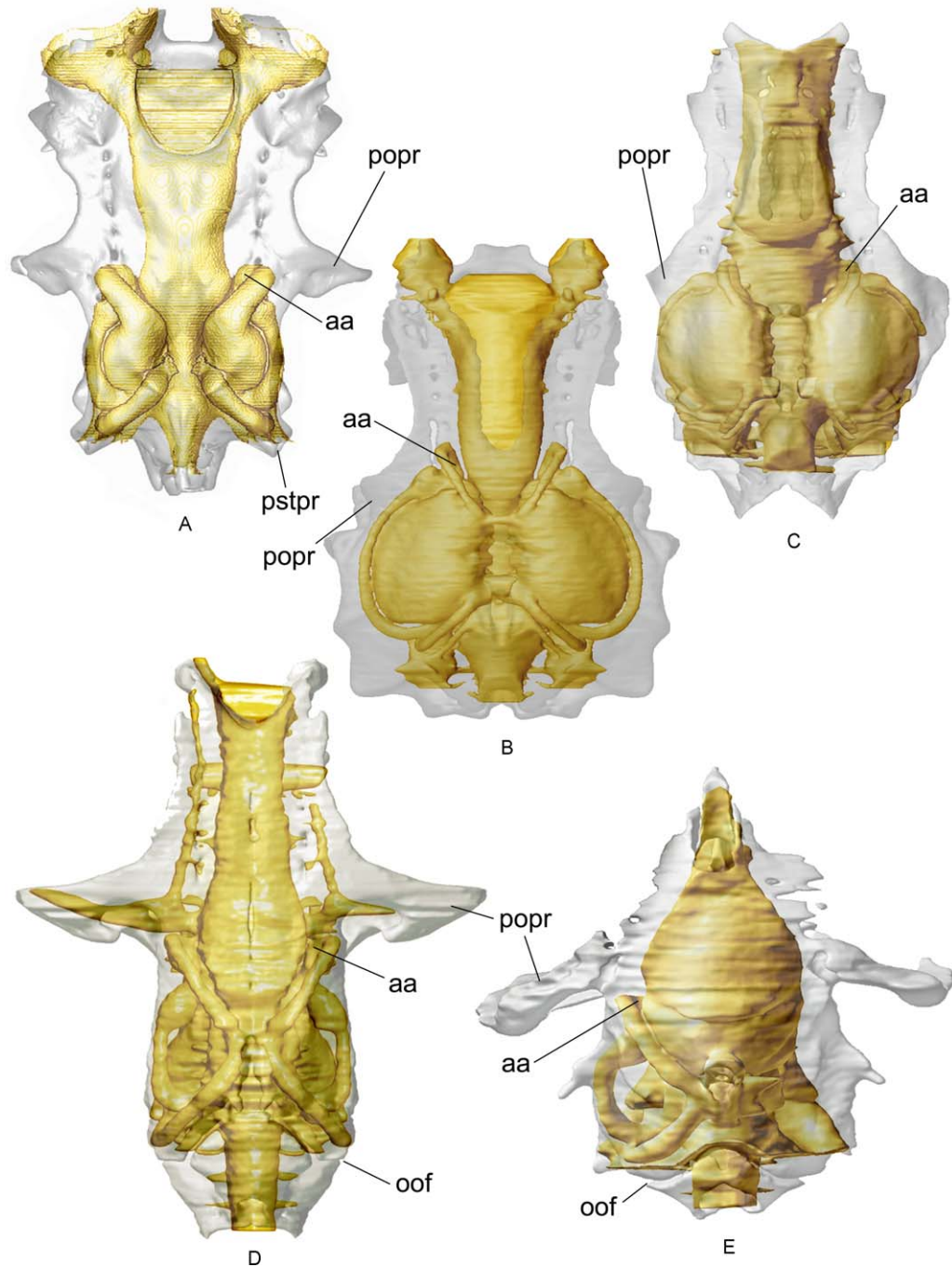


Fig. 8. Imaris® reconstructions of the braincase (rendered as a translucent object) and the cranial endocast in: A, *Notorynchus* (Maisey, 2004a); B, *Tribodus* (Lane, 2010b); C, *Egertonodus* (Lane, 2010b); D, *Cladodoides* (Maisey, 2005); E, “*Cobelodus*” (Maisey, 2007). All in dorsal view, anterior to top. Not to scale. aa: anterior ampulla; oof: otico-occipital fissure; popr: postorbital process; pstpr: post-otic process.

Fig. 8. Reconstitutions sous Imaris® des boîtes crâniennes (rendues translucides par l’outil « transparence ») et des moulages endocrâniens, en vue dorsale avec la région antérieure dirigée vers le haut, chez : A, *Notorynchus* (Maisey, 2004a) ; B, *Tribodus* (Lane, 2010b) ; C, *Egertonodus* (Lane, 2010b) ; D, *Cladodoides* (Maisey, 2005) ; E, “*Cobelodus*” (Maisey, 2007). Pas à l’échelle. aa : ampulla antérieure ; oof : fissure otico-occipitale ; popr : processus postorbitaire ; pstpr : processus post-otique.

seems to lie in a single plane). *Tristychius* may also possess a chondrified medial capsular wall, perilymphatic fenestrae and a glossopharyngeal canal, but its posterior semicircular canal was apparently not separated from the

rest of the labyrinth and did not make a complete circuit, and its anterior ampullae seem to have been located behind the level of the postorbital processes. Two additional apomorphic characters (separation of the utricular

and saccular regions, single connection of the posterior semicircular canal) unite neoselachians and hybodonts, but the arrangement is still unknown in *Acronemus* and *Tristychius*. One character apparently unites neoselachians and hybodonts but excludes *Acronemus* and *Tristychius* (out-of-plane orientation of the external semicircular canal). Collectively, these features strongly corroborate the hypothesis that hybodonts and neoselachians are closely related (Compagno, 1973; Lane, 2010a; Maisey, 1984; Maisey et al. 2004), and that *Acronemus* and *Tristychius* are allied to these forms although their relationships are still poorly resolved.

The lateral otic process may represent a synapomorphy of xenacanth and ctenacanth (which are also characterized by an extremely elongate occipital region), but its presence in iniopterygians is puzzling; possibly it was acquired independently, or it may have been primitively present in the common ancestors of crown-group chondrichthyans and subsequently lost in holocephalans, and either lost or modified in elasmobranchs (see Discussion below). This process is absent in neoselachians and extinct elasmobranchs inferred to have possessed a neoselachian-like non-otolithic phonoreceptor.

Exogenous sand grains are known in many extant elasmobranchs, but have not been reported in chimaeroids and are unknown in all the fossil chondrichthyans examined. However, similar grains have been reported in some acanthodians as well as outside the gnathostome crown-group (Sahney and Wilson, 2001). This distribution pattern suggests that open-ended endolymphatic ducts were primitively present in gnathostomes, but is uninformative about the evolution of LFSDP in elasmobranchs.

The endolymphatic fossa in extant elasmobranchs seems to include at least two morphological characters with differing phylogenetic distribution patterns. One of these (isolation of the endolymphatic fossa from the otico-occipital fissure) is phylogenetically widespread among chondrichthyans, including neoselachians, hybodonts, xenacanth, *Tamiobatis*, *Cladodoides*, and symmoriiforms, but the other (closure of the otico-occipital fissure) displays a more restricted distribution, being known at present only in neoselachians, hybodonts and holocephalans. In *Pucapampella* and *Doliodus*, the fissure is persistent and is connected to a posterior dorsal fontanelle as in some early osteichthyans, since a posterior tectum is absent. The only discernible difference between the posterior dorsal fontanelle of osteichthyans, *Doliodus* and *Pucapampella* on one hand and the endolymphatic fossa of other chondrichthyans on the other is absence or presence of a posterior tectum. Presence of the tectum seems to be correlated with wedging of the occipital arch between the otic capsules, which is also absent in *Doliodus*, *Pucapampella* and osteichthyans.

5. Discussion

The present list of 22 features of the otico-occipital region includes 16 previously published ones (Maisey, 2001a) (original numbers are given below in parentheses after each character, e.g., “M1”), plus four new charac-

ters (8, 20–22). One of the original characters (M29) has been reformulated as two characters here (3 & 5), and one further character (2) has been taken from another source (Schaeffer, 1981):

1. Exogenous sand grains present within endolymphatic ducts and sacculus (M28).
2. Hypotic lamina present below otic capsule.
3. Posterior tectum separates posterior dorsal fontanelle from otico-occipital fissure, forming endolymphatic fossa (M29 in part).
4. Occipital block wedged between otic capsules posteriorly (M33).
5. Otico-occipital fissure closed in adult (M29 in part).
6. Lateral otic process present (M31).
7. Extensive medial wall to otic capsule present (M23).
8. Endolymphatic fossa has chondrified floor.
9. Perilymphatic fenestrae present (M24).
10. Closure of embryonic metotic fissure, forming the glosso-pharyngeal canal (M30).
11. Isolation of the posterior semicircular canal from the other canals (M18).
12. Posterior semicircular canal describes an almost complete circuit (M19).
13. Separation of saccular and utricular regions (M20).
14. Posterior canal has only a single connection with the vestibular region (M21).
15. Anterior ampulla located between or in front of postorbital process (M32).
16. Out-of-plane orientation of external semicircular canal (M26).
17. Isolation and elaboration of the sensory crista neglecta (M22).
18. Crus distally between anterior and external (horizontal) semicircular canals (M25).
19. Anterior and external canals share a common opening into the vestibular region (M27).
20. Endolymphatic fossa small, houses paired ducts.
21. Lagenar chamber absent.
22. Post-otic process present.

In Fig. 9, crown-group elasmobranchs (neoselachians) are represented by *Notorynchus*, and crown-group holocephalans (chimaeroids) are represented by *Chimaera*. Holocephalimorphs are represented by extant chimaeroids plus iniopterygians, since details of the otic region are not available for the majority of extinct holocephalans. The characters have been plotted onto two alternative phylogenetic scenarios, which are based on recently published proposals that differ principally in how various Paleozoic chondrichthyans are related to the crown group (Coates and Sequeira, 2001; Ginter, 2005). In both scenarios, holocephalans are the sister to a group comprising extant elasmobranchs plus hybodonts, *Acronemus*, and *Tristychius*. In one (Fig. 9A), all cladodont and diplodont Paleozoic sharks fall outside the crown-group Chondrichthyes (Ginter, 2005); in the other (Fig. 9B), symmoriiform sharks are more closely related to holocephalans than to other cladodonts and diplodont chondrichthyans (Coates and Sequeira, 2001). According to both hypotheses, a group comprising all diplodont and cladodont chondrichthyans

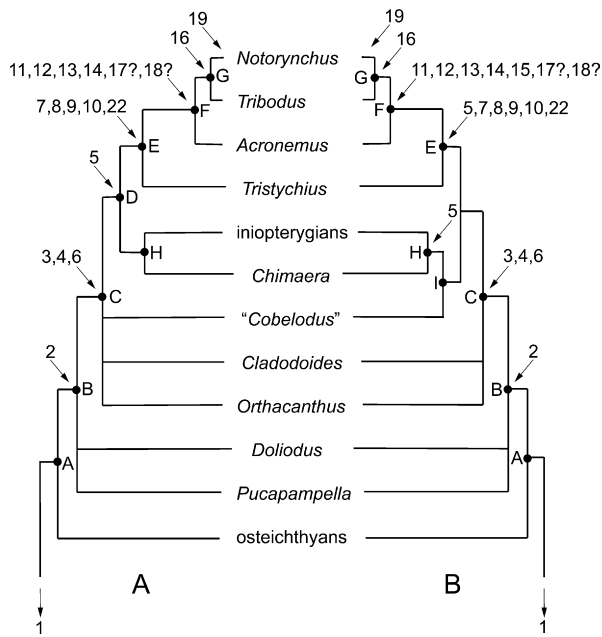


Fig. 9. Alternative scenarios of the evolution of characters associated with LFSDP in extant elasmobranchs. A. After Ginter (2005). B. After Coates and Sequeira (2001). Character numbers as listed in text. In both models, character 1 (sand grains; below node A) is plesiomorphic for gnathostomes, and character 2 (hypotic lamina) is most parsimoniously interpreted as primitively present in all chondrichthyans and lost in extant holocephalans. Node A (crown gnathostomes) is not supported by any of the apomorphic features discussed here. In model A (left), node D (crown chondrichthyans) is supported by character 5 (otico-occipital fissure closed) and node E is supported by characters 7–10 (medial capsular wall, endolymphatic fossa with chondrified floor, perilymphatic fenestrae, glossopharyngeal canal). In model B (right), character 5 shifts from node D and appears twice (at nodes E and H). Character 20 (small fossa containing endolymphatic ducts) in model B supports node I (“Cobelodus” plus holocephalans), whereas in model A the character appears independently in “Cobelodus” and holocephalans (node H). The position of characters 17–18 is speculative, as they are known only in extant elasmobranchs but are linked functionally with characters 11–15. Character 6 (lateral otic process) is a potential synapomorphy at node C and was perhaps independently lost in “Cobelodus” and chimaeroids because it may be present in iniopterygians. The process is either lost in “higher” elasmobranchs or possibly modified into a post-otic process (character 22) at node E. Character 19 (common opening of anterior and external canals) may be restricted to extant elasmobranchs (represented here by *Notorynchus*). Character 21 (absence of lagenar chamber) may be restricted to chimaeroids.

Fig. 9. Scénarios alternatifs de l'évolution des caractères associés à la LFSDP chez les élasmobranchés actuels. A. D'après Ginter (2005). B. D'après Coates et Sequeira (2001). Numérotation des caractères telle que dans le texte. Pour les deux hypothèses phylogénétiques, le caractère 1 (grains de sable; sous le nœud A) est plésiomorphe pour les gnathostomes, et le caractère 2 (lamine hypotique) est, selon le principe de parcimonie, interprété comme primitivement présent chez tous les chondrichthyens et perdu chez les holocéphales actuels. Le nœud A (crown-group gnathostomes) n'est supporté par aucun des caractères apomorphiques discutés ici. Selon l'hypothèse A (à gauche), le nœud D (crown-group chondrichthyens) est supporté par le caractère 5 (fissure otico-occipitale fermée) et le nœud E est supporté par les caractères 7–10 (mur capsulaire médian, fosse endolymphatique avec plancher chondrifié, fenêtre périlymphatique, canal glossopharyngien). Selon l'hypothèse B (à droite), le caractère 5 est déplacé du nœud D aux nœuds E et H. Selon l'hypothèse B, le caractère 20 (petite fosse contenant les conduits endolymphatiques) supporte le nœud I («Cobelodus» plus les holocéphales), alors que selon l'hypothèse A, ce caractère apparaît indépendamment chez «Cobelodus» et les holocéphales (nœud H). La position des caractères 17–18 est spéculative, car ils sont uniquement connus chez les élasmobranchés actuels

would be paraphyletic. According to the first hypothesis, cladodont chondrichthyans could be mono- or paraphyletic, but they are decidedly paraphyletic in the second. Importantly, in neither scenario do holocephalans represent the sister group to all shark-like chondrichthyans (including batoids, which would fall within neoselachians). In both hypotheses, the hypotic lamina was primitively present in basal chondrichthyans (node B, character 2) and has been lost secondarily in chimaeroids. The distribution of two characters is affected by the choice of scenario (closure of the otico-occipital fissure, character 5; small endolymphatic fossa, character 20). Character 5 is a synapomorphy of crown-group chondrichthyans in A, but appears twice in B (in elasmobranchs and in holocephalans). Character 20 is a synapomorphy of “Cobelodus” and holocephalans in B, but appears twice in A (in holocephalans and “Cobelodus”).

Thus, closure of the occipital fissure (character 5) is a potential synapomorphy of neoselachians, hybodonts and holocephalans that would exclude the majority of Paleozoic chondrichthyans from the crown-group Chondrichthyes. Interestingly, a similar phylogenetic pattern is suggested by tooth morphology (Ginter, 2005); neoselachians, holocephalans, hybodonts, protacrodontids, orodontiforms and eugeneodontiforms share a “euselachian-type” morphology, contrasting with a supposedly more primitive gestalt shared by xenacanthiforms, phoebodontiforms, ctenacanthiforms, and symmoriiforms. The “euselachian-type” tooth and closure of the otico-occipital fissure could therefore represent synapomorphies of a monophyletic group that includes crown-group chondrichthyans, whereas fossil chondrichthyans possessing “primitive-type” teeth (with interlocking basal plates, including forms with cladodont and diplodont teeth) and/or a persistent otico-occipital fissure would fall outside the group, as stem chondrichthyans. It is important to note that both of these phylogenetic scenarios are congruent with the evolution of a semi-directional non-otolithic macular phonoreceptor in chondrichthyans possessing a fused otico-occipital region. Unfortunately, no data are presently available concerning braincase morphology in protacrodontids and orodontiforms, very little is known about the braincase in eugeneodontiforms, and ontogenetic data are incomplete for extant chimaeroids. Although chimaeroids have only a small endolymphatic opening and the occipital arch is attached to the otic capsules even in the earliest stages so far described, it is still unknown whether the endolymphatic opening of chimaeroids becomes secondarily separated from the embryonic otico-occipital fissure by a posterior tectum as in extant elasmobranchs.

et fonctionnellement dépendants des caractères 11–15. Le caractère 6 (processus otique latéral) est une possible synapomorphie au nœud C et pourrait avoir été indépendamment perdu chez «Cobelodus» et chez les chiméroïdes, car il pourrait être présent chez les inioptérygiens. Ce processus est, soit perdu chez les élasmobranchés «dérivés», soit potentiellement modifié en un processus post-otique (caractère 22) au nœud E. Le caractère 19 (ouverture commune des canaux antérieur et externe) pourrait être restreint aux élasmobranchés actuels (représentés ici par *Notorynchus*). Le caractère 21 (absence de chambre pour la *lagna*) pourrait être restreint aux chiméroïdes.

Even if a simple phonoreceptor system was present in some extinct chondrichthyans with an unchondrified medial capsular wall and an unfloored endolymphatic fossa (e.g., *Cladodoides*, symmoriiforms, xenacanth), such a system is unlikely to have been directionally sensitive to the kinetic component of sound waves, which probably could not have been channeled across the macula neglecta in the absence of a well-defined pathway (since perilymphatic fenestrae and a posterior canal duct are apparently absent). Under these circumstances, it is unlikely that a neoselachian-like non-otolithic semi-directional phonoreceptor system was present in chondrichthyans with a persistent otico-occipital fissure. At the present time, no morphological features of the otic capsule have been recognized that might indicate the presence of a functional *otolithic* phonoreceptor in fossil chondrichthyans. Although it is conceivable that some early elasmobranchs were capable of detecting sound via the saccular macula alone, studies of extant elasmobranchs (Corwin, 1981a, 1981b, 1989) suggest that this would have been directionally ambiguous in the absence of a channeled non-otolithic component and therefore of little value in identifying and locating prey.

The findings presented here corroborate the hypothesis that the inner ear of extant elasmobranchs is highly derived toward LFSDP (Corwin, 1977, 1978, 1981a, 1981b, 1989; Maisey, 2001b) and add support to the proposal that morphological features associated with the evolution of a non-otolithic phonoreceptor are recognizable in fossils (Maisey, 2004b). Skeletal labyrinth morphology is strikingly similar in osteichthyans, extant chimaeroids and early chondrichthyans, suggesting that the elasmobranch non-otolithic phonoreceptor evolved from a primitive gnathostome gestalt in which the otic region resembled that found in extant osteichthyans (which have thus conserved the plesiomorphic gnathostome condition), and arose in the common ancestors of hybodonts and neoselachians after their divergence from the lineage leading to extant chimaeroids.

Supposed similarities in the skeletal labyrinth of placoderms and extant elasmobranchs (Stensiö, 1963) do not withstand critical examination in the light of new data concerning early chondrichthyans (Maisey, 2005). Importantly, no apomorphic features of the inner ear have been recognized in early chondrichthyans that would support a close relationship with placoderms. Some features of labyrinth morphology in placoderms could nevertheless represent independent specializations, in which case their distribution within the group may provide a new source of phylogenetically informative data. There is no evidence that the incertae sedis Devonian gnathostome *Ramirosuarezia* possessed any of the characters associated with LFSDP in extant elasmobranchs. It apparently also lacked certain crown-group gnathostome characters such as a posterior dorsal fontanelle and endolymphatic ducts, although it clearly possessed jaws associated with toothed plates and apparently possessed paired ceratohyals (Pradel et al., 2009b). Absence of an otico-occipital fissure in *Ramirosuarezia* is open to interpretation as either a primitive or a derived feature. If *Ramirosuarezia* is a chondrichthyan, it could be related to crown-group

chondrichthyans in model A, or to either crown-group elasmobranchs or holocephalans in model B. There is little in its cranial morphology to suggest a relationship with coeval, cladistically primitive chondrichthyans such as *Pucapampella* or *Doliodus*. The lateral otic process in *Tamiobatis* and xenacanth is probably not homologous with the neoselachian post-otic process (Maisey, 2005, 2007), unless it is supposed that the latter underwent considerable modification following obliteration of the metotic fissure and enclosure of the glossopharyngeal nerve. A post-otic process is nevertheless present in *Acronemus* and perhaps *Tristychius* (see earlier comments) and its absence in hybodonts could therefore be interpreted as a secondary loss, in which case its presence may represent a synapomorphy at node E (character 22).

Our analysis suggests that the suite of characters associated with low-frequency phonoreception in extant elasmobranchs was acquired progressively, some characters being more widely distributed among fossil chondrichthyans than others. While there are currently several competing phylogenetic hypotheses for chondrichthyans, the present findings suggest that LFSDP evolved only once, within a group of elasmobranchs whose otico-occipital fissure became secondarily closed during ontogeny. The fossil record provides several important clues suggesting that a fully developed non-otolithic semi-directional phonoreceptor like that found in extant elasmobranchs was present in only a few extinct chondrichthyans such as hybodonts and possibly *Acronemus*. However, some of the features associated with LFSDP in extant elasmobranchs apparently have a wider phylogenetic distribution than others, suggesting that certain components of the phonoreceptor system were superimposed upon others and that the system evolved progressively rather than all at once. For example, wedging of the occipital block between the otic capsules, the appearance of a posterior tectum separating the posterior dorsal fontanelle from the otico-occipital fissure, and closure of the fissure in the adult all seem to be important evolutionary precursors for the elasmobranch LFSDP system (perhaps by creating a more rigid otico-occipital region, especially adjacent to the posterior semicircular canal), although these features also occur in chondrichthyans lacking such a system (e.g., chimaeroids). The evolution of a chondrified floor to the endolymphatic fossa and of chondrified medial capsular walls in neoselachians and hybodonts undoubtedly further enhanced the rigidity of the otic region, and more importantly helped define the vestibular perilymphatic fenestrae and canals associated with a fully functional non-otolithic LFSDP system, enabling the channeling of kinetic sound waves along a well-defined pathway across a tympanic membrane and over the macula neglecta contained within the posterior canal duct. In this regard, *Tristychius* may represent an important transitional form in which vestibular fenestrae were apparently present although the posterior semicircular canal was not fully isolated (since a crus commune was supposedly present) (Dick, 1978), suggesting that a posterior canal duct was absent and that the macula neglecta was limited in its ability to provide semi-directional sensitivity to near-field displacement sound waves.

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