doi:10.1038/nature20806

Table of Contents

Part A. Supplementary Notes

1. Geological setting

The neurocranium of *Dwykaselachus oosthuizeni* Oelofsen (1986) (SAM - South African Museum - K5840) was preserved within a nodule of silicified radiolarian tests, collected from the base of the Prince Albert Formation (Ecca Group, Karoo Supergroup), about 300mm above the contact with the underlying glacial diamictites of the Dwyka Group (Karoo Supergroup (Oelofsen 1986). Zircon crystal dating of volcanic ash layers within the lower portion of the Prince Albert Formation has produced dates of 289.6 (+/- 3.0) mya and 288.0 (+/- 3.4) mya (Bangert *et al*. 1999) or alternately 273.7 ± 2.7 Ma (Mckay *et al*. 2015), indicating an Early Permian age (early Artinskian or latest Kungurian) for *Dwykaselachus*. Zircons within the latter study were selected from the youngest concordent zircon population which was interpreted as being co-eruptive, and therefore capable of yielding a more precise age.

The Dwyka and Ecca Groups comprise the two lowermost geological units of the Karoo Supergroup. They were deposited in an intracontinental retroarc foreland basin to the north of the Cape Fold Belt (Catuneanu 1998), resulting from crustal shortening induced by subduction of the palaeo-Pacific plate beneath the Gondwana plate (de Wit & Ransome 1992). The skull of *Dwykaselachus* was discovered in the southerly foredeep, the deepest part of the wedge-shaped basin, adjacent to the Cape Fold Belt mountains (Catuneanu *et al*., 2002). Paleolattitude for this part of the basin was between 50 and 70 degrees south (Smith *et al*. 1981).

During the initial deposition of the Dwyka and Ecca Groups, the Karoo Basin was transgressed by an interior seaway (Catuneanu *et al*. 2002) opening towards palaeo north (Visser 1994). Dwyka Group diamictites were deposited by melting oceanic ice sheets (Visser 1994) during the collapse of the middle

Carboniferous to early Permian south polar continental icecap (Catuneanu *et al.* 2002). Persistence of occasional dropstones into the lower 30 metres of the pelagic Prince Albert Formation sediments suggest persistence of icebergs derived from continental glaciers during the early deposition of this formation (Visser 1994, Cole 2005). The dark, fine grained, finely laminated shales of the lower Prince Albert Formation were derived from suspension settling of mud under anoxic bottom conditions (Visser 1994). Fossil evidence suggests that initially, at least in the southern parts of the basin, marine conditions predominated (Cole 2005). More cherty layers resulted from slow suspension fall out of siliceous skeletal material, perhaps during times of sediment starvation (Visser 1994). Intercalated carbonate nodule bearing layers suggest phases of reduced salinity (Herbert & Compton 2007) consistent with melt mediated salinity fluctuations reported by Sheffler *et al*. (2006). The preservation of *Dwykaselachus* within cherty radiolarian ooze is consistent with a phase of fully marine deposition.

2. Comparative anatomy

Institutional abbreviations

AM, Australian Museum, Sydney, Australia; **AMNH**, American Museum of Natural History, New York, USA; **BGS-GSE**, British Geological Survey – Geological Survey England, Keyworth, UK; **CMNH**, Carnegie Museum of Natural History, Pittsburgh, USA; **FMNH**, Field Museum of Natural History, Chicago, USA; **HM**, Hunterian Museum, University of Glasgow, UK; **HU MB**, Humboldt Museum, Berlin, Germany; **MHNAO**, Museo de Historia Natural Alcide d'Orbigny, Cochabamba, Bolivia; **NHM**, The Natural History Museum, London, UK; **NMS**, National Museum of Scotland, Edinburgh, UK; **OUZC**, Ohio University Zoology Collection, Athens; **SAM**, South African Museum, Cape Town, SA; **UALVP**, University of Alberta Laboratory of Vertebrate Palaeontology, Alberta; **UCL GM**, Grant Museum, University College London, UK; **UMCZ**, University Museum of Zoology, Cambridge, UK.

Morphological description

*Note on FMNH PF 13242 "*Cobelodus*",* Ozarcus mapesae*, and* Cobelodus aculeatus*.*

In the present analysis, *FMNH PF 13242* (Extended Data Fig. 2a, b) described by Maisey (2007) and cautiously attributed to *Cobelodus* (Zangerl & Case 1976) (Extended Data Fig. 2c), is interpreted as conspecific with *Ozarcus mapesae* (Pradel *et al.,* 2014) (Extended Data Fig. 2d, e).

FMNH PF 13242 is an isolated, three-dimensional, concretion-preserved braincase from the Fayetteville Shale of Arkansas. In many respects this specimen is closely comparable to *Dwykaselachus* (Extended Data Fig.2f, g). Other, likely symmoriiform braincases recovered from the same horizon and locality as FMNH PF 13242 include specimens OUZC 5300 – OUZC 5305, of which Maisey singled out OUZC 5300 because of its preserved articulation with jaws, gill arches and teeth (Maisey 2007, Figs. 33-

35). Recatalogued as AMNH FF 20544, this specimen was erected as the holotype of a new genus and species, *Ozarcus mapesae* by Pradel *et al*. (2014) (Extended Data Fig. 2d, e). Although Maisey (2007, p.60) originally recognized that OUZC 5300 (AMNH FF 20544, *Ozarcus*) and FMNH PF 13242 ("*Cobelodus*") could be the same taxon, Pradel *et al*. (2014, Supplementary Information) concluded that the two braincases represented different genera because of the smaller 'jugular canal relative to the (postorbital) arcade in *Ozarcus* as compared to "*Cobelodus*"'.

In addition to being derived from the same horizon and locality, these braincases are similarly sized, and in lateral view FMNH PF 13242 and AMNH FF 20544 map closely onto one another (Extended Data Figs 2a, d). Both show a characteristic projection dividing uncalcified spaces within the interorbital walls; in both the postorbital arcade (lateral commissure) curves smoothly towards the orbit floor (trabecular plate) without a prominent lateroventral prong; in both the otic region and occipital arch are similarly shaped and proportioned; the periotic process of FMNH PF 13242 maps onto an irregularity in the surface of the lateral otic ridge in AMNH FF 20544, and the dorsolateral extremity of the hypotic lamina in FMNH PF 13242 overlaps precisely with an identical feature in AMNH FF 20544; both specimens show the same concave profile in the lateral wall of the occipital cotylus.

A corresponding set of comparisons with *Cobelodus aculeatus* (Zangerl & Case 1976) is not possible because the vast majority of *C. aculeatus* crania are dorsoventrally flattened. Nevertheless, the ventral surfaces of all three can be compared, and all show the same 'wasp-waisted' parachordal plate with a distinct midline ridge, a deep 'U'-shaped notch in the floor of the occipital cotylus, and a postorbital arcade that is deflected posteriorly. But details of *Cobelodus aculeatus* differ from both *Ozarcus* and FMNH PF 13242: the basicranial fenestra of *C. aculeatus* is either absent (Zangerl & Case 1976) or positioned more anteriorly (Maisey 2007, Fig. 39: FMNH PF 7347), the periotic process is either absent (Zangerl & Case 1976) or positioned closer to the postorbital process and arcade (Maisey 2007, Fig. 39: FMNH PF 7347), and the supraorbital shelves are broad, like those of *Akmonistion* (Zangerl & Case 1976; Coates & Sequeira 1998; Maisey 2007) (Extended Data Fig. 2h).

For these reasons, we suggest that FMNH PF 13242 ("*Cobelodus*") (Extended Data Fig. 2a, b) is an incomplete *Ozarcus* braincase, with the anterior 50% of the orbit missing (Extended Data Fig. 2d, e). Therefore, in the following comparative description and analysis we combine data from FMNH PF 13242 and OUZC 5300/AMNH FF 20544 to serve as a single operational taxonomic unit.

Comparative morphology of Dwykaselachus

The *Dwykaselachus* (SAM K5840) braincase is preserved with minimal postmortem distortion and breakage (Oelofsen, 1986), and consists exclusively of thin sheets of tessellated calcified cartilage (Fig. 1; Extended Data Figs. 1, 3, 5-8), with no evidence of multiple layering or trabecular reinforcement. As far as possible, the present work uses terminology employed in Maisey's (2007) description of FMNH PF 13242. Other

comparable braincases include *Akmonistion* (Coates & Sequeira 1998), *Denaea* (Williams 1985, Maisey 2008b), *Symmorium* (Williams 1985), *Kawichthys* (Pradel *et al.* 2011), and *Ozarcus* (Pradel *et al*. 2014). The *Dwykaselachus* braincase is almost 125mm in total length (Oelofsen 1986). Skeletal proportions from the similarly sized *Symmorium reniform*, near-complete skeletal remains of which are preserved in FMNH PF 2202, suggest that the total length of the *Dwykaselachus* individual may have been nearly 1.5m.

Ethmoid region. The ethmoid region has a broad, gently convex anterior margin (cf. Oelofsen 1986), and includes a pair of almost complete nasal capsules (Extended Data Fig.3). There is no clear evidence of a precerebral fontanelle, and the area reconstructed as such by Oelofsen (1986) is a wedge-shaped space between the anterior walls of the nasal capsules, which is seperated from the cranial cavity and was probably filled with cartilage in life (Extended Data Fig. 3a). In FMNH PF 13242 (Maisey 2007) the ethmoid region appears to be missing, whereas in *Cobelodus aculeatus* (Zangerl & Case 1976 fig.3; Maisey 2007 Figs. 39, 48) the reconstructed precerebral fontanelle occupies the same position as the pre-nasal space in *Dwykaselachus*. In *Akmonistion* the precerebral fontanelle is unknown (Coates & Sequeira 1998 *contra* Maisey 2007, Fig. 50). Thus far, *Falcatus* (Lund 1985 Fig. 9A, 10B, Maisey 2007 Fig. 56A) provides the best evidence for a precerebral fontanelle in a symmoriiform, but in this fish the posterior rim of the fontanelle lies dorsal to the anterior part of the orbit and posterior to the nasal capsules. This kind of fontanelle is evidently absent in *Dwykaselachus*.

In agreement with Oelofsen (1986), the anterior rim of the *Dwykaselachus* snout bears a smooth internasal groove joining left and right nasal capsules (Extended Data Fig. 3d, f) resembling the internasal groove of sibyrhynchids (Pradel 2010). In lateral view the internasal plate is angled antero-dorsally, also comparable to the palatal crests of sibyrhynchids (Pradel 2010, Fig. 16). There is no ventral ethmoid keel.

The nasal capsules are large, and abut one another at the midline (Extended Data Fig. 3a, b). The enclosed capsule space is greater than hemispherical, and probably contained most of the olfactory organ. The main opening, directed anterolaterally and slightly dorsally, probably admitted incurrent and excurrent ducts. The capsule rear extends into a wide olfactory nerve canal, and the left and right canals unite into an olfactory trunk directly behind the capsular walls. The capsule floor, anterior and medial to the olfactory canal, includes an opening for a branch of the profundus nerve. Anterior and lateral to the profundal foramen, a narrow, ventrolaterally directed channel connects the capsule chamber to a subtriangular, subnasal space (Extended Data Figs 3c, d, 5a). This subnasal space might have been cartilage-filled in life, buttressing the anterior wall of the orbit. However, the communicating duct suggests the presence of a subnasal chamber, opening ventrally into the pre-oral cavity. Oelofsen (1986) identified these spaces as ventral openings for each nasal capsule. Williams (1985, Text-Fig. 6B; see also Maisey 2007 Fig. 49C) identified similar structures in *Denaea* as nostrils. We doubt that these openings housed nostrils, but note the complexity of

certain extant chondrichthyan olfactory organs (Howard *et al*. 2013), in which supplementary ducts augment function and regulate odorant molecule flow over sensory epithelia.

Orbit and interorbital walls. The large orbits are almost twice the length of the otic region (Fig. 1, Extended Data Fig. 5a). The flattened supraorbital shelf on left and right sides probably results from postmortem compression (Oelofsen 1986). The locations of cranial nerve foramina and the optic pedicel resemble those of FMNH PF 13242, except that in *Dwykaselachus* these features are clustered in the posterior third of the orbit (Extended Data Figs 5a, 6b). Like *Ozarcus*/FMNH PF 13242, *Dwykaselachus* has a septum-like interorbital wall (Extended Data Figs. 3e, 7) anterior to the large opening for the optic nerve. In *Ozarcus*/FMNH PF 13242 (Maisey 2007) this region is identified as the internasal plate, but in *Dwykaselachus* the interorbital septum is shown to be mid-orbit level, posterior to the orbital articulation for the palatoquadrate. Presence of such an interorbital septum resembles chimaeroid conditions, but, in agreement with Maisey (2007), because the septum is ventral to the forebrain space (rather than dorsal) it represents a tropibasic neurocranial morphotype, unlike platybasic adult chimaeroids. Left and right orbits are interconnected by broad openings anteriorly (Extended Data Figs. 5a, 7) and posteriorly; the posterior recess resembles the posterior myodome of actinopterygians (Patterson 1975). The calcified walls of both interorbital openings indicate that these are not preservational artefacts.

The anterior wall of the orbit, the orbitonasal lamina, is unusually broad (Fig. 1; Extended Data Figs. 3e, 5b). The antorbital foramen lies at the junction of the orbitonasal lamina with the medial wall of the orbit. A broad groove connects this foramen with the superficial ophthalmic foramen in the posterior wall of the orbit (Extended Data Fig. 6a, b). Unlike *Orthacanthus* (Shaeffer 1981) and *Cladodoides* (Maisey 2005), both of which preserve similarly grooved paths for the superficial ophthalmic nerves, in *Dwykaselachus* the superficial ophthalmic trunk feeds directly into an intracranial space between the nasal capsules above the channel for the olfactory tracts. However, there is no evidence of a cartilage floor, or any trace of an enclosed ethmoid canal (cf. chimaeroids: Didier 1995). Notably, de Beer and Moy-Thomas (1935) and de Beer (1937) argue that the chimaeroid ethmoid canal is not part of, or derived from, the cranial cavity *sensu stricto* because it lies outside the 'dura mater'. They provide an explanatory scenario, in which an extracranial space is enclosed by the orbitonasal lamina rising in height to match the increased size of the orbit in chimaeroid fishes. Holmgren (1942) offers a different scenario, in which the ethmoid canal is interpreted as endocranial space separated by the formation of an interorbital septum. Patterson's (1965) review of chimaeroid phylogeny is undecided between these alternative interpretations. Evidence from *Dwykaselachus* might slightly favour Holmgren's (1942) interpretation, but further work is needed on the crania of 'classic' early holocephalans such as *Helodus* and *Deltoptychius*. At present, the convergent paths of the superficial ophthalmic trunks in *Dwykaselachus* and chimaeroids (Extended Data Fig. 9) might be homologous, but important details of phylogenetic origin of the chimaeroid ethmoid canal remain unresolved.

Supraorbital shelf. The lateral margins of the broad supraorbital shelf (Fig. 1; Extended Data Figs 5b, 6a, b), are poorly preserved where it thins out towards the orbital rim. The dorsalmost section was probably arched in life, continuing the smooth curvature of the postorbital rim. Dorsally, the supraorbital shelves show linear arrays of foramina marking exits for twigs of the superficial ophthalmic trunk that supplied the supraorbital sensory canal.

Suborbital shelf. Like that of *Akmonistion* (Coates & Sequeira 1998) and *Ozarcus* (Pradel *et al*. 2014) the suborbital shelf (trabecular plate) of *Dwykaselachus* is narrow and parallel sided (Fig. 1; Extended Data Fig. 5b). In all three genera the ventrolaterally expanded and ridged, orbital (palatobasal) articulation for the palatoquadrate, lies far to the anterior. Extended Data Figures 3d and 5b show the structure clearly in *Dwykaselachus*, and its relation to the nasal capsules. *Cladodoides* (Maisey 2005) displays a constrasting and perhaps plesiomorphic condition where the articular flange extends below the optic nerve foramen and anterior to the notch and groove for the efferent pseudobranchial artery. Maisey (2007) interprets the position of this articular region in FMNH PF 13242 as similar to the *Cladodoides* condition. In *Dwykaselachus*, the groove for the efferent pseudobranchial artery is faint, and there is no notch for the passage of the artery around the lateral margin of the suborbital shelf. Likewise, there is no opening in the dorsal surface of the shelf for the internal carotid artery.

Postorbital arcade. Like *Cobelodus* and FMNH PF 13242, the *Dwykaselachus* postorbital arcade (Extended Data Fig. 6a, b) joins the suborbital shelf, rather than the ventrolateral wall of the otic capsule (cf. Maisey 2007). As in *Cobelodus*, *Akmonistion* and other symmoriids, the postorbital arcade is large, wide, and anteroposteriorly slender. The near-circular jugular opening in *Dwykaselachus* (Extended Data Fig. 6b) is smaller than that of FMNH PF 13242. The rim of the opening extends from the anterior border of the trigeminal nerve foramen, and terminates ventrally just anterior to the facial nerve foramen. Thus both nerve foramina lie behind the level of the arcade and there is no trigeminofacial recess. Comparison with the dorsoventrally flattened specimens of *Akmonistion* suggests that these parts of the cranium are reasonably similar: the actual area in which such a recess might have been present is not well preserved, and at least some of the pocket-like features identified as such (especially those in Coates & Sequeira Fig.3) are edges of a similarly sized jugular foramen.

In ventral view the laterally extending edge of the arcade resembles that of *Akmonistion* (Extended Data Fig. 2h). In both taxa the articular surface for the palatoquadrate is located posteriorly, medial to thickened lateral rim of the arcade (Extended Data Fig. 6c, d). In lateral view, the arcade rim forms a sweeping, crescent-shaped prong (Fig. 1), the ventral extremity of which is grooved and pierced for the exit

of a mandibular branch of the trigeminal nerve. The posterior articular surface consists of a tall, slightly dorsomedially sloping groove, extending from the ventral prong to the level of the periotic process.

Basicranium and arterial supply to the head. The basicranium of *Dwykaselachus* has a simple cruciform outline (Fig. 1; Extended Data Fig. 2g), much like *Akmonistion* (Extended Data Fig. 2h). Where the postorbital arcade meets the rear of the suborbital shelf, the basicranium shows a groove for the orbital artery. The basicranial fenestra is situated level with these in the ventral midline. Directly posterior to the postorbital arcade, the base of the otic region is waisted, but the hypotic lamina flares laterally, extending as a nearly horizontal plate beneath the otic capsules (Extended Data Figs 6c, d, 8b), a condition markedly unlike the FMNH PF 13242 hypotic lamina that curves dorsolaterally to join the otic capsular wall.

The cranial arterial supply was mostly embedded within the basicranial cartilage (Fig. 1; Extended Data Fig. 5a). The median dorsal aorta is marked by a midline foramen in the rear of the chordal plate (Extended Data Figs. 6c, d, 8b). This passes anteriorly as an enclosed canal for a short distance (Extended Data Fig. 7), but calcified remains cease before its divergence into the lateral dorsal aortae. The entrance of the efferent hyoid artery is marked by a prominent foramen that is dirceted laterally and slightly posteriorly. This matches a similarly directed foramen in *Akmonistion* (Coates & Sequeira 1998; re-identified by Maisey 2007 as the foramen for the lateral dorsal aorta, although this appears unlikely because of the opening orientation). The basicranial fenestra (Extended Data Fig. 5a) shows no foramina or associated grooves. Consequently, the arrangement of the blood supply to the head via the internal carotids, if present, and the efferent pseudobranchial artery, is largely unknown (as in FMNH PF 13242, Maisey 2007). The small foramen with posterolateral groove situated between the orbital artery opening and the foramen for the efferent hyoid might provide an exit for a palatal branch of the facial nerve. The location relative to other openings resembles conditions in *Cladodoides* (Maisey 2005).

Otic region. Prominent ridges of the otic wall and roof overlie the semicircular canals, and define the boundaries of major fossae (Extended Data Fig. 5b). Some areas of the otic wall are weakly calcified and missing, especially the covering of the ampulla of the posterior semicircular canal, ventral to the lateral otic ridge (Extended Data Figs 5a, 6d). This region is unfinished on both sides of the braincase, and in both instances calcified cartilage edges project laterally but not ventrally. As such, *Dwykaselachus* is unlikely to have possessed a ventral otic process similar to that of *Kawichthys* (Pradel *et al*. 2011). Additionally, there is no lateral otic process like those of *Tamiobatis* (Williams 1998) or *Akmonistion* (Coates & Sequeira 1998).

A large periotic process projects dorsolaterally from the anterior part of the lateral otic ridge, cf. FMNH PF 13242 (Maisey 2007) (Extended Data Figs 5, 6c, d). The robust process is incomplete distally, but sufficiently calcified to show that it was forked in life. The otic roof slopes dorsally and medially towards the central, chimney-like opening of the endolymphatic ducts at the apex of the median otic ridge. The full dorsal

extent of the walls of this opening is unknown; the distal profile is truncated by damage to the external surface of the nodule. The endolymphatic duct opening is closed posteriorly and separated from the otico-occipital fissure by a calcified posterior tectum bearing a low median crest (Extended Data Figs. 5b, 7).

Occipital region. The occipital unit of *Dwykaselachus* (Extended Data Figs 6c, d, 8a, b) encloses a foramen magnum and notochordal canal of similar widths, and a narrower dorsal aortic canal. As in FMNH PF 13242, the notorchordal canal rim bears dorsal and ventral paroccipital processes, and foramen magnum is situated dorsal to the level of the glossopharyngeal nerve exit (Maisey 2007). In posterior view, the occipital plate presents a near-rectangular outline, somewhat wider than that of FMNH PF 13242. *Dwykaselachus* is further distinguished by the presence of a tall, paired occipital crest, the height of which reaches the height of the dorsal otic ridge (Extended Data Fig. 8a, b). Each half of the crest extends anterodorsally from the apex of the foramen magnum (the right side is complete; the left side mostly missing), overlaps a low median crest on the posterior tectum, and follows the rear wall of the posterior dorsal fontanelle.

In lateral view (Fig. 1) the persistent otico-occipital fissure separating the occipital arch from the otic capsule (Extended Data Fig. 5a) is narrower than that of FMNH PF 13242. The suprachordal occipital plate fits closely around, but not between, the walls of the posterior semicircular canals (Extended Data Fig. 6d, 8a). However, the ventral, parachordal component of the occipital arch intrudes between the saccular chambers; in *Dwykaselachus* slightly more deeply than in FMNH PF 13242. Correspondingly, in FMNH PF 13242 two spino-occipital foramina are visible in lateral view, but in *Dwykaselachus* only one such foramen is visible. However, an intra-cranial perspective (Extended Data Fig. 7) shows that in both genera five canals for spino-occipital nerves perforate the ventrolateral wall of the foramen magnum. The short notochordal canal extends anteriorly only as far as the anterior rim of the occipital arch, level with the anteriormost spino-occipital nerve canal.

Cranial endocast including otic labyrinth.

Short olfactory nerve canals unite in the midline just posterior to the nasal capsules, and a long central space for the olfactory tracts and telencephalon passes between the orbits to join the mesencephalon cavity (Extended Data Fig. 4). No swelling or other marker clearly indicates the boundary between the olfactory tracts and the olfactory lobes/telencephalon. The floor of this region is at mid-orbit height, formed by the dorsal surface of the interorbital wall. The superficial ophthalmic nerves entered the endocranial space just above the union of olfactory nerve canals, with the trajectory of the superficial ophthalmic nerves directed towards the midline region, medial to the nasal capsules (Extended Data Figs 3c; 4a).

The large hypophyseal space is isolated from the roof of the mouth (Extended Data Fig. 7). Unlike FMNH PF 13242, in *Dwykaselachus* the anterior wall of the compartment is complete and the narrower, posterior part is overarched by the accentuated dorsum sellae (Goodrich 1930, de Beer 1937) (Extended Data

Fig. 7). The elevated mid-region of the endocranium (and mid-region of the brain) correlates with the exaggerated height of the dorsum sellae (de Beer 1937, Maisey 2007), the large diameter of the orbit, and height of the interorbital wall. Consequently, the anterior part of the roof of the cavity enclosing midbrain narrows and descends markedly at the junction with the telencephalon chamber (Extended Data Fig. 9a). Correspondingly, the roof of the cerebellar and vestibulolateral chamber is somewhat higher than the level of the otic labyrinth (Extended Data Figs 4b, 7) and medullary region, matching conditions in FMNH PF 13242 and chimaeroids, but quite unlike modern elasmobranchs and early chondrichthyans such as *Cladodoides* (Maisey 2005) and *Orthacanthus* (Schaeffer 1981).

Posteriorly, the hindbrain (medullary) chamber and otic labyrinth appear to be canted backwards, again resembling FMNH PF 13242 and modern chimaeroids. The vestibular or labyrinth space is continuous with the cranial cavity: there is no medial wall to the otic capsule (Extended Data Fig. 7). Outgroup comparisons with *Cladodoides* (Maisey 2005) and other early gnathostomes (Davis *et al*. 2012) indicate that this is the primitive condition. The crus commune space is confluent with the dorsolateral part of the medullary region. Medial to the crus, the endocast is raised into an elaborate chimney-like endolymphatic duct canal (Extended Data Fig. 4), taller than that of FMNH PF 13242 and modern chimaeroid examples. The anterior wall of this laterally narrow, midline space, is perforated by a circular foramen, communicating with the rear of the cerebellar chamber. The anterior semicircular canals hug the posterolateral boundary of the vestibulolateral space, and converge on the posterior of the base of the infilling of the endolymphatic ducts.

The small-radius external (horizontal) semicircular canal fits comfortably within the span of anterior and posterior canals (Extended Data Fig. 4a). The distinctive, inclined angle of the external canal is shared with those of FMNH PF 13242 and chimaeroids (Maisey 2007): a straight line projected through the canal intersects the anterior ampullae, but posteriorly passes below foramen magnum. External and anterior ampullae meet the utricular space independently; all three form well-defined bulges in the lateral wall of the vestibular chamber. In *Dwykaselachus* the posterior ampulla is separated more distinctly from the vestibular chamber than that of FMNH PF 13242, but there is no trace of pre-ampullary canal.

Part B. Morphometric and Phylogenetic Analysis

1. List of taxa

Acanthodes: Benznosov 2009; Coates 1994; Davis *et al.* 2012; Heidtke 1993; Jarvik 1977, 1980; Miles 1968, 1973a, b; Nelson 1968; specimens AMNH 1037b, 10370, 10376, 19628; CMNH 30725b, 30726, 4591; FMNH PF2875; GM C145, 146, 180; HM V8251, 252; HU MB.F.4209, 4277, 4284, 4285, 7286, MB3b, 4a & b, 5a & b, 7a & b, 8a & b, 11a & b, 12a, 13a &b, 14a &b, 16a &b, 17a & b, 18a & b, 23 (resin copy), 24, MM L1693, 1698, 9432B, W1994; NHM P.11287, P.13139, 13140, 14558, 1728, 34912, 34914, 4057, 49941, 49944, 49959, 49967, 49979, 49980, 49990, 49995,

49996, 60928, 60939, 62138, 7335; NMS 2001.7.1, 3; UCL GM C1126; UMZC GN9, 11, 13, 14, 15a &b, 16, 39, 756.

Akmonistion: Coates & Sequiera 1998, 2001a,b; Coates *et al.* 1998.

Brochoadmones: Bernacsek & Dineley 1977; Gagnier & Wilson 1996b; Hanke & Wilson 2006; specimens UALVP 32672, 41487, 41493, 41494, 41495.

Callorhinchus/Hydrolagus: Cole 1896; De Beer 1937; De Beer & Moy-Thomas 1935; Didier 1995; Didier *et al*. 1994, 1998, 2012; Howard *et al*. 2013; Kesteven 1937; Patterson 1965, 1992; Pradel *et al*. 2008; Stahl 1999.

Chondrenchelys: Finarelli & Coates 2012, 2014; Lund 1982; Moythomas 1935; specimens NMS 1885.54.5/5A, 1891.53.33, 1998.35.1, 2002.68.1; BGS-GSE 13328; HM V.7173.

Cladodoides: Gross 1937, 1938; Maisey 2005.

Cladoselache: Bendix-Almgreen 1975; Harris 1938a, b; Maisey 1989a, 2007; Schaeffer 1981; Woodward & White 1938; specimens CMNH 8110, 8111, 8207, NHM P9273, P9285.

Cobelodus: Zangerl & Case 1976.

Cowralepis: Carr *et al*. 2009; Ritchie 2005; Long *et al.* 2009.

Debeerius: Grogan & Lund 2000: specimens CM 35479, 35480, 48831, 62811.

Denaea: Maisey 2008b; Williams 1985.

Dicksonosteus: Goujet 1975, 1984.

Doliodus: Miller *et al.* 2003; Maisey *et al.* 2009, 2013.

Dwykaselachus: Oelofsen 1986: specimen SAM K5840 (Oosthuizen No. G50).

Egertonodus: Maisey 1982, 1983; Lane 2010.

Entelognathus: Zhu *et al*. 2013.

Falcatus: Lund 1985; Maisey 2007.

Gladbachus: Heidtke & Krätschmer 2001; Heidtke 2009; Burrow & Turner 2003, 2013.

Guiyu: Zhu *et al*. 2009.

Hamiltonichthys: Maisey 1989b.

Helodus: Patterson 1965; Stahl 1999; specimens NHM P.6706, 8207, 8209, 8212, 8213.

Iniopera: Zangerl & Case 1973; Pradel *et al*. 2009b, 2011; Pradel 2010; Pradel *et al*. 2010.

Janusiscus: Giles *et al*. 2015.

Kathemacanthus: Gagnier & Wilson 1996a; Hanke & Wilson 2010; specimens UALVP 32402, 42269, 43113.

Kawichthys: Pradel *et al*. 2011.

Lebachacanthus: Heidtke 1982, 1999.

Ligulalepis: Basden *et al*. 2000; Basden & Young 2001; specimen AM F101607.

Mimipiscis: Gardiner & Bartram 1977; Gardiner 1984; Choo 2011; Giles & Friedman 2014.

Onychoselache: Dick & Maisey 1980; Coates & Gess 2007.

Orthacanthus: Hiedtke 1982; Hotton 1952; Schaeffer 1981; Maisey 1983.

Ozarcus and FMNH PF 13242: Maisey 2007; Pradel *et al.* 2014.

Psarolepis: Yu 1998; Zhu & Schultze 1997; Zhu *et al.* 1999; Qu *et al.* 2013a.

Ptomacanthus: Brazeau 2009; Denison 1979; Miles 1973a; specimens NHM P.19999, 24919b.

Pucapampella: Maisey 2001a; Maisey & Anderson 2001; Maisey & Lane 2010; Janvier & Maisey 2010.

Ramirosuarezia: *Pradel et al.* 2009a; uncatalogued peel of MHNAO 1313 provided by Phillipe Janvier to MIC.

Squalus: Schaeffer 1981; Gans & Parsons 1964; Marinelli & Strenger 1959.

Synechodus: Maisey 1985; NHM P.6135, 41675.

Tamiobatis: Schaeffer 1981; Williams 1998.

Tribodus: Lane 2010.

Triodus: Soler-Gijon & Hampe 1998; Heidtke *et al*. 2004.

Tristychius: Dick 1978; Coates & Gess 2007; specimens NMS 1972.27.455A, 1974.51.5A; HM V8299.

Wapitiodus: Mutter *et al*. 2007.

2. Morphometric data

Supplementary Table 1: Orbital length, otic capsule length and basicranial length for holocephalan and non-holocephalan taxa. The natural log of orbital and otic length, normalized to the basicranial length of the skull, has been calculated as a measure of the relative size of these regions of the skull. See Main Text Figure 3.

Taxon	Group	Orb	Oti	BCL	Ln[Orbit/BCL]	Ln[Otic/BCL]
Ligulalepis	Non-holocephalan	4.6	4.6	12.5	-1.000	-1.000
Mimipiscis	Non-holocephalan	6.7	5.1	15.5	-0.839	-1.112
Psarolepis	Non-holocephalan	3.9	6.4	19.1	-1.589	-1.093
Dicksonosteus	Non-holocephalan	6.0	9.8	27.8	-1.533	-1.043
Pucapampella	Non-holocephalan	15.0	18.0	41.0	-1.006	-0.823
Acanthodes	Non-holocephalan	15.0	16.0	44.0	-1.076	-1.012
Synechodus	Non-holocephalan	14.6	23.1	58.5	-1.388	-0.929
Squalus	Non-holocephalan	26.0	26.0	59.0	-0.819	-0.819
Doliodus	Non-holocephalan	22.0	26.0	74.0	-1.213	-1.046
Egertonodus	Non-holocephalan	38.0	36.0	112.0	-1.081	-1.135
Gladbachus	Non-holocephalan	31.0	43.0	112.0	-1.285	-0.957
Tristychius	Non-holocephalan	41.0	44.0	142.0	-1.242	-1.172
Cladodoides	Non-holocephalan	22.0	23.0	62.0	-1.036	-0.992
Orthacanthus	Non-holocephalan	56.0	85.0	236.0	-1.438	-1.021

Tamiobatis	Non-holocephalan	95.0	112.0	297.0	-1.140	-0.975
Tribodus	Non-holocephalan	30.0	39.5	89.0	-1.087	-0.812
Triodus	Non-holocephalan	24.0	37.0	69.0	-1.056	-0.623
Lebachacanthus	Non-holocephalan	45.0	57.5	130.0	-1.061	-0.816
Wapitiodus	Non-holocephalan	28.0	30.7	67.0	-0.872	-0.780
Callorhinchus adult	Holocephalan	29.0	20.0	100.0	-1.238	-1.609
Callorhinchus 'late embryo'	Holocephalan	8.0	5.5	21.0	-0.965	-1.340
Callorhinchus pre-hatchling	Holocephalan	4.5	3.5	12.5	-1.022	-1.273
Callorhinchus stage 31+	Holocephalan	2.5	2.0	5.0	-0.693	-0.916
Chondrenchelys	Holocephalan	6.0	3.4	15.0	-0.916	-1.484
Kawichthys	Holocephalan	11.3	7.5	19.0	-0.520	-0.930
Iniopera	Holocephalan	11.0	8.2	25.4	-0.837	-1.131
Cobelodus	Holocephalan	31.0	19.0	60.0	-0.660	-1.150
Ozarcus	Holocephalan	43.0	23.0	76.0	-0.570	-1.195
Akmonistion	Holocephalan	33.0	24.0	79.0	-0.873	-1.191
Cladoselache	Holocephalan	46.0	35.0	110.0	-0.872	-1.145
Dwykaselachus	Holocephalan	62.0	39.0	124.0	-0.693	-1.157
Falcatus	Holocephalan	10.0	8.0	22.0	-0.788	-1.012
Denaea	Holocephalan	14.0	13.0	30.0	-0.762	-0.836

Supplementary Table 2: Median percentages for the length of the orbit relative to BCL, the length of the otic capsule relative to BCL and the length of the orbit relative to the otic capsule for the holocephalan and non-holocephalan samples. Holocephalan taxa have significantly larger orbits than non-holocephalan taxa, whereas non-holocephalans have larger otic regions. The contrast in the size of the two regions relative to each other is striking across the groups.

	Median % Orbit vs. BCL	**Median % Otic capsule vs. BCL**	**Median % Orbit vs. Otic capsule**
Holocephalans	44.4%	31.6%	141.3%
Non-holocephalans	33.9%	37.1%	84.6%

3. Character list

The character list is developed primarily from sets assembled by Coates and Sequeira (1998, 2001a,b), Brazeau (2009), Pradel *et al*. (2011), Davis *et al*. (2012), and Zhu *et al.* (2013). Other material has been incorporated from classic studies by Patterson (1965), Schaeffer (1981); Maisey (1984); Didier 1994; and Stahl 1999.

Skeletal Tissues

1. **Tessellate calcified cartilage: absent (0); present (1).** Presence of the tessellate condition includes irregularly shaped and widely spaced tiles, near-hexagonal tiles with abutting intertesseral joints, and tesserae concealed beneath an outer sheet of continuously calcified cartilage. Tessellated calcified endoskeletal cartilage (Dean & Summers 2006; Dean *et al*. 2009; Maisey 2013) is unique to fossil and living shark-like fishes, has long been used as a chondrichthyan synapomorphy (Maisey 1984; Lund & Grogan 1997, 2004a,b; Coates & Sequeira 2001a,b; Maisey 2001; Brazeau 2009; Davis et al. 2012; Grogan *et al*. 2012; Pradel *et al.* 2014).
2. **Multilayered tesserae in the outer wall of the neurocranium: absent (0); present (1).** Pradel *et al.* (2011). Present in *Tamiobatis*, *Orthacanthus* (Pradel *et al.* 2011; Schaeffer 1981) and *Akmonistion* although not figured as such (Coates & Sequeira 1998). Specimens of *Tristychius* show limited areas of layered tesserae (pers. obs. MIC), but these might be the inner and outer calcified rinds of collapsed cartilage. Schaeffer (1981) codes multilayered tesserae as present in *Cladodoides*, but Maisey (2005) states that this condition is absent.
3. **Perichondral bone: present (0); absent (1).** Janvier (1996); Donoghue & Aldridge (2001); Brazeau (2009); Davis *et al.* (2012).
4. **Extensive endochondral ossification: absent (0); present (1).** Forey (1980); Gardiner (1984); Brazeau (2009); Davis *et al.* (2012).
5. **Dentine kind: mesodentine or semidentine (0); orthodentine (1).** Donoghue *et al*. (2000); Brazeau (2009); Davis *et al.* (2012).
6. **Cosmine: absent (0); present (1).** Cloutier & Ahlberg (1996); Janvier (1996); Brazeau (2009); Davis *et al.* (2012).
7. **Acrodin tooth caps: absent (0); present (1).** Adapted from Zhu *et al.* (2013, 2009), Friedman & Brazeau (2010).

Dermal Skeleton: scales and fins

8. **Lepidotrichia or lepidotrichia-like scale alignment: present (0); absent (1).** Davis *et al.* (2012).
9. **Trunk scales monocuspid (0); multicuspid (1).** Revised after Davis *et al.* (2012). It has long been accepted that some Palaeozoic chondrichthyan scales show evidence of sustained growth (Nelson 1970, Zangerl 1981, Reif 1985), indicating that the non-growing condition is the derived state, and is possibly a synapomorphy uniting crown chondrichthyans. Morphological evidence of sustained, incremental growth can include presence of a variably multicuspid crown (state '1': see *Kathemacanthus* or *Tamiobatis*) versus a monocuspid crown (state '0': see *Hamiltonichthys*).
10. **Scale growth concentric: absent (0); present (1).** Hanke & Wilson (2004); Brazeau (2009); Davis *et al.* (2012).
11. **Body scales with peg-and-socket articulation: absent (0); present (1).** Gardiner (1984); Coates (1999); Brazeau (2009); Davis *et al.* (2012).
12. **Body scales with convex base: absent (0); present (1).** Brazeau (2009); Davis *et al.* (2012). A convex scale base is present in numerous acanthodian-grade and placoderm-grade fishes, and in most instances presence indicates lamellar structure and sustained scale growth (cf. discussions in Nelson 1970 and Reif 1985).
13. **Body scales with flat base: absent (0); present (1).** Brazeau (2009) ; Davis *et al.* (2012).
14. **Body scales with basal canal or open basal vascular cavity: absent (0); present (1).** Chondrichthyan placoid scales are distinguished, in part, by the presence of a basal canal (Reif 1978). Early chondrichthyan scales that depart from the standard placoid morphology also exhibit basal canals, e.g. *Akmonistion* (Coates & Sequeira 2001a, fig. 12E) and *Antarctilamna* (Young 1982, p.830). However, the scales of *Gladbachus* and most taxa traditionally classified as acanthodians (Denison 1979) lack basal canals, including the decidedly chondrichthyan-like genus *Brochoadmones* (Hanke and Wilson 2006, fig.8).
15. **Neck canal: absent (0) present (1).** Maisey (1984); Lund & Grogan (1997). Although considered a classic feature of placoid scales, the presence of a neck canal is more widespread among early vertebrates. Data on scales attributable to placoderm bodies are sparse (Burrow & Turner 1998, 1999), and acanthodians are not as well documented as might be expected. Osteichthyan scores are in part from Qu *et al*. (2013a, b). Chondrichthyan scores are from specimens and published descriptions, with notable exceptions of *Cladoselach*e, pers. obs. MIC from specimen CMNH 8207, and *Chondrenchelys* (redescribed by Finarelli & Coates 2014) in which canals are observable at the margins of the scale crown and base.
16. **Sensory line canal perforates scales (0); passes between scales (1); scales C-shaped (2).** Davis (2002); Friedman & Brazeau (2010); Davis *et al.* (2012); Zhu *et al*. (2013); Giles *et al.* (2015).

17. **Sensory line network preserved as open grooves (sulci) in dermal bones (0); sensory lines pass through canals enclosed within dermal bones (1).** (Davis 2002); Davis *et al.* (2012); Zhu *et al.* (2013).

Dermal Skeleton: skull

18. **Dermal skull roof includes large dermal plates (0); consists of undifferentiated plates, tesserae or scales (1).** Forey (1980); Gardiner (1984); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).
19. **Tessera morphology: large interlocking polygonal plates (0); microsquamose, not larger than body squamation (1).** Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).
20. **Series of paired median skull roofing bones that meet at the dorsal midline of the skull (rectilinear skull roof pattern): absent (0); present (1).** Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).
21. **Large unpaired median bone contributing to posterior margin of skull roof: absent (0); present (1).** Zhu *et al.* (2013).
22. **Pineal opening perforation in dermal skull roof: present (0); absent (1).** Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).
23. **Parietals (preorbitals of placoderms) surround pineal foramen/eminence present (0); absent, uninterrupted suture (1).** Zhu *et al.* (2009, 2013).
24. **Consolidated cheek plates: absent (0); present (1).** Davis (2002); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).
25. **Dermal intracranial joint: absent (0); present (1).** Zhu *et al.* (2009, 2013)

Dermal Skeleton: operculogular series

26. **Bony hyoidean gill-cover series (branchiostegals): absent (0); present (1).** Davis (2002); Hanke & Wilson (2004); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).
27. **Opercular (submarginal) plate: present (0); absent (1).** Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).
28. **Gular plates: absent (0); present (1).** Gardiner (1984); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).

Branchial skeleton

29. **Gill skeleton mostly beneath otico-occipital region (0); posterior to occipital region (1).** Zangerl (1981); Lund & Grogan (1997); Stahl (1999). Chondrichthyan gill skeletons are generally located posterior to the braincase. Holocephalans represent a notable exception to this

condition (hence Zangerl's 'Subterbranchialia'), considered here as a secondarily primitive arrangement. The absence of direct articulation between chondrichthyan pharyngobranchials and the basicranium (unlike osteichthyan examples) is probably linked to the posterior displacement of the gill skeleton.

30. **Interhyal: absent (0); present (1).** Maisey (1984); Davis *et al.* (2012); Zhu *et al.* (2013).

31. **Hypohyals: absent (0); present (1).** Friedman & Brazeau (2010); Pradel *et al.* (2014). Friedman & Brazeau (2010) discuss hypohyal presence as a possible osteichthyan synapomorphy (the traditional view), and predetermine the hypohyals of *Debeerius* (Grogan & Lund 2000) as independently derived, while offering no comment on the hypohyal of *Cobelodus* (Zangerl & Case 1976). Alternatively, Pradel *et al.* (2014) argue for the presence of hypohyals in the last common ancestor of gnathostomes.

32. **Basihyal absent, hyoid arch articulates directly with basibranchial (0); present (1).** Pradel *et al.* (2014); see also discussion in Carr *et al.* (2009).

33. **Pharyngobranchials absent (0); present (1).** Pradel *et al*. (2014).

34. **Separate supra- and infra-pharyngobranchials absent (0); present (1).** Gardiner (1984); Pradel *et al*. (2014). Formerly, character state '1' was assumed to be an osteichthyan specialization because *Acanthodes*, in a traditional stem-osteichthyan position, has only single pharyngobranchials, as do known fossil and Recent chondrichthyans (see discussion in Gardiner 1984). However, Pradel *et al*. (2014) reversed the polarity of this character, hypothesizing that the dual pharyngobranchial condition present in *Ozarcus* represents primitive conditions for crown gnathostomes.

35. **Pharyngobranchials directed anteriorly (0); posteriorly (1).** Pradel *et al*. (2014). Posteriorly directed pharyngobranchials characterize the vast majority of chondrichthyans, including several Palaeozoic taxa (*Orthacanthus*, *Debeerius, Tristychius*, and others). However, those of *Gladbachus* and the infrapharyngobranchials of *Ozarcus* (Pradel *et al.* 2014) are oriented anteriorly, as in osteichthyes.

36. **Hypobranchials directed anteriorly (0); hypobranchials of second and more posterior gill arches directed posteriorly (1).** Maisey (1984). Hypobranchials are generally present in early osteichthyans, chondrichthyans and *Acanthodes*. Posteriorly directed hypobranchials appears to be a synapomorphy of Recent elasmobranchs and several fossil clades including xenacanths and hybodontids.

Dentition

37. **Oral dermal tubercles borne on jaw cartilages: absent (0); present (1).** Hanke & Wilson (2004); Brazeau (229); Davis *et al.* (2012); Zhu *et al.* (2013).

38. **Pharyngeal teeth or denticles: absent (0); present (1).** Pharyngeal denticles are widespread among early gnathostomes. None, however, seem to be present in placoderm grade taxa and 'absent' scores have been inserted where preservation is sufficiently complete to allow a plausible judgement. Early osteichthyan pharyngeal denticles usually consist of multiple crowns supported on a plate-like base. Early chondrichthyan examples are often in the form of small whorls, notable for having an apparently fused base, unlike tooth whorls on the mandibular arch (Zangerl & Case 1976; Coates & Sequeira 2001a).
39. **Tooth whorls: absent (0); present (1).** Maisey (1984); Davis (2002); Hanke & Wilson (2004); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).
40. **Bases of tooth whorls: continuous plate (0); some or all whorls consist of separate tooth units (1).** Adjusted from Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013); conditions in early chondrichthyans discussed by Maisey and colleagues (Maisey *et al*. 2013).
41. **Lingual torus: absent (0); present (1).** Among early chondrichthyans, one of the most distinctive features of isolated teeth is the exposed platform on the lingual side of the toothbase. This platform or ledge, the 'lingual torus' (Ginter *et al.* 2010), is notably absent in outgroups, and Mesozoic and Recent elasmobranchs.
42. **Basolabial shelf: absent (0); present (1).** The basolabial shelf (Ginter *et al.* 2010) projects ventrally into a gutter at the base of the lingual surface of tooth crown(s) in the next, ontogenetically senior, member of a tooth family.
43. **Tooth whorl restricted to symphysial region (0); distributed along jaw margin (1).** Hanke & Wilson (2004); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013). Revised in light of discussion by Tucker and Fraser (2014): the restriction of tooth whorls to the symphysial region appears to be the more general condition, whereas continuous distribution of tooth whorls along the jaw margin represents a likely chondrichthyan synapomorphy.
44. **Toothplates absent (0); present (1).**
45. **Toothplates consolidated into one to three large posterior plates, and one to three smaller anterior tooth plates, occupying each quadrant of the jaw: absent (0); present (1).** Adapted from Stahl (1999), the character captures conditions in chondrenchelyids and cochliodonts, as well as more derived taxa.
46. **Toothplate complement restricted to two pairs in the upper jaw and a single pair in the lower jaw: absent (0); present (1).** After Patterson (1965); as a condition of toothplates, the character is coded as inapplicable for taxa lacking toothplates.
47. **Dermal plates on biting surface of jaw cartilages: absent (0); present (1).** Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).

48. **Mandibular teeth fused to dermal plates on biting surfaces of jaw cartilages: absent (0); present (1).** Hanke & Wilson (2004); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013). Coded as present in *Ramirosuarezia*, although we acknowledge that it is possible that the apparent teeth might be no more than enlarged outgrowths of the dermal bone, as has been identified in *Bothriolepis* (Rücklin *et al.*, 2012).
49. **Large dermal plates forming outer arcade of biting edge: absent (0); present (1).** Gardiner (1984), Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013**).**

Mandibular arch

50. **Palatoquadrate otic process large: absent (0); present (1).** Coates & Sequeira (2001a); Davis (2002); Brazeau (2009); Zhu *et al.* (2009, 2013). Scored as absent in holocephalans because there is no portion of the upper jaw posterior to the rear margin of the orbit. Pradel *et al*. (2011) speculate that no such process was present in *Kawichthys* because the articulation for the upper jaw is on the ventral surface of the postorbital process. The current matrix is coded accordingly.
51. **Palatoquadrate with ventromedial fossa for adductor muscle insertion (0); ventromedial fossa absent, adductor muscle insertion mostly or exclusively on lateral surface, or bypassing it laterally (1).** Adapted from Friedman (2007) character 154: placoderm-grade palatoquadrates generally include a ventral or medial fossa for the jaw adductor muscles (Miles 1971; Schaeffer 1975; Young 1979, 1986; Goujet 1984) because the close and broad connection between the endoskeletal upper jaw and dermal cheek bones leaves little or no room for a lateral fossa.
52. **Oblique ridge or groove along medial face of palatoquadrate: absent (0); present (1).** Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).
53. **Palatoquadrate articulation with the postorbital process directed anteriorly (0); laterally (1); dorsally (2).** Among chondrichthyans and other early gnathostomes in which the palatoquadrate articulates with the postorbital process, the orientation of the articular surface varies considerably. In genera such as *Acanthodes*, *Orthacanthus* and *Tamiobatis*, the articular area faces anteriorly; in symmoriids such as *Cobelodus*, *Akmonistion* and *Dwykaselachus* the area faces anterolaterally or laterally; in *Tristychius* and other putative early elasmobranchs the surface may be a dorsally directed trough or groove.
54. **Palatoquadrate fused to the neurocranium: absent (0); present (1).** Homoplastic among crown group gnathostomes, in the present analysis the possibility of convergent instances of fusion among fossil relatives of modern chimaeroids appears likely. *Debeerius* was described as "autodiastylic" by Groagan and Lund (2000). Here it is scored as having a palate that is continuous with the neurocranium after further observation of specimen CM48510. Although the

palate is fused to the neurocranium in *Iniopera* (Pradel 2010), this is scored with an additional character state '2' to reflect the strong likelihood that autostylic jaw suspension is not, as originally thought, a characteristic of the group (Stahl 1980; Zangerl 1996).

55. **Mandibular knob: absent (0); present (1).** Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013). The mandibular knob (mesial or preglenoid articular process or condyle) is usually considered the secondary or auxiliary part of the double articulation present in chondrichthyan jaws (Hotton 1952; Maisey 1989a; Lane & Maisey 2012). The primary articulation is the cotylus or glenoid, accommodating the quadrate condyle, positioned laterally or posterolaterally. No such process is present in stem gnathostomes, *Gladbachus*, or, apparently, *Pucapampella* (Janvier & Maisey 2010, fig.7B).

56. **Jaw articulation located on rearmost extremity of mandible: absent (0); present (1).** Davis *et al.* (2012); Zhu *et al.* (2013).

57. **Dental trough or sulcus adjacent to oral rim on Meckel's cartilage and palatoquadrate: absent (0); present (1).** Standard feature of chondrichthyans, although no trace of such a recess is present along the jaws of *Gladbachus*; similarly absent in toothplate-bearing holocephalans including *Helodus* (pers. obs. MIC). *Iniopera* includes a crest to support fused tooth whorls, but no sulcus.

58. **Scalloped oral margin on Meckel's cartilage and palatoquadrate: absent (0); present (1).** Characteristic of symmoriiform chondrichthyans, including *Akmonistion*, *Ozarcus* and *Cladoselache*, as well as the holocephalan *Helodus* (pers. obs. MIC). Such scalloped pockets for tooth families suggests that the dental lamina might have been subdivided into a series of discrete 'crypts', sensu Tucker and Fraser (2014).

59. **Mandibular symphysis fused: absent (0); present (1).** In numerous toothplate-bearing early gnathostomes, the halves of the lower jaw are fused across the mandibular symphysis. For the purposes of the present analysis this character might represent a further synapomorphy of holocephalans and less derived members of the stem lineage.

60. **Dermal plates on mesial (lingual) surfaces of Meckel's cartilage and palatoquadrate: absent (0); present (1).** Zhu *et al.* (2013).

Neurocranium

61. **Parasphenoid: absent (0); present (1).** Gardiner (1984); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).

62. **Precerebral fontanelle: absent (0); present (1).** Schaeffer (1981); Lund & Grogan (1997); Coates & Sequeira (1998, 2001a,b); Maisey (2001a); Brazeau (2009); Pradel *et al*. (2011) Davis *et al.* (2012); Zhu *et al.* (2013). Evidence for a precerebral fontanelle can be difficult to pin down

in fossil braincases. The fontanelle is reported as present in *Gladbachus* (Heidtke & Krätschmer 2001), but the notch in the cranial roof extends posterior to the level of the postorbital processes. If this represents a fontanelle rather than simply the anteromedial limit of cranial roof calcification, it would be precerebellar rather than precerebral opening. Conditions in *Cobelodus* are uncertain. Zangerl and Case (1976), Williams (1985) and Maisey (2007) show no clear evidence of a precerebral fontanelle in *Cobelodus aculeatus* or *Denaea*, except for indications of the wedge-shaped area identified as such in *Dwykaselachus* by Oelofsen (1986). Even in elasmobranchs with a largely pre-nasal precerebral fontanelle, the posterior limit of this opening is posterior to the nasal capsules. Pradel *et al*. (2011) find only a small, midline notch in *Kawichthys*, anterior to the orbits.

63. **Pronounced sub-ethmoidal keel: absent (0); present (1).** Schaeffer (1981); Coates & Sequeira (1998); Brazeau (2009). A keel is present in *Egertonodus* (Maisey 1983), where it separates left and right anterior extremities of the palatoquadrates. A similar keel is present in *Orthacanthus* (*Xenacanthus*), labeled as the 'rostrum' in Schaeffer (1981, fig.6). No such keel is present in *Dwykaselachus* or *Akmonistion* (Coates & Sequeira 1998), but a keel is reported as present in *Ozarcus* (Pradel *et al.* 2014). *Cladoselache* and *Cobelodus* (Maisey 2007) are incomplete anteriorly, thus coded as uncertain. This keel appears to be absent in *Doliodus* (Maisey *et al.* 2009; 2013, fig. 8a).

64. **Rostral bar: absent (0); present (1).** Adapted from Maisey (1985): characteristic of elasmobranch crania, this outgrowth of the internasal plate contributes support for rostral soft tissue, and may interconnect with other rostral cartilages.

65. **Internasal groove absent (0); present (1).** Identified by Pradel (2010) in *Iniopera*, this horizontal groove passes between the nasal capsules across the anterior of the snout. A second example is present in *Dwykaselachus*.

66. **Orbitonasal lamina dorsoventrally deep: absent (0); present (1).** Patterson (1965); Davis *et al.* (2012); Zhu *et al.* (2013). Chimaeroids and other members of the holocephalan clade are characterized by the dorsoventral expansion ('upgrowth', Patterson 1965) of the orbitonasal lamina. Much of this might be linked to the development of an ethmoid canal, or possible preconditions in fossil holocephalans lacking an ethmoid canal (Patterson 1965). Examples occur in modern chimaeroids and Palaeozoic genera including *Debeerius*, *Chondrenchelys*, and *Helodus*.

67. **Canal or channel for the olfactory tracts and telencephalon elongate: absent (0); present (1).** In chimaeroids the cavity for the forebrain extends anteriorly, medially and ventrally relative to the orbits, before diverging into the rear of the nasal capsules. In lateral view, this anterior

division of the endocranial space (between the optic nerve foramen and the rear of the nasal capsule) covers at least one third of the total endocranial cavity length.

68. **Position of myodome for superior oblique eye muscles: posterior and dorsal to foramen for nerve II (0); anterior and dorsal to foramen (1).** Young (1986); Coates & Sequeira (2001a); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).

69. **Supraorbital shelf broad with convex lateral margin: absent (0); present (1).** Coates & Sequeira (1998); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013). Classic examples are present in *Akmonistion*, *Cladoselache*, *Kawichthys* and *Iniopera*.

70. **Interorbital space narrow: absent (0); present (1).** Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).

71. **Palatobasal (or orbital) articulation posterior to the optic foramen** (0); **anterior to the optic foramen** (1). Adapted from Pradel *et al.* (2011, character 26), which develops a discussion from Maisey (2005) on the homology between ethmoidal articulations in Palaeozoic sharks and the orbital articulation of living orbitostylic sharks. Here, coding is simplified: the outgroup condition (state '0') exemplified by *Dicksonosteus* (Goujet 1984, fig. 12) and osteichthyans, is seemingly retained in *Pucapampella*, whereas the derived condition (state '1') is expressed in most known sharks. Contra Pradel *et al*. (2011), *Cobelodus* is coded as uncertain because the region where the orbital arcticulation is located in more complete crania, such as those of *Ozarcus*, *Akmonistion* and *Dwykaselachus*, appears to be missing.

72. **Optic pedicel: absent (0); present (1).** Dupret *et al*. (2014); Zhu *et al.* (2009, 2013). Among Osteichthyes a pedicel is present in *Ligulalepis*, and perhaps in *Psarolepis*. A pedicel is present in chondrichthyans such as *Cladodoides* (clearly visible in the original specimen but reduced in renderings of CT scans) and *Pucapampella*, but is absent in *Tristychius* and hybodontids. *Ozarcus* (Pradel *et al.* 2014) is tentatively coded as pedicel present, because of an elliptical outgrowth posterior to large opening for optic nerve.

73. **Ophthalmic foramen in anterodorsal extremity of orbit communicates with cranial interior: absent (0); present (1).** In *Dwykaselachus* the foramen in the anterodorsal and medial extremity of the orbit appears to have transmitted the superficial ophthalmic branch of the anterior lateral line nerve and the profundus nerve from the orbit, into the neurocranial interior, passing dorsal to the forebrain and medial to the bulk of the nasal capsules (Extended Data Fig. 9a). This condition also occurs modern chimaeroids: in adults the nerve trunk passes directly into the ethmoidal canal, but in late embryo stages, the nerve passes into the interior space of the developing chondrocranium (Extended Data Fig. 9b, c) prior to the ethmoid canal becoming separated from the rest of the endocranial cavity by the development of a cartilage floor beneath the ophthalmic trunk and above the telencephalon. De Beer and Moy-Thomas (1935), argue that

the ethmoidal canal is a secondarily enclosed extracranial space because the dura mater, which lies directly above the forebrain but ventral to the ethmoid canal nerves, marks the primary endocranial roof. Alternatively, Holmgren (1942) proposes that the ethmoid canal is an endocranial space that is separated from the main cranial cavity by the formation of an interorbital septum. Patterson (1965) reviews available evidence but is undecided between these scenarios. *Dwykaselachus* evidence tends to support an endocranial origin, but location of the dura mater in *Dwykaselachus* is unknown. The membrane might already have been separated from the ethmoid cartilage roof as a result of the ophthalmic trunk re-entering the cranium. Consequently, the extent of De Beer and Moy-Thomas's defined endocranial (endomeningeal) space is unknown; for this reason, we use the less restrictive term 'cranial interior' in the character statement.

74. **Bucco-hypophyseal duct open (0); closed (1).** Bucco-hypophyseal openings are primitively present in crown gnathostomes. The opening has closed independently in major clades, including elasmobranchs (primitively present in hybodontids: Maisey 1982) and holocephalans (possibly present in the holocephalan *Helodus*: Patterson 1965). Although a basal fenestra is present in FMNH PF 13242 (Maisey 2007) and *Dwykaselachus*, there appears to be no direct connection to the hypophyseal space. The character is retained in the present analysis as a plausible synapomorphy of more deeply nested groups.

75. **Internal carotids: entering single or paired openings in the basicranium from a posterolateral angle (0); entering basicranial opening(s) head-on from an extreme, lateral angle (1); absent (2).** Canals and grooves within the basicranial cartilage reveal details of the cranial arterial supply in early chondrichthyans (Schaeffer 1981; Coates & Sequeira 1998; Maisey 2005). However, conditions in symmoriiforms are not entirely clear. Maisey (2007) speculates that in FMNH PF 13242 the internal carotids entered the basal fenestra, but later exited the basicranial cartilage into the floor of the orbit before re-entry into endocranial space. Here, FMNH PF 13242 is coded as uncertain, although it might represent an apomorphic condition. Pradel (2010) reconstructs *Iniopera* as lacking internal carotids like modern chimaeroids (state '2'); *Kawichthys* is coded as uncertain (Pradel *et al.* 2011).

76. **Canal for efferent pseudobranchial artery within basicranial cartilage: absent (0); present (1).** Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).

77. **Ascending basisphenoid pillar pierced by common internal carotid: absent (0); present (1).** Miles (1973b); Brazeau (2009); Friedman & Brazeau (2010); Davis *et al.* (2012); Zhu *et al.* (2013).

78. **Spiracular groove on basicranial surface: absent (0); present (1).** Davis *et al.* (2012); Zhu *et al.* (2013).

79. **Spiracular groove on lateral or transverse wall of jugular canal: absent (0); present (1).** Davis *et al.* (2012); Zhu *et al.* (2013).

80. **Orbit larger than otic capsule: absent (0); present (1)**. Lund & Grogan (1997) and Grogan & Lund (2000) have drawn attention to the likely phylogenetic signal in holocephalan cranial proportions. For the present analysis, a data set is provided (Supplementary Table 1) documenting maximum oribit length, otic capsule capsule length (measured from hindmost part of the posterior semicircular canal to the anteriormost part of the anterior canal) and basicranial length.

81. **Postorbital arcade: absent (0); present (1).** Pradel *et al.* (2011). Here, 'postorbital arcade' is used in the sense of Maisey's (2007) description of the postorbital process and associated wall enclosing the jugal opening. The general condition of the chondrichthyan postorbital arcade is to have a broad postorbital wall extending ventrally or anteroventrally from the postorbital process to the basicranium. This wall forms a complete arcade surrounding the jugular canal. A lateral portion of the wall, in non-holocephalans at least, probably developed from an embryonic 'lateral commissure', a topic discussed at length elsewhere (De Beer 1937; Gardiner 1984; Maisey 2007; Coates & Friedman 2010; Pradel 2010; Zhu *et al*. 2013). For discussion about possible lateral commissure contribution to holocephalan postorbital arcades, see De Beer (1937) and Pradel (2010).

82. **Postorbital process articulates with palatoquadrate: absent (0); present (1).** Schaeffer (1981); Coates & Sequeira (1998); Maisey (2001a); Pradel *et al.* (2011); Davis *et al.* (2012); Zhu *et al.* (2013). The 'archaeostylic' (Maisey 2008) condition (state '1') is characteristic of early chondrichthyans such as *Cladodoides*, *Pucapampella* and *Gladbachus*, as well as acanthodian grade genera such as *Acanthodes* and *Promesacanthus*. A weak and perhaps secondarily derived version of archaeostyly is present in *Synechodus* (Maisey 1985).

83. **Postorbital process and arcade width not more than maximum width of braincase (excluding arcade) (0); process and arcade width exceeds maximum width of braincase (1); process and arcade reduced to the dorsal part (2).** Symmoriiforms, have a characteristic, anterioposteriorly slender arcade (Maisey 2007) enclosing an exceptionally large opening for the jugular vein (Zangerl & Case 1976; Williams 1985; Maisey 2007). Ventral perspectives of the *Dwykaselachus* baincase indicate that a similarly large opening was present in *Akmonistion*.

84. **Jugular canal in postorbital arcade small (0); canal large (1); canal absent (2).** Adapted from Pradel *et al.* (2011); scored as inapplicable for taxa in which the postorbital arcade is reduced to the dorsal part. A large canal is defined here as one in which the dorsal rim is level with or dorsal to the level of the lateral otic ridge, and the ventral margin is ventral to the level of the pituitary vein.

85. **Trigeminofacial recess: absent (0); present (1).** For detailed discussion, see Goodrich (1930), Pradel (2010), Pradel *et al*. (2011) and Davis *et al.* (2012). Notably, this characteristic of the crown gnathostome braincase is secondarily absent in modern holocephalans, *Kawichthys* (Pradel *et al*. 2011), FMNH PF 13242 (Maisey 2007; Pradel *et al.* 2011), *Dwykaselachus*, and putative stem holocephalans including *Iniopera* (Pradel 2010), *Helodus* (Patterson 1965; pers.obs. MIC) and *Chondrenchelys* (Finarelli & Coates 2014). The trigeminofacial recess identified in *Akmonistion* (Coates & Sequeira 1998 figs 3A, B) is probably the rim of the jugular opening: compare with Extended Data Fig. 5b. For this reason, *Akmonsition* is coded as uncertain. Pradel *et al.* (2009a, fig. 5c) identify a possible recess in *Ramirosuarezia*, although detail of the interior morphology is unknown.

86. **Postorbital fossa: absent (0); present (1).** Zhu *et al.* (2013).

87. **Hyoid ramus of facial nerve (N. VII) exits through posterior jugular opening: absent (0); present (1).** Friedman (2007); Brazeau (2009); Friedman & Brazeau (2010); Davis *et al.* (2012); Zhu *et al.* (2013).

88. **Posterior postorbital process and supravagal process: absent (0); present (1).** In many jawed, stem-gnathostomes (placoderms), the braincase bears a 'Y'-shaped lateral outgrowth, the anterior component of which is identified as the posterior postorbital process and the posterior part as the supravagal process (Young 1980, text-fig. 24). Notably, this structure is present in *Entelognathus* but absent in *Ramirosuarezia* and crown group gnathostomes including the otherwise primitively proportioned braincase of *Gladbachus*.

89. **Periotic process: absent (0); present (1).** Maisey (2007) describes the periotic process of FMNH PF 13242, tentatively restores the process in *Cobelodus aculeatus* and notes its presence in a several other symmoriiform sharks. A well-formed example is present in *Dwykaselachus*.

90. **Lateral otic process: absent (0); present (1).** Schaeffer (1981); Coates & Sequeira (1998); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013). The lateral otic process is generally linked to the neurocranial articulation with the head of the hyomandibula (Schaeffer 1981; Coates & Sequeira 1998). Clear examples are present in *Orthacanthus* and *Tamiobatis*, where the process is most prominent dorsally, projects laterally almost as far as the postorbital process, and the anterolateral face is distinctly concave below the level of the lateral otic ridge. The short but heavily mineralized lateral otic process of *Akmonistion* (Coates & Sequeira 1998, figs 1a, c and 4) is notably absent in FMNH PF 13242, *Cobelodus*, *Kawichthys* and *Dwykaselachus*.

91. **Sub-otic occipital fossa: absent (0); present (1).** In genera such as *Orthacanthus* and *Tamiobatis* (Schaeffer 1981) a distinctive concavity flanked by the lateral otic process and the posteriorly projecting occipital arch, lies beneath the rear of the otic capsule. No such fossa is present in *Cladodoides* (Maisey 2005) or *Akmonistion* (Coates & Sequeira 1998).

92. **Otic capsule extends posterolaterally relative to occipital arch: absent (0); present (1).** Maisey (1985): suggested synapomorphy of crown elasmobranchs.

93. **Postotic process: absent (0); present (1).** Pradel *et al.* (2011) characterize this as different from the lateral otic process because it projects posteriorly, contains the glossopharyngeal nerve canal but does not contain the posterior semicircular canal (identified in *Synechodus* as the lateral otic process: Maisey 1985).

94. **Otic capsules: widely separated (0); approaching dorsal midline (1).** In stem gnathostomes left and right semicircular canal arrays are widely separated: the commissural union of anterior and posterior semicircular canals lies close to, but does not overlap dorsally, the boundary between myencephalic and metencephalic regions of the neurocranial cavity. Examples of the primitive condition are depicted clearly in jawless (Gai *et al.* 2011; Janvier 1985, 1996) and jawed taxa (Stensio 1963; Young 1980, 1986; Goujet 1984). In these genera, a dorsal view of the cavity enclosing the hindbrain-midbrain junction is uninterrupted, irrespective of whether otic labyrinths are large (*Dicksonosteus*) or small (*Brindabellaspis*). In crown gnathostomes, the plesiomorphic condition persists early in ontogeny, but the adult condition is markedly different. The crus commune of left and right otic capsules approaches the dorsal midline above or posterior to the level of the hindbrain-midbrain junction. This condition is present in taxa both with and without substantial walls dividing the labyrinth from the main endocranial cavity (Schaeffer 1981; Lane 2010; Pradel 2010). In taxa where the endocranial spaces are not directly visible, the condition can, occasionally, be scored from neurocranial roof ridges overlying anterior and posterior canals (e.g. *Akmonistion*: Coates & Sequeira 1998). *Janusiscus* (Giles *et al.* 2015, fig. 2) appears to retain the primitive condition.

95. **Endocranial cavity (infill) anterior to otic capsules smoothly convex dorsally and anteriorly: absent (0); present (1).** Endocranial cavities in most early gnathostomes more-or-less reflect the principal divisions between forebrain, midbrain and hindbrain (numerous examples shown in Janvier 1996). In this respect, *Kawichthys* and *Iniopera* are unusual because the endocranial spaces are remarkably simple and featureless. In both genera, the endocranial roof anterior to the otic region is slightly domed dorsally and anteriorly, without narrowing above the orbits or broadening towards the nasal capsules and precerebral fontanelle (notably, both crania are just over 20mm long).

96. **Roof of skeletal cavity for cerebellum and mesencephalon significantly higher than dorsal-most level of semicircular canals: absent (0); present (1).**

97. **Roof of the endocranial space for telencephalon and olfactory tracts offset ventrally relative to level of mesencephalon: absent (0); present (1).** The roof of the forebrain cavity is distinctly lower than the height of midbrain endocranial cavity in chimaeroid crania (Kesteven 1932;

Howard *et al*. 2015). This change in level is abrupt or stepped rather than a gradual sloping of the forebrain, and coincides with narrowing of the endocranial cavity. However, these two features (narrowing and ventral offset) are not co-dependent. For contrasting conditions, see cranial endocasts of early actinopterygians in which the forebrain and olfactory tract space narrows but remains at the level of the orbit roof (Gardiner 1984; Giles & Friedman 2014).

98. **Labyrinth cavity separated from the main neurocranial cavity by a cartilaginous or ossified capsular wall (0); skeletal medial capsular wall absent (1).** Pradel *et al*. (2011); Davis *et al.* (2012); Zhu *et al.* (2013).

99. **Crus commune connecting anterior and posterior semicircular canals present (0); absent (1).** As noted by Daniel (1922), Maisey (1984, 2001b), Maisey & Lane (2010), Pradel *et al.* (2011) and others, modern elasmobranchs exhibit a derived condition in which the posterior semicircular canal is separated from the anterior canal.

100. **Sinus superior: absent or indistinguishable from union of anterior and posterior canals with saccular chamber (0); present, elongate and nearly vertical (1).** Davis *et al.* (2012); Zhu *et al.* (2013). Primitively absent, this is secondarily lost in hybodontids (Maisey & Lane 2010). Notably, in *Squalus* (Marinelli & Strenger 1959, Abb. 195-197), although there is no crus commune, the sinus persists, above the level of the saccular chamber, although difficult to distinguish from a dorsally and posteriorly extended utricular chamber. A sinus superior is scored present in *Kawichthys* on the basis of its similarity to the labyrinth configuration of *Iniopera*.

101. **Angle of external semicircular canal: in lateral view, straight line projected through canal intersects anterior ampulla, external ampullae, and base of foramen magnum: absent (0); present (1).** Maisey (2007) notes the unusually tilted angle of the external canal in FMNH PF 13242; this is markedly similar to conditions in *Dwykaselachus* as well as modern chimaeroids (examples shown in Pradel et al. (2013) supplementary movie; Finarelli & Coates (2014) fig. 6a).

102. **Left and right external semicircular canals approach or meet the posterodorsal midine of the hindbrain roof: absent (0); present (1).** This highly unusual labyrinth arrangement is present in *Iniopera* (Pradel 2010, fig. 27) and the limited remains of *Kawichthys* (Pradel *et al*. 2011, fig. 12) are sufficiently complete to demonstrate that this genus exhibits the same condition. This specialized arrangement is very likely linked to the unusually elevated level of the external canal in both taxa.

103. **Perilymphatic fenestra: absent (0); present (1).** Pradel *et al*. (2011). Fenestrae communicate with the posterior semicircular canals. The derived condition is synapomorphic for crown elasmobranchs (Daniel 1922) and seems likely to include hybodontids (Maisey & Lane 2010) and *Tristychius*.

104. Endolymphatic ducts: posteriodorsally angled tubes (0); tubes oriented vertically through median endolymphatic fossa/endolymphatic foramen (1). Schaeffer (1981); Coates & Sequeira (1998, 2001); Davis (2002); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).

105. Posterior dorsal fontanelle/external opening for endolymphatic ducts anterior to crus commune: absent (0); present (1). In taxa where the crus commune is absent, the level of the fontanelle or duct is assessed relative to the dorsal origin of the anterior semicircular canal.

106. Posterior dorsal fontanelle connected to persistent otico-occipital fissure (0); posterior tectum separates fontanelle from fissure (1). Schaeffer (1981); Coates & Sequeira (1998); Pradel *et al.* (2011).

107. Subcircular endolymphatic foramen: absent (0); present (1). Pradel *et al*. (2015) character 15 defines this feature as a 'small, rounded and unfloored endolymphatic fossa'; see also Maisey & Lane (2010) who recognized this feature as a likely holocephalan synapomorphy. The present character describes the opening as a foramen because there is no fossa as such (cf. *Squalus*, or *Tamiobatis*). In other respects the general homology hypothesis is the same, that this condition is present in chimaeroids, other holocephalans and symmoriids.

108. Dorsal otic ridge forms a horizontal crest posteriorly, and flanks the anterior rim of the endolymphatic fossa: absent (0); present (1). Coates & Sequeira (1998, 2001); Pradel *et al.* (2011).

109. Dorsal ridge divided posteriorly by an anteroposteriorly elongate recess enclosing the exits of the endolymphatic ducts: absent (0); present (1). The presence of a slot-shaped opening is characteristic of the otico-occipital roof in ctenacanths, *Cladodoides*, *Tristychius* and hybodontids.

110. Endolymphatic or parietal fossa: absent (0); present (1). Pradel *et al*. (2011). Character state 1 indicates presence of a cartilage floor within the posterior dorsal fontanelle. The floor is perforated laterally or medially by further openings for the endolymphatic ducts and perilymphatic chamber. Clear examples of the fossa are present in *Orthacanthus* and *Egertonodus*. Examples of an endolymphatic opening in which a floor is absent include *Cobelodus*, *Pucapampella* and *Cladodoides.*

111. Ventral cranial fissure: absent (0); present (1). Janvier (1996); Coates & Sequeira (2001); Maisey (2001); Davis (2002); Brazeau (2009); Pradel *et al.* (2011); Davis *et al.* (2012); Zhu *et al.* (2013). Contra Davis *et al.* (2012), *Chondrenchelys*, despite condition of the basicranium of NMS 2002.68.1, is revised to state '0': fissure absent (Finarelli & Coates **2014**).

112. Endoskeletal intracranial joint: absent (0); present (1). Janvier (1996, and references therein); Davis *et al.* (2012); Zhu *et al.* (2013).

113. **Metotic (otic-occipital) fissure: absent (0); present (1).** Schaeffer (1981); Janvier (1996); Coates & Sequeira (1998); Maisey (2001); Davis (2002); Brazeau (2009); Pradel *et al*. (2011); Davis *et al.* (2012); Zhu *et al.* (2013). Consistent with Pradel *et al*. (2011), *Kawichthys* is scored as uncertain. In *Akmonistion* (Coates & Sequeira 1998, fig. 4), FMNH PF 13242 (Maisey 2007, fig. 7), and *Dwykaselachus* (Extended Data Fig. 5b) the posterior rim of the otic roof is gently concave. The condition in *Kawichthys* is different: the posterior margin of the otic roof is convex, and projects posteriorly. In this context, it is also noteworthy that the glossopharyngeal nerve exits the endocranium by means of a foramen in the otic wall.

114. **Hypotic lamina: absent (0); present (1).** Schaeffer (1981); Maisey (1984, 2001); Brazeau (2009); Pradel *et al*. (2011); Davis *et al.* (2012); Zhu *et al.* (2013). Pradel *et al.* (2013) define a hypotic lamina as 'a lateral extension of the parachordal plate which floors the glossopharyngeal canal'. They demonstrate that in *Callorhinchus*, although the parachordal plate is extended laterally, it barely underlies the otic capsule, and is thus unlikley to form the floor of the glossopharyngeal canal or channnel through the metotic fissure. This contrasts with conditions in modern elasmobranchs, as well as Palaeozoic taxa including *Cladodoides*, *Tamiobatis* and symmoriiforms such as *Cobelodus*, FMNH PF 13242 and *Dwykaselachus*, in which a hypotic lamina is undoubtedly present.

115. **Glossopharyngeal nerve path: directed laterally, across floor of the saccular chamber and exits via foramen in side wall of the otic capsule (0); directed posteriorly, and exits through metotic fissure or foramen in posteroventral wall of otic capsule (1); exits laterally through a canal contained ventrally (floored) by the hypotic lamina (2); exits through a foramen anterior to the posterior ampulla (3).** Schaeffer (1981); Coates & Sequeira (1998, 2001); Brazeau (2009): Davis *et al.* (2012); Zhu *et al.* (2013); Pradel *et al*. (2011, 2013). The plethora of conditions exhibited by the glossopharyngeal canal are here reduced to four: the apparently derived condition of passing posteriorly from the endocranium (state '1'), and the alternative laterally directed pattern, beneath the otic capsule and above the hypotic lamina, secondarily derived (state '2') in elasmobranchs and in *Iniopera* and *Kawichthys* (state '3') in which the glossopharyngeal exit is situated ventral and anterior to location of posterior canal ampulla. This not considered homologous with the outgroup condition exhibited by *Dicksonosteus* (Goujet 1984).

116. **Basicranial morphology: platybasic (0); tropibasic (1).** Brazeau (2009); Pradel *et al.* (2011); Davis *et al.* (2012); Zhu *et al.* (2013). Here, the definition of tropibasic versus platybasic follows discussions in Maisey (2007) and Pradel *et al* (2011), and reference of the term is confined to adult morphologies. A tropibasic skull displays an interorbital septum ventral and anterior to the bulk of the cranial cavity. We agree with Pradel *et al.* (2011) that *Kawichthys* is tropibasic, and

score *Dwykaselachus* and FMNH PF 13242 similarly. *Cobelodus* is scored uncertain because the endocranial conditions are unknown.

117. Canal for dorsal aorta and/or lateral dorsal aortae within basicranial cartilage: absent (0); present (1). Schaeffer (1981); Coates & Sequeira (1998); Brazeau (2009); Pradel *et al.* (2011).

118. Dorsal aorta divides into lateral dorsal aortae posterior to occipital level (0); anterior to level of the occiput (1). Pradel *et al*. (2011). *Pucapampella* is coded tentatively as state '0', after Janvier and Maisey's (2010, fi. 9b) illustration of basicranial material with infilled canals. Other codings are in agreement with interpretations of dorsal aortic conditions from Giles *et al.* (2015).

119 Ventral portion of occipital arch wedged between rear of otic capsules: absent (0); present (1). Schaeffer (1981); Coates & Sequeira (1998); Maisey (2001a); Brazeau (2009); Pradel *et al.* (2011); Davis *et al.* (2012); Zhu *et al.* (2013). Generally present in conventional fossil and recent chondrichthyans: the ventral part of the arch is overlapped by the wall of the posterior semicircular canal, obscuring the anteriormost exits of the occipito-spinal nerve foramena in lateral view. This condition is absent *Acanthodes*, *Gladbachus*, *Doliodus*, *Pucapampella*, and osteichthyan outgroups (notably including early actinopterygians in which the occipital arch is similarly proportioned to those of symmoriiforms).

120 Dorsal portion of occipital arch wedged between otic capsules: absent (0); present (1). Schaeffer (1981); Coates & Sequeira (1998); Maisey (2001a); Brazeau (2009); Pradel *et al.* (2011); Davis *et al.* (2012); Zhu *et al.* (2013). This condition is most clearly displayed by *Cladodoides*, *Tamiobatis*, *Orthacanthus* and elasmobranchs. In symmoriiforms and holocephalans the degree of occipital arch instrusion between the otic capsules is minimal at the level of the foramen magnum and more dorsally. In most respects, the condition in these groups is barely distinguishable from osteichthyans.

121. Occipital crest anteroposteriorly elongate, and extends from the roof of the posterior tectum: absent (0); present (1). Here, the occipital crest is distinguished from those of *Orthacanthus* and hybodontids that rise from the occipital arch wedged deeply between the posterior semicircular canals of left and right otic capsules (Schaeffer 1981; Maisey 1982). The occipital crest of *Callorhinchus* develops as median keel of the posterior tectum and extends posteriorly to the level of the foramen magnum (see Finarelli & Coates 2014, fig. 6a-c). The same condition is present in *Kawichthys* (Pradel *et al*. 2011, fig. 5) and *Iniopera* (Pradel 2010, fig. 5). In *Dwykaselachus* the posterior tectum bears only an anterioposteriorly short crest that terminates at the concave anterior margin of the occipital fissure (Extended Data Fig. 5b). The same condition is present in FMNH PF 13242 (Maisey 2007, fig. 7) and *Akmonistion* (Coates & Sequeira 1998, fig. 4). The condition in *Helodus* is uncertain: Patterson (1965) reconstructs the cranial roof as detail-free because the best available specimen (P 8212) is incompletely exposed.

122. Unconstricted basicranial notochord: absent (0); present (1). Zhu *et al.* (2009, 2013); Pradel *et al.* (2011).

Axial skeleton, paired fins and girdles

123. Calcified vertebral centra: absent (0); present (1). Maisey (1985); suggested synapomorphy of crown elasmobranchs.

124. Chordacentra: absent (0); present (1). Stahl (1999); Coates and Sequeira (2001): chordacentra, or circumchordal rings (Stahl 1999) are an established characteristic of holocephalans (Patterson 1965; Lund 1982; Finarelli & Coates 2014). Examples occur as complete, tightly packed rings in the majority of modern chimaeroids (absent in *Callorhinchus*) and as anteroposteriorly broader half-rings in Palaeozoic examples (Finarelli & Coates 2014). Similar, half-ring chordacentra occur in certain symmoriiforms, most notably in *Damocles* (Lund 1986; CM 48760). A distinctive line of likely chordacentra (here coded as uncertain) is also present in the caudal extremity of *Akmonistion* (Coates & Sequeira 2001). However, no traces of such centra whatsoever are visible in *Debeerius*, in agreement with Grogan & Lund (2000), and the condition of *Helodus* remains uncertain because the axial region is obscured by scales and/or poor specimen preparation.

125. Chordacentra polyspondylous and consist of narrow closely packed rings: absent (0); present (1). Derived from Patterson (1965).

126. Synarcual: absent (0); present (1). Stahl (1999); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013). It seems highly unlikely that the synarcuals of 'placoderms' are homologous with those of holocephalans, but there appears to be no simple alternative means of characterizing these structures as different. Both can occur associated or unassociated with dorsal fins. Both appear to represent fusion of all parts of the vertebral skeleton.

127. Macromeric dermal pectoral girdle (0); micromeric or lacking dermal skeleton entirely (1). Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).

128. Scapular process with posterodorsal angle. Absent (0); present (1). Coates & Sequeira (2001a); Davis *et al.* (2012); Zhu *et al.* (2013).

129. Dibasal pectoral fin: absent (0); present (1). Lund & Grogan (1997); Stahl (1999). Holocephalans exhibit a highly stereotypical pectoral fin endoskeleton. Palaeozoic genera exhibiting well-preserved examples include *Helodus*, *Debeerius* and *Chondrenchelys*.

130. Meptapterygial whip: absent (0); present (1). Coates & Sequeira (2001a,b); Giles *et al*. (2015).

131. Pelvic girdle with fused puboischiadic bar: absent (0); present (1). Maisey (1984); Coates & Sequeira (2001a).

132. **Mixipterygial/mixopterygial claspers: absent (0), present (1).** Maisey (1984); Coates and Sequeira (2001a,b). In contrast to the claspers of placoderm clades (Long *et al*. 2015), those of male chondrichthyans, both fossil and Recent, are supported by an axial rod plus terminal cartilages and spurs, and these are linked to the metapterygium-like pelvic basipterygium by a series of short intermediate cartilages (Compagno, 1999). The entire musculoskeletal entity is variously named the mixopterygium (Compagno 1999), mixipterygium (Trinajstic *et al*. 2014) or mixipodium (Liem & Summers 1999). This pattern of clasper support is known in modern and fossil chondrichthyans.

133. **Pre-pelvic clasper or tenaculum: absent (0); present (1).** After Patterson (1965).

Fin spines and other spines of the dermal skeleton

134. **Dorsal fin spines: absent (0); present (1).** Zhu *et al*. (2001); Zhu & Yu (2002); Friedman (2007); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).

135. **Dorsal fin spines with rows of large denticles on posterior surface: absent (0); present (1).** Maisey (1989b); Davis *et al.* (2012); Zhu *et al.* (2013).

136. **Dorsal fin spine at anterior (pectoral level) location only**: absent (0); present (1). Coates & Sequeira (2001a); Ginter *et al.* (2010). This character is coded as inapplicable in taxa with a continuous dorsal fin extending throughout the length of the trunk.

137. **Anal fin spine: absent (0); present (1).** Maisey (1986); Davis (2002); Brazeau (2009). Coded as inapplicable where anal fin is absent.

138. **Pectoral fin spines: absent (0); present (1).** Davis (2002); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).

139. **Cephalic spines: absent (0); present (1).** Maisey (1989b).

Median fins

140. **Number of dorsal fins, if present: one (0); two (1); continuous dorsal fin (2); continuous dorsal to caudal fin (3).** Coates & Sequeira (2001a); Brazeau (2009); Davis *et al.* (2012); Zhu *et al.* (2013).

141. **Posterior or pelvic-level dorsal fin with calcified base plate: absent (0); present (1).** Coates & Sequeira (2001a,b). Present in *Tristychius*, hybodontids, modern elasmobranchs, *Ctencanthus costellatus* and *Goodrichthys*. For the purposes of the present analysis, *Tamiobatis*, a token 'ctenacanth' is coded as having a posterior dorsal fin baseplate. If coded as lacking such a plate, the present data set yields a spurious result with this character as a synapomorphy of hybodontids and more crownward elasmobranchs.

142. Posterior dorsal fin with delta-shaped cartilage: absent (0); present (1). Coates & Sequeira (2001a,b). Present in a wide variety of symmoriids including *Falcatus* (Lund 1985) but absent in *Cladoselache*.

143. Anal fin: absent (0); present (1). Coates & Sequeira (2001a,b); Giles et al. (2015).

144. Caudal neural and/or supraneural spines short (0); long (1). Coates & Sequeira (2001a,b). See comparative description and discussion in Coates and Sequeira 2001b.

145. Caudal axis upturned steeply supporting high aspect ratio (lunate) tail: absent (0), present (1). Coates and Sequeira (2001a,b). Present in symmoriids including *Cladoselache*.

4. Character state transitions and taxon exclusion tests

Supplementary Table 3: Apomorphy table mapping unambiguous character state transitions on the strict consensus cladogram of the 240 MPTs. Characters were optimized using DELTRAN. Node numbers in the table correspond to those presented in Extended Data Figure 9a.

Branch Optimized			Character	Description	Character CI	State Change		
Node 1	to	Node 2	26	Branchiostegals	0.50	0	to	1
Node 2	to	Node 3	88	Posterior postorbital process	1.00	1	to	0
Node 3	to	Node 4	50	PQ otic process large	0.25	0	to	1
			81	Postorbital arcade	0.50	0	to	1
			86	Postorbital cavity	1.00	1	to	0
			113	Metotic & occipital cranial fissure	0.25	0	to	1
Node 4	to	Node 5	12	Scale base convex	0.25	0	to	1
			18	Dermal skull plates	1.00	0	to	1
			20	Paired dermal plates	0.50	1	to	0
			21	Large median cran. dermal bone in posterior	1.00	1	to	0
			24	Cheek plates	1.00	1	to	0
			27	Submarginal/opercular plate	1.00	0	to	1
			137	Anal finspines	0.50	0	to	1
Node 5	to	Node 6	43	Adsymphyseal whorl/gape margin	1.00	0	to	1
			47	Jaw dermal plates	1.00	1	to	0
Node 6	to	Node 7	3	Perichondral bone	0.33	0	to	1
			19	Dermal skull tesserae	1.00	0	to	1
			26	Branchiostegals	0.50	1	to	0

Node 7	to	Node 8	1	Tessellate calcified cartilage	1.00	0	to	1
			8	Lepidotrichia	1.00	0	to	1
			76	Efferent pseudobranchial canal	1.00	0	to	1
			117	Dorsal aorta canal in basicranium	0.20	0	to	1
Node 8	to	Node 9	14	Scale basal canal	0.50	0	to	1
			40	Whorls fused/separate teeth	1.00	0	to	1
			55	Mandibular knob	0.50	0	to	1
			104	Endolymphatic duct orientation	1.00	0	to	1
			106	Postdorsal fontanelle posterior tectum	1.00	0	to	1
			119	Basioccip. arch wedged	1.00	0	to	1
			138	Pectoral fin spines	0.50	1	to	0
Node 9	to	Node 18	16	Sensory line scales	1.00	1	to	2
			80	Orbit large	0.33	0	to	1
			85	Trigeminofacial recess	0.50	1	to	0
			97	Telencephalon roof offset ventrally	1.00	0	to	1
			107	Subcircular endolymphatic foramen.	1.00	0	to	1
			118	Dorsal aorta split	0.33	0	to	1
			136	Dorsal finspine only at pectoral level	1.00	0	to	1
			143	Anal fin	0.50	1	to	0
Node 18	to	Node 24	41	Lingual torus	0.33	0	to	1
			42	Basolabial shelf	0.50	0	to	1
			58	Scalloped margin	0.50	0	to	1
			84	Jugular canal	1.00	0	to	1
			89	Periotic process	0.50	0	to	1
			145	Lunate tail	1.00	0	to	1
Node 24	to	Node 26	69	Supraorbital shelf wide	0.33	1	to	0
			74	Bucco-hypophyseal space	0.20	0	to	1
			116	Platybasic/tropibasic	0.25	0	to	1
Node 18	to	Node 19	29	Gill skeleton position	0.50	1	to	0
			44	Toothplates	0.50	0	to	1
			50	PQ otic process	0.25	1	to	0

			56	Jaw artic. posterior	1.00	0	to	1
			59	Mandibular symphysis fused	0.50	0	to	1
			62	Precerebral fontanelle	0.50	1	to	0
			72	Optic pedicel	0.33	1	to	0
			113	Metotic cranial fissure	0.33	1	to	0
Node 19	to	Node 21	54	PQ fused to neurocranium	1.00	0	to	1
			66	Orbito-nasal lamina dorsoventrally deep	1.00	0	to	1
			84	Jugular canal	1.00	0	to	2
			129	Dibasal pectoral fin	1.00	0	to	1
Node 21	to	Node 22	117	Dorsal aorta canal in basicranium	0.20	1	to	0
Node 22	to	Node 23	39	Tooth whorls	0.25	1	to	0
			124	Chordacentra	1.00	0	to	1
Node 19	to	Node 20	95	Domed endocranial space	1.00	0	to	1
			102	External semicircular canals meet	1.00	0	to	1
			115	Glossopharyngeal path	0.67	1	to	0
Node 9	to	Node 10	36	Hypobranchial direction	1.00	0	to	1
			120	Occipital arch dorsal wedge	1.00	0	to	1
			141	Posterior dorsal baseplate	1.00	0	to	1
Node 10	to	Node 16	41	Lingual torus	0.33	0	to	1
			42	Basiolabial Shelf	0.50	0	to	1
			108	Dorsal ridge with horizontal crest	0.33	0	to	1
Node 16	to	Node 17	2	Multilayered tesserae	0.50	0	to	1
			90	Lateral otic process	0.50	0	to	1
			91	Subotic occipital fossa	1.00	0	to	1
Node 10	to	Node 11	98	Medial capsular wall	0.50	1	to	0
			99	Crus commune	1.00	0	to	1
			103	Perilymphatic fenestra	1.00	0	to	1
			113	Metotic cranial fissure	0.33	1	to	0
			117	Dorsal aorta canal in basicranium	0.20	1	to	0
Node 11	to	Node 13	72	Optic pedicel	0.33	1	to	0
			100	Sinus superior	0.50	1	to	0
			135	Dorsal finspine posterior denticles	1.00	0	to	1

Node 13	to	Node 14	139	Cephalic spines	1.00	0	to	1
Node 14	to	Node 15	9	Trunk scales mono/polycuspid	0.25	1	to	0
			131	Puboischiadic bar	0.50	0	to	1
Node 11	to	Node 12	64	Rostral bar	1.00	0	to	1
			74	Bucco-hypophyseal space	0.20	0	to	1
			75	Internal carotids	1.00	0	to	1
			83	Postorb. arcade shape	0.67	0	to	2
			92	Otic capsules extend posteriorly	1.00	0	to	1
			93	Postotic process	1.00	0	to	1
			115	Glossopharyngeal path	1.00	1	to	2
			123	Vertebral centra	1.00	0	to	1
Node 4	to	Node 27	4	Endochond bone	1.00	0	to	1
			79	Spiracular groove on lateral commissure	1.00	0	to	1
Node 27	to	Node 28	23	Parietals surround pineal	1.00	1	to	0
			87	Hyoid ramus of facial nerve exit	0.50	0	to	1
Node 28	to	Node 29	25	Dermal intracranial joint	1.00	0	to	1
			81	Postorbital arcade	0.50	1	to	0
			112	Intracranial joint	1.00	0	to	1
			122	Unconstricted cranial notochord	1.00	0	to	1

Supplementary Table 4: Taxon deletion test results

Results of sequential taxon deletion analysis on chondrichthyan phylogeny. Chondrichthyan taxa were deleted one at a time and subjected to a maximum parsimony analysis in PAUP*. The impact of the taxon deletion was assessed through the number of nodes lost upon excluding the taxon. These are reported in the second column. The recovery of selected significant nodes observed in the strict consensus of all of the taxa is given in the remaining columns. The topology of chondrichthyan phylogeny recovered in the all-taxa analysis is exceedingly stable, with minimal impact of taxon deletion on resolution and only two instances of significant nodes disappearing in the taxon-pruned analyses. Node numbers given refer to the numbering scheme in Extended Data Fig. 10a

Taxon Deletion	Loss of resolution (nodes lost)	Total group Chondrichth--yes (Node 8)	Crown clade chondrichth--yes (Node 9)	"Cladodont" sharks with elasmobranchs (Node 10)	Symmoriiforms with total group holocephalans (Node 18)	Inioperans with holoceph- -alans (Node 19)	Monophyletic symmoriifor--ms (Node 24)
Akmonistion	**26**	**X**	**X**	**X**	**X**	**X**	**X**
Chondrenchelys	**21, 22**	**X**	**X**	**X**	**X**	**X**	**X**
Cladodoides	***None***	**X**	**X**	**X**	**X**	**X**	**X**

Cladoselache	***None***	**X**	**X**	**X**	**X**	**X**	**X**
Cobelodus	***None***	**X**	**X**	**X**	**X**	**X**	**X**
Debeerius	***None***	**X**	**X**	**X**	**X**	**X**	**X**
Doliodus	***None***	**X**	**X**	**X**	**X**	**X**	**X**
Dwykaselachus	***None***	**X**	**X**	**X**	**X**	**X**	**X**
Egertonsodus	**13, 14**	**X**	**X**	**X**	**X**	**X**	**X**
Gladbachus	***None ****	**X**	**X**	**X**	**X**	**X**	**X**
Hamiltonichthyes	***None***	**X**	**X**	**X**	**X**	**X**	**X**
Helodus	***None***	**X**	**X**	**X**	**X**	**X**	**X**
Iniopera	**21, 22, 23**	**X**	**X**	**X**	**X**	**X**	**X**
Kawichthyes	**22**	**X**	**X**	**X**	**X**	**X**	**X**
Onychoselachae	**13**	**X**	**X**	**X**	**X**	**X**	**X**
Orthacanthus	***None***	**X**	**X**	**X**	**X**	**X**	**X**
Ozarcus	**24**	**X**	**X**	**X**	**X**	**X**	
Pucapampella	***None***	**X**	**X**	**X**	**X**	**X**	**X**
Synechodus	**13, 14, 15**	**X**	**X**	**X**	**X**	**X**	**X**
Tamiobatis	**10**	**X**	**X**		**X**	**X**	**X**
Tristychius	**14, 15**	**X**	**X**	**X**	**X**	**X**	**X**

*** Excluding *Gladbachus* from the analysis results in the formation of a novel topology. When *Gladbachus* is removed *Pucapampella, Doliodus,* and the taxa traditionally referred to as "acanthodians" form an unresolved clade that is the sister to crown clade Chondrichthyes.**

Part C. Supplementary References

Bangert, B., Stollhofen, H., Lorenz, V. & Armstrong, R. The geochronology and significance of ash-fall tuffs in the glaciogenic Carboniferous-Permian Dwyka Group of Namibia and South Africa. *Journal of African Earth Sciences* **29**, 33-49 (1999).

Basden, A. M. & Young, G. C. A primitive actinopterygian neurocranium from the Early Devonian of Southeastern Australia. *J. Vertebr. Paleontol.* **21**, 754-766 (2001).

Basden, A. M., Young, G. C., Coates, M. I. & Ritchie, A. The most primitive osteichthyan braincase? *Nature* **403**, 185–188 (2000).

Bendix-Almgreen, S. E. The paired fins and shoulder girdle in *Cladoselache*, their morphology and phyletic significance. *Colloques Internationaux du Centre National de la Recherche Scientifique* **218**, 111-123 (1975).

Benznosov, P. A redescription of the Early Carboniferous acanthodian *Acanthodes lopatini* Rohon, 1889. *Acta Zoologica* **90** (supplement 1), 183-193 (2009).

Bernacsek, G. M. & Dineley, D. L. New acanthodians from the Delorme Formation (Lower Devonian) of N.W.T., Canada. *Paleontographica Abt.A* **158,** 1-25 (1977).

Brazeau, M. D. The braincase and jaws of a Devonian 'acanthodian' and modern gnathostome origins. *Nature* **457**, 305-308 (2009).

Brazeau, M. D. & Friedman, M. The characters of Palaeozoic jawed vertebrates. *Zoological Journal of the Linnean Society*, **170**, 779-821 (2014)

Burrow, C. J. & Turner, S. Devonian placoderm scales from Australia. *Journal of Vertebrate Paleontology* **18**, 677-695 (1998).

Burrow, C. J. & Turner, S. A review of placoderm scales, and their significance in placoderm phylogeny. *Journal of Vertebrate Paleontology* **19**, 204-219 (1999).

Burrow, C. J. & Turner, S. Scale structure of the putative chondrichthyan *Gladbachus adentatus* Heidtke & Krätschmer, 2001 from the Middle Devonian Rheinisches Schiefergebirge, Germany. *Historical Biology* **25**, 385-390 (2013).

Burrow, C. J., Turner, S. & Heidtke, U. H. J. The squamation of *Gladbachus adentatus* Heidtke & Kratschmer, 2001. *UNESCO-IUGCP 491: The Gross Symposium 2 Advances in Palaeoichthyology, Riga, Latvia, September* 7-14, 2003, p 16-17 (2003).

Carr, R. K., Johanson, Z. & Ritchie, A. The phyllolepid placoderm *Cowralepis mclachlani*: insights into the evolution of feeding mechanisms in jawed vertebrates. *J. Morph* **270**, 775-804 (2009).

Catuneanu, O., Hancox, P. J. & Rubidge, B. S. Reciprocal flexural behaviour and contrasting stratigraphies: a new basin development model for the Karoo retroarc foreland system, South Africa. *Basin Research* **10**, 417–439 (1998).

Catuneanu O., Hancox, P. J., Cairncross, B. & Rubidge, B. S. Foredeep submarine fans and forebulge deltas: orogenic off-loading in the underfilled Karoo Basin. *Journal of African Earth Sciences* **35** 489–502 (2002).

Choo, B. Revision of the actinopterygian genus *Mimipiscis* (= *Mimia*) from the Upper Devonian Gogo Formation of Western Australia and the interrelationships of early Actinopterygii. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **102**: 77-104 (2011)

Cloutier, R. & Ahlberg, P. E. in *Interrelationshps of Fishes* (eds Stiassny, M. L. J., Parenti, L. R. & Johnson, G. D.) 445–479. (Academic, 1996).

Coates, M. I. The origin of vertebrate limbs. *Development* Supplement, 169-180 (1994).

Coates, M. I. *Gladbachus adentatus* Heidtke & Kratschmer; is it a chondrichthyan, and if so, where does it fit in phylogeny? *Paleobios* **25**, 31-32 (2005).

Coates, M. I. & Gess, R. W. A new reconstruction of *Onychoselache Traquairi*, comments on early chondrichthyan pectoral girdles and hybodontiform phylogeny. *Palaeontology* **50**, 1421-1446 (2007).

Coates, M. I. & Friedman, M. in *Morphology, Phylogeny and Paleobiogeography of Fossil Fishes*. (eds Elliot, D.K., Maisey, J.G., Yu, X. & Miao, D.) 389–416 (Freidrich Pfeil, 2010).

Coates, M. I., Sansom, I. J. & Smith, M. M. Spines and tissues of ancient sharks. *Nature* **396**, 729-730 (1998).

Coates, M. I. & Sequeira, S. E. K. The braincase of a primitive shark. *Trans. R. Soc. Edinb. (Earth Sci.)* **89**, 63–85 (1998).

Coates, M. I. & Sequeira, S. E. K. A new stethacanthid chondrichthyan from the Lower Carboniferous of Bearsden, Scotland. *J. Vertebr. Paleontol.* **21**, 754–766 (2001a).

Cole, D. I. Prince Albert Formation. Catalogue of South African lithostratigraphic units, 4pp. South African Committee for Stratigraphy (SACS), Council for Geosciences, Dept. of Mineral and Energy Affairs S.A. (2005).

Cole, F. J. On the cranial nerves of *Chimaera monstrosa* (Linn.); with a discussion of the lateral line system and of the morphology of the chorda tympani. *Trans. R. Soc. Edinb*. **38**, 631-680 (1896).

Compagno, L. J. V. in *Sharks, Skates, and Rays, the Biology of Elasmobranch Fishes* (ed. Hamlett, W. C.) 69-92 (Johns Hopkins University, 1999).

Daniel, J. F. *The Elasmobranch Fishes* (Univ. California, 1922).

Davis, S. P. Comparative anatomy and relationships of the acanthodian fishes. *Unpublished PhD thesis, Unv. London*, 1–318. (2002).

Davis, S. P., Finarelli, J. A., & Coates, M. I. *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes. *Nature* **486**, 247-250 (2012).

De Beer, G. R. *The Development of the Vertebrate Skull* (Univ. Chicago, 1937).

De Beer, G. R. & Moy-Thomas, J. A. On the skull of Holocephali. *Philos. Trans. R. Soc. London B. Biol. Sci*. **224**: 287-312 (1935).

de Wit, M. J., Ransome, I. G. D. in *Inversion Tectonics of the Cape Fold Belt, Karoo and Cretaceous Basins of Southern Africa* (eds de Wit, M. J., Ransome, I. G. D.) 15–21 (Balkema, Rotterdam, 1992).

Dean, M. N. & Summers, A. P. Cartilage in the skeleton of cartilaginous fishes. *Zoology* **109**,164–168 (2006).

Dean, M. N., Mull, C. G., Gorb, S. N. & Summers, A. P. Ontogeny of the tessellated skeleton: insight form the skeletal growth of the round stingray *Urobatis halleri*. *J. Anat*. Doi: 10.1111/j.1469-7580.2009.01116x (2009).

Denison, R. in *Handbook of Paleoichthyology* Vol. 5 (ed. Schultze, H.-P.) (Gustav Fischer Verlag, Stuttgart, 1979).

Dick, J. R. F. On the Carboniferous shark *Tristychius arcuatus* Agassiz from Scotland. *Trans. R. Soc. Edinb.* **70**, 63–109 (1978).

Dick, J. R. F. & Maisey, J. G. The Scottish Lower Carboniferous shark *Onychoselache traquairi*. *Palaeontology* **23**, 363-374 (1980).

Didier, D. A. Phylogenetic systematics of extant chimaeroid fishes (Holocephali, Chimaeroidei). *Am. Mus. Novit.* **3119**, 1–86 (1995).

Didier, D. A., Kemper, J. M. & Ebert, D. A. in *Biology of Sharks and Their Relatives* (eds Carrier, J. C., Musick, J. & Heithaus, M. R.) 97-122 (CRC Press, 2012).

Didier, D. A., LeClair, E. & VanBuskirk, D. R. Embryonic staging and external features of development of the chimaeroid fish, *Callorhinchus milii* (Holocephali, Callorhinchidae). *Journal of Morphology* **236**, 25-47 (1998).

Didier, D. A., Stahl, B. J. & Zangerl R. Development and growth of compound tooth plates in *Callorhinchus milii* (Chondrichthyes, Holocephali). *Journal of Morphology* **222**, 73-89 (1994).

Donoghue, P. C. J., & Aldridge, R. J. in *Major events in early vertebrate evolution: palaeontology, phylogeny, genetics and development.* (ed Ahlberg P.E.) 85–105 (Taylor & Francis, 2001).

Donoghue, P. C. J., Forey, P.L. & Aldridge, R. J. Conodont affinity and chordate phylogeny. *Biol. Rev.***75**, 191–251 (2000).

Dupret, V., Sanchez, S., Goujet, D., Tafforeau, P. & Ahlberg, P. E. A primitive placoderm sheds light on the origin of the jawed vertebrate face. *Nature* **507**, 500-503 (2014).

Finarelli, J. A. & Coates, M. I. First tooth-set outside the jaws in a vertebrate. *Proceedings of the Royal Society of London Series B-Biological Sciences* **279,** 775-779 (2012).

Finarelli, J. A. & Coates, M. I. *Chondrenchelys problematica* (Traquair, 1888) redescribed: a Lower Carboniferous, eel-like holocephalan from Scotland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **105**, 1-25 (2014).

Forey, P. L. *Latimeria*: a paradoxical fish. *Proc. R. Soc. London, Ser. B* **208**, 369–384 (1980).

Friedman, M. *Styloichthys* as the oldest coelacanth: implications for early osteichthyan interrelationships. *J. Syst. Palaeontol.* **5**, 289–343 (2007).

Friedman, M. & Brazeau, M. A reappraisal of the origin and basal radiation of the Osteichthyes. *J. Vertebr. Paleontol.* **30**, 36–56 (2010).

Gagnier, P.-Y. & Wilson, M. V. H. Early Devonian acanthodians from northern Canada. *Palaeontology* **39**, 241–258 (1996a).

Gagnier P. –Y. & Wilson, M. V. H. An unusual acanthodian from Northern Canada: revision of *Brochoadmones milesi*. *Modern Geology* **20**, 235-251 (1996b).

Gai, Z., Donoghue, P. C. J., Zhu, M., Janvier, P. & Stampanoni, M. Fossil jawless fish from China foreshadows early jawed vertebrate anatomy. *Nature* **476**, 324-367 (2011).

Gans, C. & Parsons, T. S. *A Photographic Atlas of Shark Anatomy* (Academic Press, New York, 1964).

Gardiner B. G. The relationships of the palaeoniscoid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bull. Br. Mus. Nat. Hist. (Geol.)* **37**, 173–428 (1984).

Gardiner B. G. & Bartram A. W. H. in *Problems in Vertebrate Evolution* (eds Andrews, S. M., Miles, R. S., Walker & A. D.) 227-245 (Linnean Symposium Series, London, 1977).

Gess R. W. & Coates M. I. High-latitude chondrichthyans from the Late Devonian (Famennian) Witpoort formation of South Africa. *Paläontol Z.* DOI 10.1007/s12542-014-0221-9 (2014).

Giles, S. & Friedman, M. Virtual reconstruction of endocast anatomy in early ray-finned fishes (Osteichthyes, Actinopterygii). *Journal of Paleontology* **88**, 636-651 (2014).

Giles, S., Friedman, M. & Brazeau, M. D. Osteichthyan-like cranial conditions in an Early Devonian stem gnathostome. *Nature* **520**, 82-85 (2015).

Goodrich E. S. *Studies on the structure and development of vertebrates* (Univ. Chicago Press, 1930).

Goujet, D. *Dicksonosteus*, un nouvel arthrodire du Dévonien du Spitsbert. Remarques sur le squelette viscéral des Dolichothoraci. *Colloques Internationaux du Centre National de la Recherche Scientifique* **218**, 81-99 (1975).

Goujet, D. *Les Poissons Placodermes du Spitsberg* (Cahiers de Paléontologie, Section Vertebrés, Centre national de la Recherche scientifique, 1984).

Grogan, E. D. & Lund, R. *Debeerius ellefseni* (Fam. Nov., Gen. Nov., Sped. Nov.) an Autodiastylic Chondrichthyan From the Mississippian Bear Gulch Limestone of Montana (USA), the Relationships of the Chondrichthyes, and Comments on Gnathostome Evolution. *J. Morphol.* **243**, 219–245 (2000).

Grogan, E. D., Lund, R. & Greenfest-Allen, E. in *Biology of Sharks and Their Relatives* (eds Carrier, J. C., Musick, J. A. & Heithaus, M. R.) 3-29 (CRC Press, 2012).

Gross, W. Das Kopfskelett on *Cladodus wildungensis* Jaekel; 1. Teil. Endocranium und Palatoquadratum. *Senckenbergiana* **19**, 80-107 (1937).

Gross, W. Das Kopfskelett on *Cladodus wildungensis* Jaekel; 2. Teil. Der Kieferbogen. Anhang: *Protracrodus vetustus* Jaekel. *Senckenbergiana* **20**, 123-145 (1938).

Hanke, G. F., & Wilson, M. V. H. in *Recent Advances in the Origin and Early Radiation of Vertebrates*. (eds Arratia, G., Wilson, M. V. H., & Cloutier, R.) 189–216 (Freidrich Pfeil, 2004).

Hanke, G. F. & Wilson, M. V. H. Anatomy of the Early Devonian Acanthodian *Brochoadmones milesi* based on nearly complete body fossils, with comments on the evolution and development of paired fins. *J. Vertebr. Paleontol*. **26**, 526-537 (2006).

Hanke, G. F., & Wilson, M. V. H. in *Morphology, Phylogeny and Paleobiogeography of Fossil Fishes*. (eds Elliot, D.K., Maisey, J.G., Yu, X. & Miao, D.) 159–182 (Freidrich Pfeil, 2010).

Harris, J. E. The dorsal fin spine of *Cladoselache*. *Scientific Publications of the Cleveland Museum of Natural History* **8**, 1-6 (1938a).

Harris, J. E. The neurocranium and jaws of *Cladoselache*. *Scientific Publications of the Cleveland Museum of Natural History* **8**, 7-12 (1938b).

Heidtke, U. H. J. Der Xenacanthide *Orthacanthus senckenbergianus* aus dem pfälzischen Rotliegenden (Unter-Perm). *Pollichia* **70**, 65-86 (1982).

Heidtke, U. H. J. Studien über *Acanthodes*. 4. *Acanthodes boyi* n. sp., die dritte Art der Acanthodier (Acanthodii: Pisces) aus dem Rotliegend (Unterperm) des Saar-Nahe-Beckens (S-W-Deutschland. *Paläont. Z.* **67**, 331-341 (1993).

Heidtke, U. H. J. *Orthacanthus (Lebachacanthus) senckenbergianus* Fritsch 1889 (Xenacanthida: Chondrichthyes): revision, organization und phylogenie. *Frieberger Forschungsheft*, **481**, 63-106 (1999).

Heidtke, U. H. J. *Gladbachus adentatus*, die Geschichte des weltweit ältesten Hais – untersucht und beschriebenaus dem AK Geowissenschaften. *Pollichia Kurrier* **25**, 24-26 (2009).

Heidtke, U. H. J., Schwind, C. & Krätschmer K. Über die Organisation des Skelettes und die verwandschaftlichen Beziehungen der Gattung Triodus Jordan 1849 (Elasmobranchii: Xenacanthida). *Mainzer geowiss. Mitt.* **32**, 9-54 (2004).

Heidtke, U. H. J. *Gladbachus adentatus*, die Geschichte des weltweit ältesten Hais – untersucht und beschrieben aus dem AK Geowissenschaften. *Pollichia-Kurrier* **25**, 24-26 (2009).

Heidtke, U. H. J. & Krätschmer K. *Gladbachus adentatus* nov. gen. et sp., ein primitiver Hai aus dem Oberen Givetium (Oberes Mitteldevon) der Bergisch Gladbach – Paffrath-Mulde (Rheinisches Schiefergebirge). *Mainzer geowiss. Mitt.* **30**, 105-122 (2001).

Herbert, C. T. &. Compton, J. S. Depositional environments of the lower Permian Dwyka diamictite and Prince Albert shale inferred from the geochemistry of early diagenetic concretions, southwest Karoo Basin. *South Africa Sedimentary Geology* **194**, 263–277 (2007).

Holmgren, N. Studies on the head in fishes, Part III. *Acta zool., Stockh*. **23**, 129-261 (1942).

Hotton, N. Jaws and teeth of American xenacanth sharks. *Journal of Paleontology* **26**, 489-500 (1952).

Howard, L. E., Holmes, W. M., Ferrando, S., Maclaine, J. S., Kelsh, R. N., Ramsey, A., Abel R. L. & Cox P. L. J. Functional nasal morphology of chimaeroid fishes. *Journal of Morphology* **274**, 987-1009 (2013).

Janvier, P. *Les Céphalaspides du Spitsberg. Anatomie, phylogénie et systématique des Ostéostracés siluro-dévoniens. Révision des Ostéostracés de la Formation de Wood Bay (Dévonien inférieur du Spitsberg)* (Cahiers de Paléontologie, Section Vertebres, Centre National de la Recherche Scientifique, 1985).

Janvier, P. *Early Vertebrates* (Oxford Univ. Press, 1996).

Janvier, P. & Maisey, J. G. (2010) in *Morphology, Phylogeny and Paleobiogeography of Fossil Fishes*. (eds Elliot, D.K., Maisey, J.G., Yu, X. & Miao, D.) 431–459 (Freidrich Pfeil, 2010).

Jarvik, E. in *Problems in Vertebrate Evolution*. (eds Andrews, S. M., Miles, R. S., Walker & A. D.) 199-225 (Linnean Symposium Series, London, 1977).

Jarvik, E. *Basic Structure and Evolution of Vertebrates* (Academic, 1980).

Kesteven, H. L. The anatomy of the head of *Callorhynchus antarcticus*. *Journal of Anatomy* **67**, 443-474

(1932).

Lane, J. A. Morphology of the braincase in the Cretaceous hybodont shark *Tribodus linnae* (Chondrichthyes: Elasmobranchii), based on CT scanning. *Amer. Mus. Novitates* **2758**, 1-70 (2010).

Lane, J. A. & Maisey, J. G. The visceral skeleton and jaw suspension in the durophagous hybodontid shark *Tribodus limae* from the Lower Cretaceous of Brazil. *Journal of Paleontology* **86,** 886-905 (2012).

Liem, K., & Summers, A. P. in *Sharks, Skates, and Rays, the Biology of Elasmobranch Fishes* (ed. Hamlett, W. C.) 93-114 (Johns Hopkins University, 1999).

Long, J. A., Trinajstic, K. M., & Johanson, Z. Devonian arthrodire embryos and the origin of internal fertilization in vertebrates. *Nature* **457**, 1124-1127 (2009).

Long, J. A., Mark-Kurik, E., Johanson, Z, Lee, M. S. Y., Young, G. C., Zhu, M., Ahlberg, P. E., Newman, M., Jones, R., den Blaauwen, J., Choo, B. & Trinajstic, K. Copulation in antiarch placoderms and the origin of gnathostome internal fertilization. *Nature* **517**, 196-199 (2015).

Lund, R. *Harpagofututor volsellorhinus* new genus and species (Chondrichthyes, Chondrenchelyiformes) from the Namurian Bear Gulch Limestone, *Chondrenchelys problematica* and their sexual dimorphism. *Journal of Paleontology* **56**, 938-958 (1982).

Lund, R. The morphology of *Falcatus falcatus* (St. John and Worthen), a Mississippian stethacanthid chondrichthyan from the Bear Gulch Limestone of Montana. *Journal of Vertebrate Paleontology* **5**, 1-19 (1985).

Lund, R. On *Damocles serratus*, nov. gen. et. sp. (Elasmobranchii: Cladodontida) from the Upper Mississippian Bear Gulch Limestone of Montana. *Journal of Vertebrate Paleontology* **6**, 12-19 (1986).

Lund, R. & Grogan, E. D. Relationships of the Chimaeriformes and the basal radiation of the Chondrichthyes. *Reviews in Fish Biology and Fisheries* **7**, 65-123 (1997).

Lund, R. & Grogan, E. D. in *Recent Advances in the Origin and Early Radiation of Vertebrates* (eds Arratia, G., Wilson, M. V. H. & Cloutier, R.) 171–187 (Friedrich Pfiel, 2004a).

Lund, R. & Grogan, E. D. in *Recent Advances in the Origin and Early Radiation of Vertebrates* (eds Arratia, G., Wilson, M. V. H. & Cloutier, R.) 505–531 (Friedrich Pfiel, 2004b).

Maddison, W. P. and Maddison, D. R. *Mesquite: A modular system for evolutionary analysis.* Version 2.71. http://mesquiteproject.org Version 2.71 (2009).

Maisey, J. G. The anatomy and interrelationships of Mesozoic hybodont sharks. *Am. Mus. Novit.* **2724**, 1–48 (1982).

Maisey, J. G. Cranial anatomy of *Hybodus basanus* Egerton from the Lower Cretaceous of England. *Am. Mus. Novit.* **2758**, 1–64 (1983).

Maisey, J. G. Chondrichthyan phylogeny: a look at the evidence. *J. Vertebr. Paleontol*. **4**, 359–371 (1984).

Maisey, J. G. Cranial Morphology of the Fossil Elasmobranch *Synechodus dubrisiensis*. *American Museum Novitates* **2804**, 1-28 (1985).

Maisey, J. G. Visceral skeleton and musculature of a Late Devonian shark. *J. Vertebr. Paleontol*. **9**, 174–190 (1989a).

Maisey, J. G. *Hamiltonichthys mapesi* g. & sp. nov. (Chondrichthyes; Elasmobranchii), from the Upper Pennsylvanian of Kansas. *American Museum Novitates* **2931**, 1-42 (1989b).

Maisey, J. G. in *Major Events in Early Vertebrate Evolution* (ed. Ahlberg, P. E.) 263–288 (Taylor and Francis, 2001a).

Maisey, J. G. Remarks on the inner ear of elasmobranchs and its interpretation from skeletal labyrinth morphology. *J. Morph.* **250**, 236-264. (2001b).

Maisey, J. G. Braincase of the Upper Devonian shark *Cladodoides wildungensis* (Chondrichthyes, Elasmobranchii), with observations on the braincase in early chondrichthyans. *Bull. Am. Mus. Nat. Hist*. **288**, 1–103 (2005).

Maisey, J. G. The braincase in Paleozoic symmoriiform and cladoselachian sharks. *Bull. Am. Mus. Nat. Hist*. **307**, 1–122 (2007).

Maisey, J. G. The postorbital palatoquadrate articulation in elasmobranchs. *Journal of Morphology* **269**, 1022-1040 (2008a).

Maisey, J. G. Some observations on *Denaea fournieri* (Chondrichthyes, Symmoriiformes) from the Lower Carboniferous of Belgium. *Acta Geologica Polonica* **58**, 185-190 (2008b).

Maisey, J. G. The diversity of tessellated calcification in modern and extinct chondrichthyans. *Revue de Paléobiologie, Geneve* **32,** 355-371 (2013).

Maisey, J. G. & Anderson, M. E. A primitive chondrichthyan braincase from the Early Devonian of South Africa. *Journal of Vertebrate Paleontology* **21**, 702-713 (2001).

Maisey, J. G. & Lane, J. A. Labyrinth morphology and the evolution of low-frequency phonoreception in elasmobranchs. *C. R. Palevol* **9**, 289-309 (2010).

Maisey, J. G., Miller, R. & Turner, S. The braincase of the chondrichthyan *Doliodus* from the Lower Devonian Campbellton Formation of New Brunswick, Canada. *Acta Zoologica* **90** (supplement 1), 109-122 (2009).

Maisey, J. G., Turner, S., Naylor, G. J. P. & Miller, R. F. Dental patterning in the earliest sharks: implications for tooth evolution. *Journal of Morphology* DOI 10.1002/jmor.20242 (2013)

Marinelli, W. & Strenger, A. *Vergleichende Anatomie und Morphologie der Wirbeltiere*. III. 174-308 (Franz Deuticke, Wien, 1959).

McKay, M. P., Weislogel, A.L., Fildani, A., Brunt, R. L., Hodgson, D. M. & Flint, S. S. U-PB zircon tuff geochronology from the Karoo Basin, South Africa: implications of zircon recycling on stratigraphic age controls. *International Geology Review* **57**,4: 393-410, DOI: 10.1080/00206814.2015.1008592 (2015).

Miles, R. S. in *Current problems of lower vertebrate phylogeny*. (ed. T. Ørvig) 109-127 (Almqvist & Wiksell, Stockholm, 1968).

Miles, R. S. Acanthodii. in *Encyl. Sci. Tech*. 33–34, (McGraw-Hill, 1971).

Miles, R. S. Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder- girdle. *Bull. Br. Mus. Nat. Hist. (Geol.)* **24**, 111–213 (1973a).

Miles, R. S. in *Interrelationships of Fishes* (eds Greenwood, P. H., Miles, R. S. & Patterson, C.) 63–103 (Academic, 1973b).

Miller, R. F., Cloutier, R. & Turner, S. The oldest articulated chondrichthyan from the Early Devonian period. *Nature* **425**, 501–504 (2003).

Mutter, R. J., De Blanger, K. & Neuman, A. G. Elasmobranchs from the Lower Triassic Sulpher Mountain Formation near Wapiti Lake (BC, Canada). *Zool. J. Linn. Soc*. **149**, 309-337 (2007).

Moy-Thomas, J. A. The structure and affinities of *Chondrenchelys problematica* Tr. *Proceedings of the Zoological Society, London***1935**, 391-403 (1935).

Nelson, G. J. in *Current problems of lower vertebrate phylogeny*. (ed. T. Ørvig) 129-143 (Almqvist & Wiksell, Stockholm, 1968).

Nelson, G. J. Pharyngeal denticles (placoid scales) of sharks with notes on the dermal skeleton of vertebrates. *Amer. Mus. Novitates* **2416**, 1-26 (1970).

Oelofsen, B. W. in *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes.* (eds Uyeno, T., Arai, R., Taniuchi, T., Matsuura, K.) 107-124 (Ichthyological Society of Japan, Tokyo, 1986).

Patterson, C. The phylogeny of the chimaeroids. *Philosophical Transactions of the Royal Society of London*, Series B **249**, 101-219 (1965).

Patterson, C. Interpretation of the toothplates of chimaeroid fishes. *Zool. J. Linn. Soc*. **106**, 33-61 (1992).

Pradel, A. Skull and brain anatomy of Late Carboniferous Sibyrhynchidae (Chondrichthyes, Iniopterygia) from Kansas and Oklahoma (USA). *Geodiversitas* **32**, 595-661 (2010).

Pradel, A., Didier D., Casane D., Tafforeau P. & Maisey J. G. Holocephalan embryo provides new information on the evolution of the glossopharyngeal nerve, metotc fissure and parachordal plate. *PLoS ONE* **8**: e66988 doi:10.1371/journal.pone.0066988 (2013).

Pradel, A., Maisey, J. G., Tafforeau, P. & Janvier P. An enigmatic gnathostome vertebrate skull from the Middle Devonian of Bolivia. *Acta Zoologica* **90** (supplement 1), 123-133 (2009a).

Pradel, A., Langer, M., Maisey, J. G., Geffard-Kuriyama, D., Cloetens, P., Janvier, P. & Tafforeau, P. Skull and brain of a 300 million-year-old chimaeroid fish revealed by synchrotron holotomography. *Proceedings of the National Academy of Sciences* **106**, 5224-5228 (2009b).

Pradel, A., Tafforeau, P. & Janvier, P. Study of the pectoral girdle and fins of the Late Carboniferous sibyrhynchid iniopterygians (Vertebrata, Chondrichthyes, Iniopterygia) from Kansas and Oklahoma (USA) by means of microtomography, with comments on iniopterygian relationships. *Comptes Rendus Palevol* **9**, 377-387 (2010).

Pradel, A., Tafforeau, P., Maisey, J. G. & Janvier, P. A new Paleozoic Symmoriiformes (Chondrichthyes) from the Late Carboniferous of Kansas (USA) and Cladistic Analysis of Early Chondrichthyans. *PLoS ONE* **6**: e24938 doi:10.1371/journal.pone.0024938 (2011).

Pradel, A., Maisey, J. G., Tafforeau, P., Mapes, R. H. & Mallatt, J. A Palaeozoic shark with osteichthyan-like branchial arches. *Nature* **509**, 608-611 (2014).

Qu, Q.-M., Zhu, M. & Wang, W. Scales and dermal skeletal histology of an early bony fish *Psarolepis romeri* and their bearing on the evolution of rhombic scales and hard tissues. *PLoS ONE* **8,** doi:10.1371/journal.pone.0061485 (2013a).

Qu, Q., Sanchez, S., Blom, H., Tafforeau, P. & Ahlberg P. E. Scales and Tooth Whorls of Ancient Fishes Challenge Distinction between External and Oral 'Teeth'. *PLoS ONE* **8**, doi:10.1371/journal.pone.0071890 (2013b).

Reif, W.-E. Types of morphogenesis of the dermal skeleton in fossil sharks. *Paläont. Z.* **52**, 110-128 (1978).

Reif, W.-E. Squamation and ecology of sharks. *Cour. Forsch.-Inst. Senckenberg* **78**, 1-255 (1985).

Ritchie, A. *Cowralepis*, a new genus of phyllolepid fish (Pisces, Placodermi) from the late Middle Devonian of New South Wales, Australia. *Proc. Linn. Soc. N.S.W.* **126**, 215–259 (2005).

Rücklin, M., Donoghue, P. C., Johansen, Z., Trinajstic, K., Marone, F. & Stampanoni, M. Development of teeth and jaws in the earliest jawed vertebrates. *Nature* **491**, 748-751 (2012).

Schaeffer, B. (1975). Comments on the origin and basic radiation of the gnathostome fishes with particular reference to the feeding mechanism. *Colloque international C.N.R.S. (Paris)* **218**, 101-109.

Schaeffer, B. The xenacanth shark neurocranium, with comments on elasmobranch monophyly. *Bull. Am. Mus. Nat. Hist.* **169**, 1–66 (1981).

Scheffler, K., Buehmann, D. & Schwark, L. Analysis of late Palaeozoic glacial to postglacial sedimentary successions in South Africa by geochemical proxies – Response to climate evolution and sedimentary environment. *Palaeogeography, Palaeoclimatology, Palaeoecology.* **240:** 184–203 (2006).

Smith, A. G., Hurley, A. M. & Briden, J. C. *Phanerozoic paleocontinental world maps*. (Cambridge: Cambridge University Press. 1981).

Soler-Gijon, R. & Hampe, O. Evidence of *Triodus* Jordan 1849 (Elasmobranchii: Xenacanthidae) in the Lower Permian of the Autun basin (Muse, France). *N. Jb. Geol. Paläont. Mh*. **1998**, 335-348 (1998).

Stahl, B. J. Non-autostylic Pennsylvanian iniopterygian fishes. *Palaeontology* **23**, 315-324 (1980).

Stahl, B. J. in *Handbook of Paleoichthyology* Vol. 4 (ed. Schultze, H.-P.) (Friedrich Pfeil, München. 1999).

Trinajstic, K., Boisvert, C., Long, J., Maksimenko, A. & Johanson, J. Pelvic and repsoductive structures in placoderms (stem gnathostomes). *Biol. Rev*. (2014) 1-35 (2014).

Tucker A. S. & Fraser G. J. Evolution and developmental diversity of tooth regeneration. *Seminars in Cell & Developmental Biology* **25**, 71-80 (2014).

Venkatesh, B., *et al*. Elephant shark genome provides unique insights into gnathostome evolution. *Nature* **505**, 174-179 (2014).

Visser, J. N. J. (1994) in *Earth's Glacial Record* (eds Deynoux, M., Miller, J. M. G., Domack, E. W., Eyles, N., Fairchild, I. & Young, G. M.) 60-69 (Cambridge University Press, Cambridge, 1994)

Williams, M. E. The "cladodont level" sharks of the Pennsylvanian black shales of central North America. *Palaeontographica*, A, **190**, 83-158 (1985).

Williams, M. E. A new specimen of *Tamiobatis vetustus* (Chondrichthyes, Ctenacanthoidea) from the Late Devonian Cleveland Shale of Ohio. *Journal of Vertebrate Paleontology* **18**, 251-260 (1998).

Woodward, A. S. & White, E. I. The dermal tubercles of the Upper Devonian shark, *Cladoselache*. *Annals and Magazine of Natural History* **11**, 367-368 (1938).

Young, G. C. New information on the structure and relationships of *Buchanosteus* (Placodermi: Euarthrodira) from the Early Devonian of New South Wales. *Zool. J. Linn. Soc*. **66**, 309–352 (1979).

Young, G. C. A new early Devonian placoderm from New South Wales, Australia, with a discussion of placoderm phylogeny. *Palaeontographica* A**167**, 10–76 (1980).

Young, G. C. Devonian sharks from South-Eastern Australia and Antarctica. *Palaeontology* **25**, 817–843 (1982).

Young, G. C. The relationships of placoderm fishes. *Zool. J. Linn. Soc.* **88**, 1–57 (1986).

Yu, X. A new porolepiform-like fish, *Psarolepis romeri*, gen. et sp. nov. (Sarcopterygii, Osteichthyes) from the Lower Devonian of Yunnan, China. *J. Vertebr. Paleontol*. **18**, 261-264 (1998).

Zangerl, R. in *Handbook of Paleoichthyology* Vol. 3A (ed. Schultze, H.-P.) (Gustav Fischer Verlag, Stuttgart,1981).

Zangerl, R. *Cervifurca nasuta* n. gen. et sp., an interesting member of the Iniopterygidae (Subterbranchialia, Chondrichthyes) from the Pennsylvanian of Indiana, U.S.A. *Fieldiana: Geology*, **35**, 1-24 (1997).

Zangerl, R. & Case, G. R. Iniopterygia, a new order of chondrichthyan fishes from the Pennsylvanian of North America. *Fieldiana: Geology* **6**, 1-67 (1973).

Zangerl, R. & Case, G. R. *Cobelodus aculeatus* (Cope), ananacanthous shark from Pennsylvanian black shales of North America. *Palaeontographica*, A, **154**, 107–157 (1976).

Zhu, M. & Schultze, H. P. The oldest sarcopterygian fish. *Lethaia* **30**, 293-304 (1997).

Zhu, M & Yu, X. A primitive fish close to the common ancestor of tetrapods and lungfish. *Nature* 418, 767-770 (2002).

Zhu, M., Yu, X. & Janvier, P. A primitive fossil fish sheds light on the origin of bony fishes. *Nature* **397**, 607–610 (1999).

Zhu, M., Yu, X, & Ahlberg, P. E. A primitive sarcopterygian fish with an eyestalk. *Nature* **410**, 81-84 (2001).

Zhu, M., Zhao, W., Jia, L., Lu, J., Qiao, T. & Qu, Q. The oldest articulated osteichthyan reveals a mosaic of gnathostome characters. *Nature* **458**, 469-474 (2009).

Zhu, M., Yu, X., Ahlberg, P. E., Choo, B., Lu, J., Qiao, Q., Zhao, L. J., Blom, H., & Zhu, Y. A Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature* **52**, 188-193 (2013).