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The early elasmobranch *Phoebodus*: phylogenetic relationships, ecomorphology and a new time-scale for shark evolution

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Anatomical knowledge of early chondrichthyans and estimates of their phylogeny are improving, but many taxa are still known only from micro-remains. The nearly cosmopolitan and regionally abundant Devonian genus *Phoebodus* has long been known solely from isolated teeth and fin spines. Here, we report the first skeletal remains of *Phoebodus* from the Famennian (Late Devonian) of the Maïder region of Morocco, revealing an anguilliform body, specialized braincase, hyoid arch, elongate jaws and rostrum, complementing its characteristic dentition and ctenacanth fin spines preceding both dorsal fins. Several of these features corroborate a likely close relationship with the Carboniferous species *Thrinacodus gracia*, and phylogenetic analysis places both taxa securely as members of the elasmobranch stem lineage. Identified as such, phoebodont teeth provide a plausible marker for range extension of the elasmobranchs into the Middle Devonian, thus providing a new minimum date for the origin of the chondrichthyan crown-group. Among pre-Carboniferous jawed vertebrates, the anguilliform body shape of *Phoebodus* is unprecedented, and its specialized anatomy is, in several respects, most easily compared with the modern frilled shark *Chlamydoselachus*. These results add greatly to the morphological, and by implication ecological, disparity of the earliest elasmobranchs.

1. Background

Early chondrichthyans have a notoriously patchy fossil record. Frustratingly, many groups are known from no more than isolated teeth and/or fin spines, although their palaeoecological significance is evident from cosmopolitan and regionally abundant remains. One such taxon is the genus *Phoebodus* [1,2]. The characteristic tricuspid teeth (and tentatively, isolated fin spines [1]) are currently assigned to 13 species [1] known from localities worldwide, and ranging from the Middle Devonian to the Early Carboniferous [1–10]. The only available model for *Phoebodus* skeletal anatomy, and thus, the sole, albeit imprecise, indicator of its phylogenetic affinities, is *Thrinacodus gracia* [11,12] from the Serpukhovian of Bear Gulch, Montana. Previously, the hypothesized *Thrinacodus–Phoebodus* relationship was based on similarities of tooth morphology [1,7]. In most other respects, *T. gracia* is exceptional—a morphological outlier. The cranium is elongate with an acute rostrum, the dentition, although *Phoebodus*-like, is asymmetric and highly recurved [11,12], and the body is unusually slender and elongate. Many of the more precise details of the skeletal anatomy are difficult to resolve because of

the extremely flattened and partly demineralized preservation. The only alternative set of skeletal remains attributed to *Phoebodus* [13] have since been reassigned to the genus *Heslerodus* [14] and grouped with the ctenacanth [1].

Hence, the significance of the present material. Here, we describe one nearly complete skeleton and several three-dimensionally preserved skulls of *Phoebodus* that were discovered in the middle Famennian of the Maïder Basin of Morocco. Importantly, these specimens have proved amenable to computed X-ray tomography. The results add to a growing assemblage of newly detailed data transforming our knowledge of early chondrichthyan morphology and phylogeny [15–23]. In the present work, the morphological description contributes to further phylogenetic analyses that support the placement of *Phoebodus* as a genus of stem elasmobranchs. We discuss the morphological characteristics shared with the tooth form *T. gracia*, and compare the body form with that of the modern elasmobranch *Chlamydoselachus*. Lastly, we consider the implications of the phylogenetic results for the timing of the chondrichthyan crown-group origin.

2. Material and methods

Seven specimens of the new *Phoebodus* were used for this study, all collected from Madene El Mrakib, which is situated in the southern Maïder region of the eastern Anti-Atlas of Morocco (electronic supplementary material, figure S1 and Notes: §1). Five of the cited specimens are housed in the Palaeontological Institute and Museum of the University of Zurich (PIMUZ), Switzerland, and two at the Université Cadi Ayyad, Faculté des sciences et techniques, Département des sciences de la terre, Laboratoire Géosciences et Environnement in Marrakech (AA.MEM.DS.), Morocco. The skeletal remains are preserved in ferruginous concretions of reddish colour found in the Thylacocephalan Layer (formerly described as the Phyllocarid Layer [23]) in which thylacocephalan arthropods are highly abundant [23]. Index ammonoids (*Maeneceras* horizon) within the host rock suggest an early middle Famennian age [24,25]. The material includes the cranial, visceral arch, and postcranial skeletal remains of an almost complete shark, as well as six three-dimensionally preserved crania.

Computed tomograms of some of the three-dimensionally preserved skulls were acquired using a Nikon XT H 225 ST industrial CT-scanner at the University of Zurich, Switzerland. The braincase of one exceptionally well-preserved braincase, preserving parts of the otic and occiput, yielded an image stack (TIFF-stack with 1775 projections, provided via the Dryad Digital Repository) with good contrast between matrix and fossil. Data acquisition and image reconstruction parameters: 221 kV, 349 mA; filter: 2 mm of copper; voxel sizes in mm: 0.0776 in each direction; the data were exported as a raw volume. The volume was manually segmented and anatomical reconstructions were performed using the software Mimics v. 17 (<http://www.biomedical.materialise.com/mimics>; Materialise, Leuven, Belgium). Smoothing, colours, and lighting were edited in MeshLab v. 2016 (<http://www.meshlab.net>; [26]) and blender v. 2.79b (<https://www.blender.org>; Amsterdam, The Netherlands).

Our taxon and character matrix, assembled to evaluate the evolutionary relationships of *Phoebodus*, was modified from that of Coates *et al.* [20] and sources listed within. In order to simplify the search procedure, 26 stem gnathostome taxa (see electronic supplementary material, notes: §2) and 45 uninformative characters were excluded. Six characters were added or modified substantially (characters 5, tubular dentine; 20, cranial cap denticles; 52, ceratohyal condition; 66, triscuspid teeth; 99, expanded orbitonasal lamina; 100, ethmo-rostral region elongate), and the revised data matrix now contains 221 characters and 59 in-group

taxa including the addition of fossil genera *Phoebodus* and *Thrinacodus* (electronic supplementary material, notes: §3). Character and taxon sampling sources and discussion are provided in the electronic supplementary material. Phylogenetic analyses used maximum parsimony implemented in PAUP* 4.0a.165 [27]. For the nodal support, we resampled the data using 10 000 bootstrap replicants (bootstrap options in PAUP* 4.0a) and calculated Bremer support retaining suboptimal trees up to 4 extra steps.

3. Systematic palaeontology

Class: Chondrichthyes [28].

Subclass: Elasmobranchii [29].

Plesion: Phoebodontiformes [1].

Genus: *Phoebodus* [30].

Type species: *Phoebodus sophiae* Ginter *et al.*, 2010, Givetian to Famennian; distribution nearly cosmopolitan.

Other species: *Phoebodus saidselachus* sp. nov.

(a) Amended diagnosis of genus

Tooth sets separated by gaps; individual teeth with crown bearing three long main cusps with sigmoid profile, equally sized or with median cusp slightly shorter; short intermediate cusplets occasionally present; base symmetric; single orolingual button on lingual torus; arcuate basolabial projection; single aboral and lingual basal canal openings. Jaws amphistylic; otic process of the palatoquadrate dorsoventrally short; ceratohyal anteriorly blade-shaped; pharyngeal teeth present. Otic division of braincase and elongate occipital region of near equal length; hypotic lamina massive. Anguilliform body bearing multicuspid scales; two dorsal fins, each with calcified base plates and fin spines (amended from [1]).

(b) New species

Phoebodus saidselachus sp. nov.

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(c) Etymology

Named for Said Oukherbouch (Tafraoute), our Moroccan field collaborator (the Arabic word سعيد means 'happy'), and the Latin word *selachus* (shark).

(d) Material

Holotype: PIMUZ A/I 4712 (figure 1), a concretion with an almost complete individual with three-dimensionally preserved braincase, jaws, hyoid arch, and parts of gill arches, plus largely complete postcranium. Other three-dimensionally preserved cranial remains: A/I 4656, A/I 4710, AA.MEM.DS.1, AA.MEM.DS.2. Three-dimensionally preserved cranial remains of less certain affinity: PIMUZ A/I 4711, A/I 4713.

(e) Locality and horizon

Madene El Mrakib (30°44'407" N, 4°42'899" W) and Aguelmous, Maïder region, Anti-Atlas, Morocco; early middle Famennian, Devonian.

(f) Diagnosis of species

Mandibular teeth with main cusps recurved lingually, of nearly identical length, each with two distinct striae forming sharp

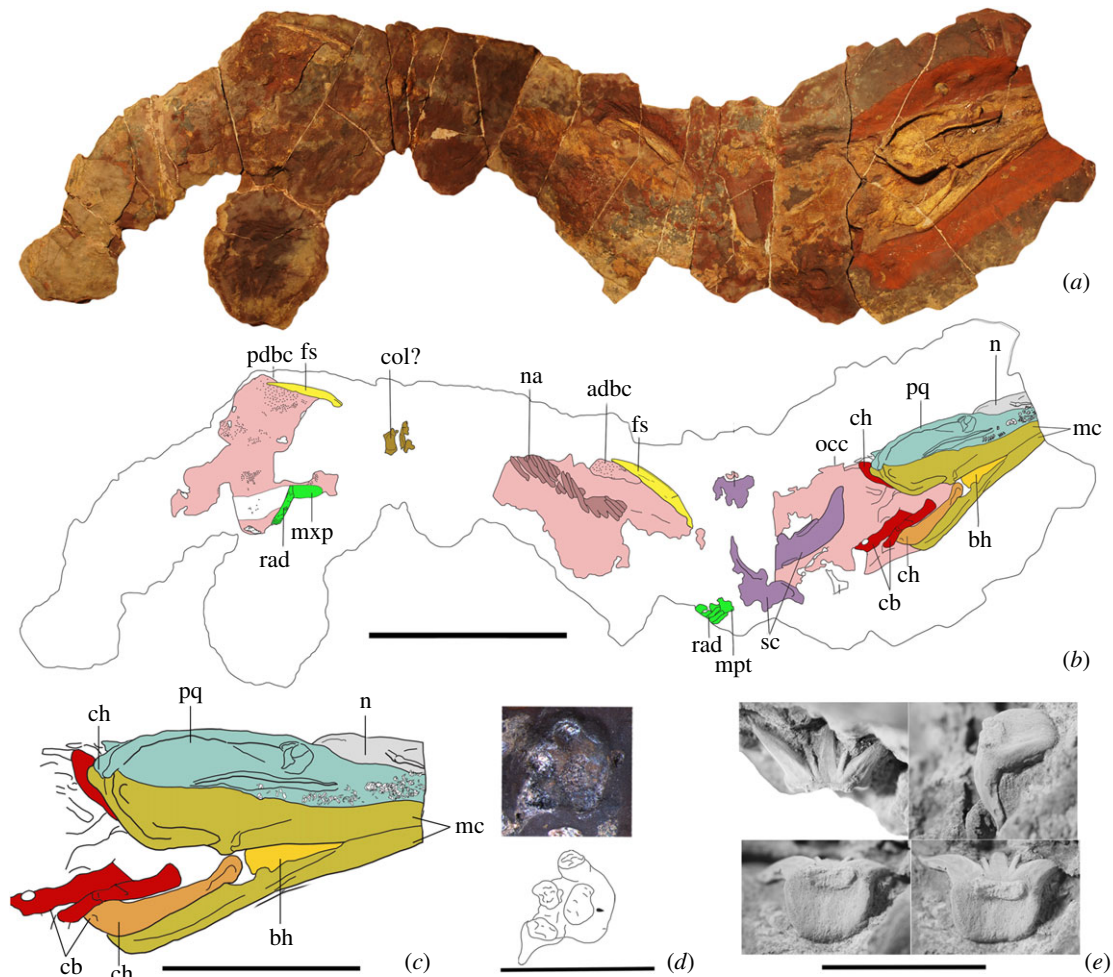


Figure 1. *Phoebodus saidselachus* sp. nov., (a–d) PIMUZ A/I 4712 and (e) PIMUZA/I 4656. (a) Ferruginous nodule containing cranial and postcranial remains; (b) drawing, scale bar, 200 mm; (c) detail of visceral skeleton, scale bar, 100 mm; (d) tooth, scale bar, 5 mm; (e) tooth in labial, aboral, baso-lateral, and linguo-basal views, scale bar, 10 mm. adbc, anterior dorsal basal cartilage; bh, basihyal; cb, ceratobranchial; ch, ceratohyal; col, cololite; fs, fin spine; mc, Meckel's cartilage; mpt, metapterygium; n, neurocranium; na, neural arches; pdbc, posterior dorsal basal cartilage; pq, palatoquadrate; rad, radials; sc, scapulacoracoid. (Online version in colour.)

edges; lateral cusps with broader diameter than the median; two intermediate cusplets reach almost half central cusp length and thickness; tooth base squarish with rounded angles in aboral view: 5.2 mm wide and 4.5 mm long; base outline concave in labial, aboral, and lateral aspects; the basolabial projection wider than the median cusp and labiolingually narrow. Dorsal fin spines with gentle posterior curvature; basal opening extends to at least 50% of total height; insertion deep; ornament of fine ctenoid ridges.

(g) Description

The morphology of *Phoebodus saidselachus* sp. nov. is based primarily on specimens PIMUZ A/I 4656 (figure 1), A/I 4710, A/I 4711 (figure 2; electronic supplementary material, figure S3), and A/I 4712 (electronic supplementary material, figures S6 and S7), presenting body scales, fin spines (electronic supplementary material, figures S6 and S8) [16]), and unambiguously *Phoebodus*-like teeth (figure 1d,e). PIMUZ A/I 4712 preserves most of the anguilliform body outline (figure 1a,b), including an elongate head and exposed jaws, albeit with an incomplete rostrum. The missing rostral apex is present in A/I 4656 (electronic supplementary material, figure S2): a second specimen of the elongate cranium (also in AA.MEM.DS.1, AA.MEM.DS.2). Four further specimens

(PIMUZ A/I 4711, A/I 4713, AA.MEM.DS.1, AA.MEM.DS.2) preserve less complete but three-dimensionally intact examples. Both PIMUZ A/I 4711 and A/I 4713 include the otico-occipital block of the neurocranium, and both display a hitherto unknown elongate occipital unit (figure 2; electronic supplementary material, figure S4). Crucially, PIMUZ A/I 4711 also includes portions of the mandibular arch, with a palatoquadrate, that, although incomplete, matches the distinctive proportions of the example visible in A/I 4712.

Exposed portions of the incompletely revealed teeth indicate that the mandibular dentition of *Phoebodus* is likely homodont. However, most teeth are broken and the diagnostic tooth bases are usually poorly visible, thus we could not verify that only one tooth form (e.g. [18,24,26,27]) occupies the jaws. In PIMUZ A/I 4656, at least seven tooth sets separated by gaps occur in each ramus of the anterior section of the upper jaws, and in A/I 4710, six tooth sets occur in the anterior section of Meckel's cartilage (electronic supplementary material, figures S2c and S3b,c). In PIMUZ A/I 4712, remains of small partly articulated tooth sets lie between the right upper and lower jaw (figure 1a,c). PIMUZ A/I 4656 shows a well-preserved tooth exposing labial, lateral, and oral surfaces (electronic supplementary material, figure S2c: tooth 4A; figure 1e); an identical tooth base is exposed in PIMUZ A/I 4710 (electronic supplementary material,

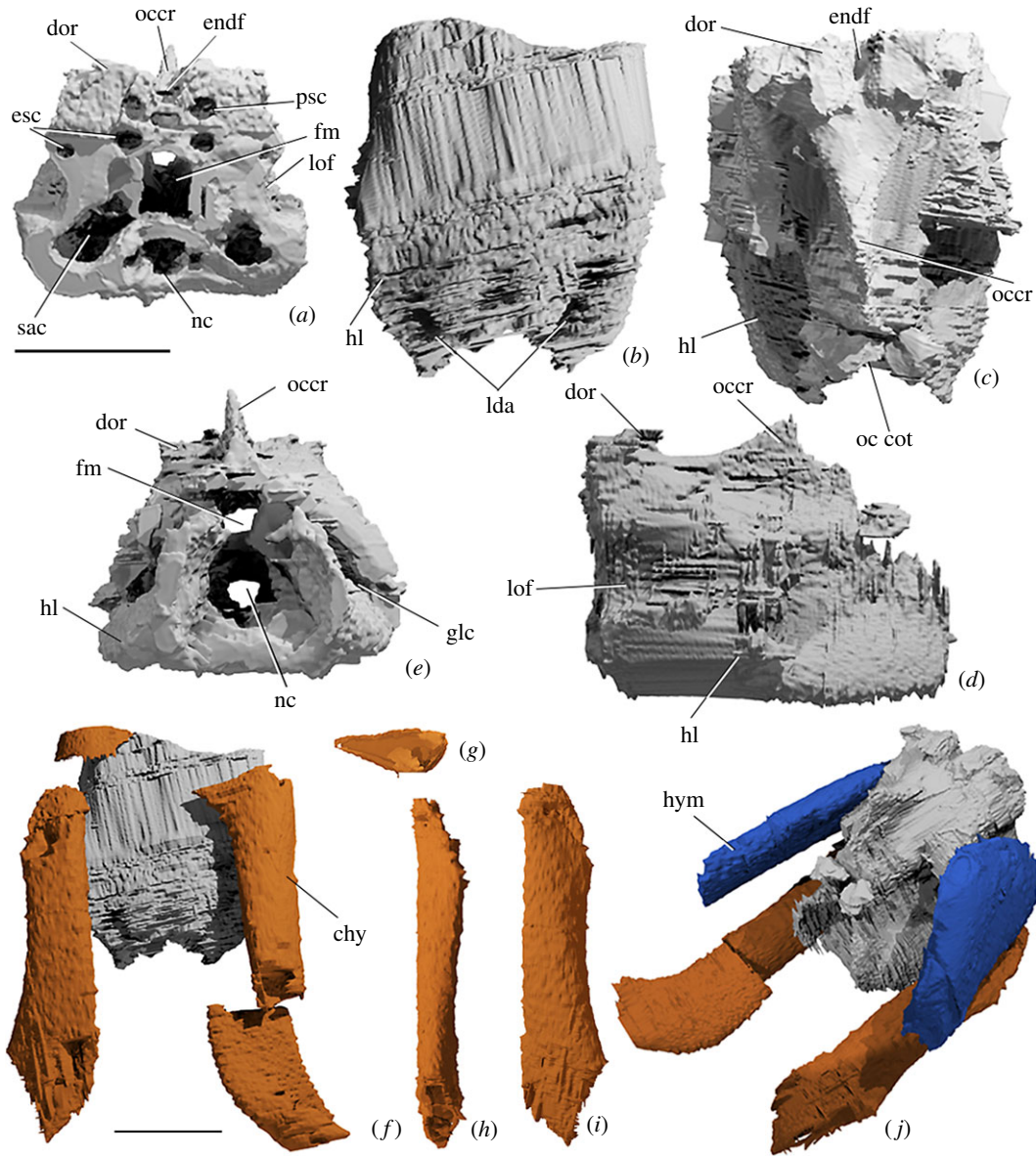


Figure 2. Otic and occipital region of *P. saidselachus* sp. nov., PIMUZ A/I 4711, reconstructed on the basis of CT scans: (a) anterior, (b) ventral, (c) dorsal, (d) lateral, and (e) posterior view. Braincase and articulated branchial arches: (f) ventral view of braincase and ceratohyals, (g) anterior aspect of ceratohyal, (h) lateral view of ceratohyal, (i) oblique lateral view of ceratohyal, (j) dorsolateral view on hyomandibula-braincase articulation. Scale bars, 30 mm. chy, ceratohyal; dor, dorsal otic ridge; endf, endolymphatic foramen; esc, external semicircular canal; fm, foramen magnum; glc, glossopharyngeal canal; hl, hypotic lamina; hym, hyomandibula; lda, lateral dorsal aorta; lof, lateral otic fossa; nc, notochordal canal; oc cot, occipital condyle; occr, occipital crest; psc, posterior semicircular canal; sac, sacculus. (Online version in colour.)

figure S3*b,c*). Labially, two large lateral cusps of nearly identical length flank a slightly smaller median cusp (figure 1*e*). All three main cusps recurve lingually and show a sigmoid outline in lateral view; each is ornamented with two distinct striae forming sharp edges. Two intermediate cusplets reach maximally half of the height and thickness of the median cusp. The tooth base is squarish with rounded angles in aboral view; from labial, aboral, and lateral aspects, the base is concave. The labiolingually narrow basolabial projection is wider than the median cusp. A large aboral foramen of the main basal canal is situated lingually to the basolabial projection. A single orolingual button, wider than the median cusp, covers around half of the labiolingual length of the tooth base (electronic supplementary material, figure S7*b*).

In dorsal and ventral views, the skull tapers anteriorly, terminating in a somewhat blunt snout (electronic supplementary material, figure S2*a,c*). The cranial shape is slender and elongate compared to other early chondrichthyans, although

much less so than in *T. gracia* [11]. CT scans of PIMUZ A/I 4711 delivered anatomical insights into the otic region including semicircular canals and the entire occipital unit (figures 2 and 3). The postorbital process is incomplete (electronic supplementary material, figure S4); only the proximal portion persists. In the otic region, the anterior and posterior semicircular canals unify to form a crus commune as in *Cladodoides*, xenacanthids, and symmoriiforms [15,20,31]. Paired endolymphatic ducts are located anterior to the crus commune (figure 3; electronic supplementary material, figure S4), although the location of the exit on the external surface is unknown. The posteriormost portion of the endolymphatic fossa is narrow and laterally flanked by prominent dorsal otic ridges (figures 2*a,c*; electronic supplementary material, figure S5*a,e*) resembling conditions in *Tamiobatis*, *Orthacanthus*, and *Tristychius* [21,31]. The glossopharyngeal canals are floored by a massive hypotic lamina, which hosts openings for the lateral dorsal aortae posteriorly (figure 2*b,c,e*), signalling that the

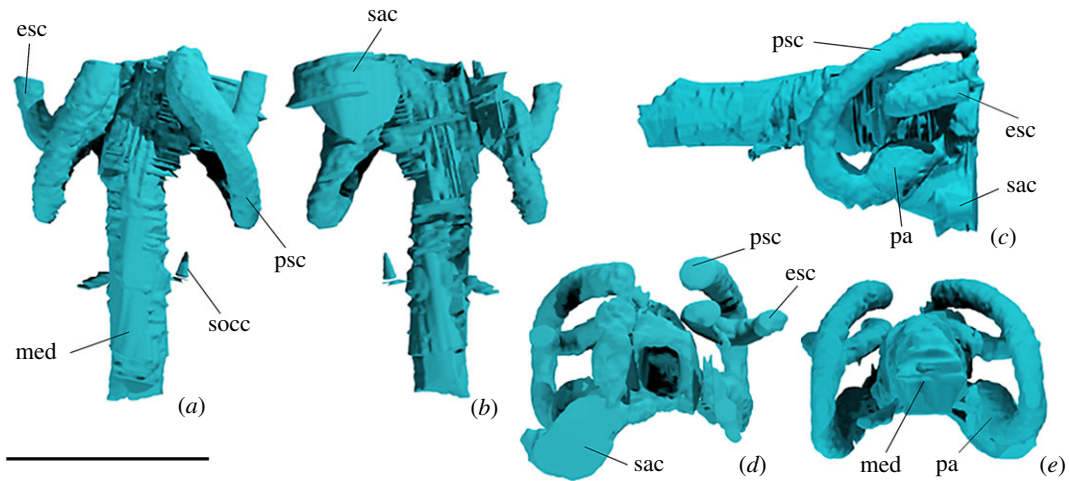


Figure 3. Otic and occipital region of the endocast of *P. saidselachus* (PIMUZ A/I 4711): (a) dorsal, (b) ventral, (c) lateral, (d) anterior, and (e) posterior views. Scale bar, 30 mm. esc, external semicircular canal; med, medulla; pa, posterior ampulla; psc, posterior semicircular canal; sac, sacculus; socc, spino-occipital. (Online version in colour.)

dorsal aorta divided posterior to the occipital level. As in *Cladodoides* and *Tristychius*, there is no prominent lateral otic process.

The occipital unit is exceptionally elongate (figure 2c; electronic supplementary material, figures S4a,b and S5e). The anterior boundary projects between the otic capsules no further than in *Tamiobatis* [31], with the division marked by a similarly formed, persistent otico-occipital fissure. The posterior part is highly apomorphic in extending caudally, so that the total length of the occipital arch accounts for approximately 50% of the entire otico-occipital portion of the braincase. No such condition is evident in *Thrinacodus* [11]. In *Phoebodus*, the greatly extended supraoccipital crest must have inserted between divisions of the epaxial musculature. Traces of three canals for the spino-occipital nerves are preserved on the right lateral side of the occipital arch.

Significantly, the palatoquadrate does not conform to the standard ‘cleaver shape’ [32]. Rather, the otic process is dorsoventrally low (figure 1a–c), barely taller than the palatine ramus, and the posterodorsal rim of the otic process is exceptionally broad. The mode of articulation with the postorbital process is unknown. The palatoquadrate ventral rim, obscured by Meckel’s cartilage and scattered teeth, is paralleled by a lateral ridge for around two-thirds of its length (figure 5; electronic supplementary material, figure S7a–c). It is unclear if this ridge is a specialized feature, or the contorted lateral (labial) margin of the tooth-bearing surface.

The dorsoventral proportions of the posterior part of Meckel’s cartilage match those of the palatoquadrate. The dorsal rim of Meckel’s cartilage is slightly concave anterior to the articulation, but straight for the remainder of the jaw. Posteroventrally, the edge of the right jaw forms a distinctive rim, matching that of the otic process; the paired rims defining an anteroposteriorly broad recess for the jaw adductor muscles. Both jaws taper gradually, anteriorly, with Meckel’s cartilage almost reaching the tip of the rostrum (electronic supplementary material, figure S2c). There are no labial cartilages.

Remains of the hyomandibula extend posteriorly from the posterior of the lateral otic shelf in PIMUZ A/I 4711 and A/I 4713 (electronic supplementary material, figure S5a,e). The hyomandibula head is dorsoventrally broad, flat, elongate, and barely curved, and the orientation is nearly horizontal. The ceratohyal, exposed, posterior to the long, triangular basihyal in PIMUZ A/I 4712 (figures 1c and 2i; electronic supplementary

material, figure S5a,e) is almost half the length of Meckel’s cartilage. The smooth ceratohyal surface shows no trace of a groove, and the posterior portion of the shaft curves dorsally, matching the posterior profile of the mandible. Anteriorly, the ceratohyal narrows, but the anteriormost quarter expands medially to form a flange that likely articulated with the basihyal. A similarly formed ceratohyal with medial flange is present in *Tristychius arcuatus* [33]. Remains of two ceratobranchials are preserved dorsal to the left ceratohyal in PIMUZ A/I 4712. Epibranchials, hypobranchials, pharyngobranchials, and other gill cartilages cannot be determined with certainty.

Traces of the body outline and general proportions preserved in PIMUZ A/I 4712 (figure 1a,b) show that *Phoebodus* was anguilliform, but less slender than *Thrinacodus*. The entire specimen measures 0.98 m from the preserved anterior tip of the rostrum to the most posterior fragment of caudal cartilage, but the complete animal is estimated as at least 1.2 m long, based on the length of the concretion, which usually follows the shape of the incorporated carcass in the Thylacocephalan Layer. The caudal region is largely eroded. The estimated body proportions are as follows: jaw length to body length, maximal 15% and body height to body length maximal 11%.

The scapulocoracoid, although poorly preserved, shows an anteriorly convex coracoid region with a broad ventral–posterior concavity, likely ventral to the articular crest for the pectoral fin radials. Posterior to the coracoid, possible fragments of a metapterygium appear to be articulated to five poorly preserved radials (figure 1a,b).

On the ventral side of the specimen, below the second dorsal fin spine, the concretion extends into a fin-like protrusion. Cartilage remains probably document the former presence of pelvic fins and their position (figure 1a,b).

Fin spines are associated with anterior and posterior dorsal fins (figure 1a,b; electronic supplementary material, figure S6a,b). Both spines are closely aligned to the body outline; their orientation could have been altered taphonomically, but their positions relative to the body axis appear unchanged. The anterior fin spine is longer and thicker than the posterior fin spine; each is slightly recurved with a deep insertion. The ribbed ornament consists of fine costae (between 25 and 30 across the broadest span of the anterior fin spine surface), with transverse ridges creating the classic zipper-like appearance of ‘ctenacanth’ spines (electronic supplementary

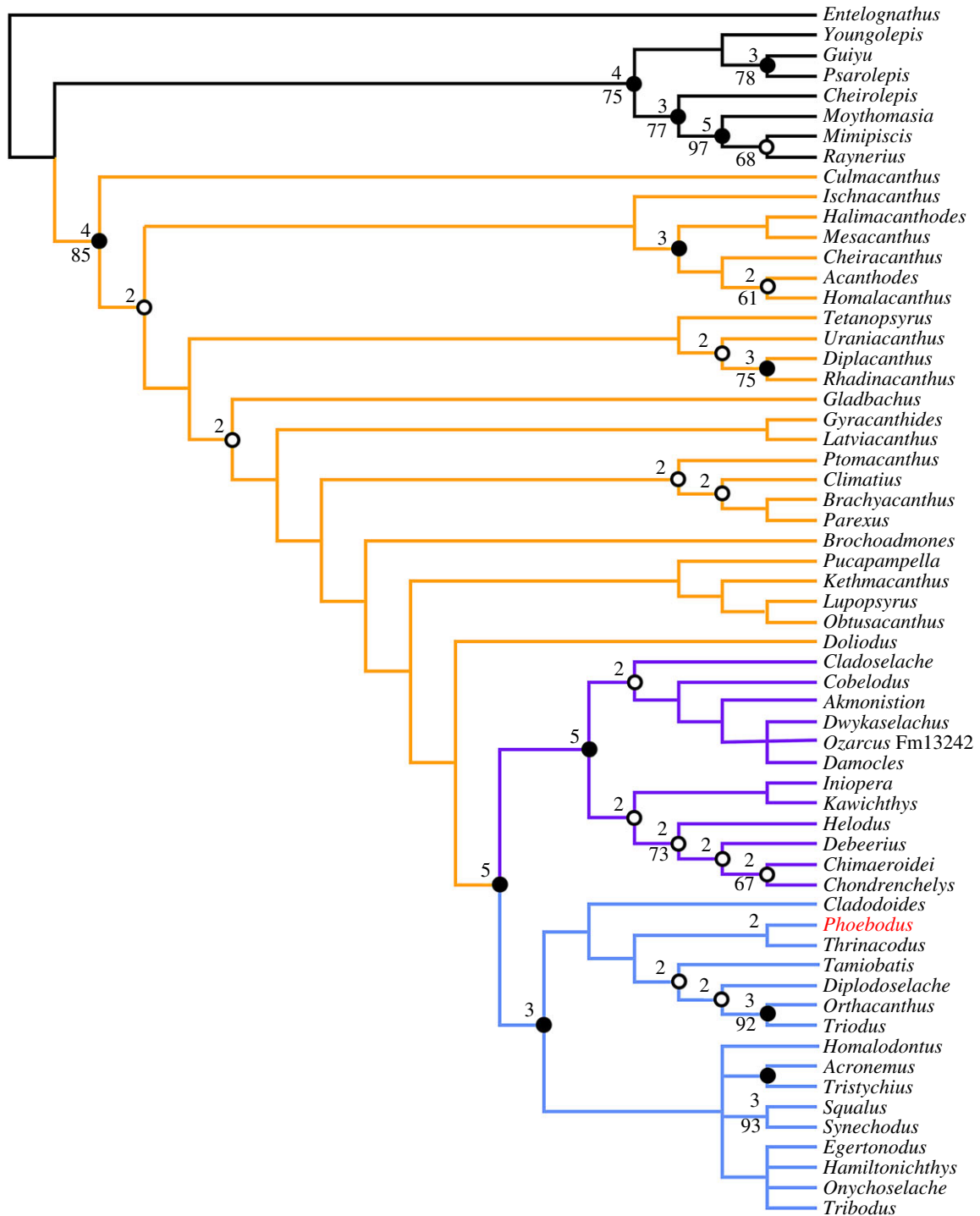


Figure 4. Cladogram (strict consensus tree) showing the placement of *Phoebodus* and *Thrinacodus* within the elasmobranchs. Colour coding: black, stem group gnathostome (outgroup) and Osteichthyes (*Entelognathus* to *Raynerius*); orange, stem Chondrichthyes including Acanthodii (*Culmacanthus* to *Doliodus*); purple, Holocephali (crown Chondrichthyes; *Cladoselache* to *Chondrenchelys*); blue, Elasmobranchii (crown Chondrichthyes, *Cladodoides* to *Tribodus*). White circles: bootstrap support of knot greater than 50% and/or Bremer decay values greater than 1; black circles: bootstrap support greater than 75% and/or Bremer decay values greater than 3. (Online version in colour.)

material, figure S6c). The basal opening appears to have exceeded 50%, perhaps 60% of the total spine length. There are no traces of posterior denticles or a prominent anterior keel. The general appearance is closest to the Mississippian nominal species *Ctenacanthus venustus* (figure 10A, B in [34]; [35]). Dorsal fin radials are absent, but cartilage traces posteroventral to both fin spines likely preserve remains of basal plates (adbc, pdbc, figure 1a,b).

Neural arches are discernible ventral to the anterior dorsal fin spine (figure 1a,b), but there are no traces of centra or other contributory cartilages to the vertebral column.

4. Results

The phylogenetic analysis recovered 105 equally most parsimonious trees (MPTs) of 513 steps (consistency index 0.46; retention index 0.77; RC 0.36). The strict consensus of these MPTs unites *Phoebodus* and *Thrinacodus*, and this clade branches as sister taxon to *Tamiobatis* and xenacanth. The larger, more inclusive clade of xenacanth, phoebodontids, and ctenacanth, extends from the elasmobranch stem lineage (figure 4). Bootstrap support values are generally low across the tree, but decay (Bremer support) values are high for the

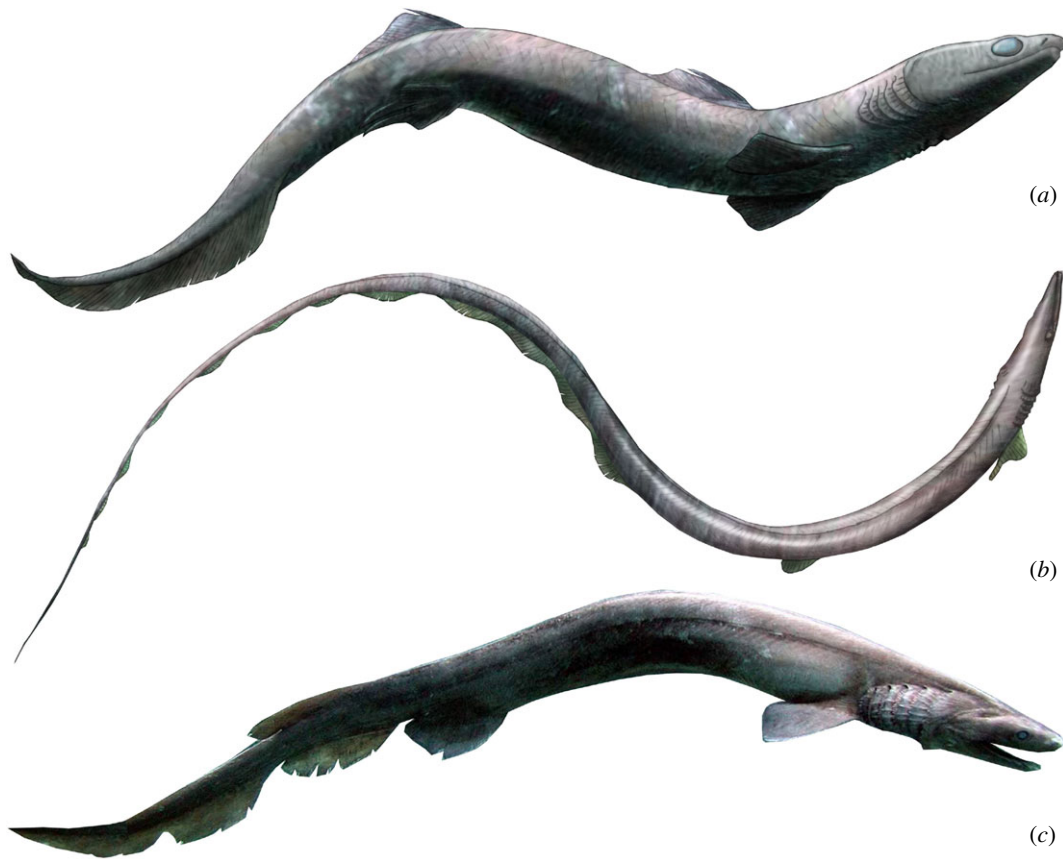


Figure 5. Possible body reconstruction of (a) *P. saidselachus* sp. nov., Late Devonian, (b) *T. gracia* [11], Early Carboniferous, and (c) picture of *C. anguineus* [44], Recent. (Online version in colour.)

chondrichthyan crown node and the major subdivisions: elasmobranch and holocephalan total groups.

5. Discussion

(a) Phylogenetic relationships

The consensus of relationships among crown-group chondrichthyans (figure 4) is consistent with results obtained from parent matrices [20] and from an independently revised analysis [22] of the Coates *et al.* [36] dataset. Importantly, synapomorphies supporting the elasmobranch total group that can be scored for *Phoebodus* capture features of the hyoid arch (character 51), the neurocranium (characters 156, 158, and 171), and the median fins (character 200). On this basis, *Phoebodus* can be considered a reasonably well-supported member of the elasmobranch stem lineage. However, relationships among clades within the early elasmobranchs are less secure. Phoebodonts, ctenacanth, and xenacanth are linked only by the presence of hypohyals (character 53) and a raised number of tooth families (i.e. generative tooth sets) along the jaw margins (character 68). Hypohyals, reported in *Thrinacodus* [11] but unknown in *Phoebodus*, have a distinctly patchy and possibly homoplastic distribution [22], and it seems likely that tooth sets could have proliferated quite independently to populate the differently shaped jaws of xenacanth and phoebodonts.

A reduced, dorsoventrally short, otic process of the palatoquadrate (character 82) appeared to be a likely synapomorphy of *Phoebodus* and other stem elasmobranchs, but the current analysis results indicate otherwise. Similarly so for the distally spatulate or bladed ceratohyal (character 52) present

in *Phoebodus* and *Tristychius*. In the absence of further examples, and few are known, this specialized form emerges as independently derived. On the other hand, a robust, smooth-surfaced ceratohyal with a posterior lateral fossa (character 51) survives the test of synapomorphy and might be used to identify further, candidate early elasmobranchs. *Gogoselachus* [37] is one such from the early Frasnian of Western Australia, known from few remains but including a well-preserved ceratohyal as well as teeth already compared with 'euselachians' [1].

Data from isolated teeth, collected over the past 144 years, have driven previous hypotheses of *Phoebodus* relatedness to other early chondrichthyans. Now, the apparent phylogenetic signal drawn from teeth can be compared with the signal from a larger set of morphologic characters, and the results are largely congruent. Ginter *et al.*'s [7] tooth-based distinction between *Phoebodus* and *Heslerodus* (contra [13]) is reinforced by the marked differences in jaw and braincase morphologies. The proposed relationship between phoebodontids and xenacanthids based on dental similarities [1,38] is supported by the present phylogenetic results, but not the proposed clade 'Cladodontomorphi' [1]. The likely close relationship between phoebodonts and thrinacodonts, again based on tooth morphology [7,39], is also upheld. Both taxa have teeth with three main cusps of similar size (character 66), and both are characterized by elongate body morphologies with long, slender heads and jaws. But, *Thrinacodus* exhibits several anomalous skeletal conditions beyond differences in body shape and dorsal fin distribution. *Thrinacodus* lacks an elongate occipital division of the braincase [11]. The palatoquadrate, as restored, retains the plesiomorphic 'cleaver shape', although published images (figure 14 in [11]) suggest that the otic process might, in fact, resemble

that of *Phoebodus*. The hyoid arch has a short hyomandibula, a short ceratohyal, a hypohyal, and no basihyal. The axial column is far more extensively skeletonized, with intervertebral and basidorsal components of vertebrae, where there are none preserved in *Phoebodus*. Resolving such differences is beyond the scope of the present work: *T. gracilis* is some 30 million years younger than *P. saidselachus*, very likely more derived within the phoebodontid clade, and preserved quite differently.

(b) Morphological specializations and palaeobiological context

Phoebodus saidselachus is the earliest known cartilaginous fish with an anguilliform body, and the earliest to have an elongate, tapering rostrum that contributes to the near-terminal gape. This specialized, garpike-like [40] condition is otherwise shared uniquely with *Thrinacodus* in the deep history of chondrichthyans. Further to this, *P. saidselachus* is the earliest known conventional chondrichthyan not to exhibit a cleaver-shaped palatoquadrate. For these reasons, *Phoebodus* adds significantly to the morphological diversity of the earliest elasmobranchs, to pre-Carboniferous chondrichthyans, and to crown-gnathostomes in general. Moreover, if the *Phoebodus* tooth form is accepted as a signal of both clade presence and, further to that, the presence of an anguilliform shark, then these data add to estimates of vertebrate disparity across a broad swathe of Middle and Late Devonian sites globally [1].

The jaws, dentition, axial skeleton, and body shape, although imperfectly preserved, provide clues about biomechanical function and ecomorphology of *Phoebodus*. The low otic process on the palatoquadrate (figure 1c) implies a reduced surface for adductor muscle attachment and weaker bite force than in other contemporary chondrichthyans (relative to body size). Correspondingly, the gracile proportions of the lower jaw are consistent with a low closing mechanical advantage [39], and add support to the hypothesis that mandible shape space and the trophic radiation of vertebrates is explored broadly before the end of the Devonian [41]. This distinctive combination of extended jaws and narrow rostrum suggests a feeding strategy involving a swift snapping action, perhaps like that of modern garpike [40]. If so, then the hyoid apparatus might be sufficiently robust to augment suction during prey capture and transport [42], as, in fact, it now appears to be, with specialized ceratohyal and large basihyal.

In certain respects, the frilled shark *Chlamydoselachus* [43] provides a living analogue of *Phoebodus*. Both taxa share an anguilliform body shape: the length-to-height proportions are similar, and while dorsal fin spines and fins are absent except for a small second dorsal in *Chlamydoselachus*, in the likely derived phoebodontid *Thrinacodus*, such fins are entirely absent (figure 5). Further similarities occur in the dentition. In *Phoebodus* and *Chlamydoselachus*, the dentition consists of generative tooth sets separated by gaps. Moreover, the individual teeth are remarkably similar: compare *Phoebodus depressus* (figure 30 in [1]) with *Chlamydoselachus anguineus* (figure 44 in [45]). Both dentitions can be characterized as grasping and functionally restricted to prey sizes that can be swallowed whole. However, very little is known of the actual feeding behaviour of the slow-moving *Chlamydoselachus*, and both ram-feeding and lurking in combination with sudden prey-snatching are proposed feeding strategies [43,45]. Reported stomach contents include epipelagic squids, scyliorhinid, and squaloid sharks [45,46]. At present, phoebodontid stomach

contents are known only in *Thrinacodus*, and they include remains of small chondrichthyans and crustaceans [11]. Possible prey for *Phoebodus* could have been thylacocephalan arthropods or cephalopods (ammonoids, bactritids, orthocerids), which occur in great numbers in the host rocks of the Moroccan phoebodontids [23,47].

The skeletal material of *Phoebodus* was found in the Maïder Basin, which is a small epicontinental marine basin at the southern margin of the Palaeotethys [48–50]. A rough estimation of the palaeodepth suggests a maximum of 400 m in the Maïder Basin depocentre, and about 100–300 m at Madene el Mrakib [51]. *Phoebodus* teeth were found mostly in localities where moderately deep to moderately shallow water conditions prevailed during the Late Devonian, consistent with previous suggestions that this genus occupied middle parts of the water column [1]. This coincides with environmental conditions of the Maïder Basin where hypoxic to dysoxic conditions occurred repeatedly at the sea floor during the Famennian [23,47]; thus, benthic life was rare and its diversity was low.

(c) Recalibrating the chondrichthyan crown

The placement of *Phoebodus* as a well-supported member of the elasmobranch stem lineage allows use of the characteristic teeth to establish a new minimum age for the chondrichthyan crown clade. Most recently, the estimated date of the crown divergence was Upper Frasnian, based on the phylogenetic placement [36] of *Cladodoides* [15]. The type species of *Phoebodus*, *Ph. sophiae* [30] in Ginter *et al.* [1] (electronic supplementary material, figure S7g), is known from the late Givetian, and *Ph. fastigatus* [2] in Ginter *et al.* [1] (electronic supplementary material, figure S7f), is known from the middle Givetian. It follows that a conservative, hard minimum, divergence date of elasmobranch from holocephalan lineages can now be placed some 10 Ma earlier, near the end of the Givetian stage of the Middle Devonian Series: 382.7 ± 1.6 Ma [52]. Thus, the new date continues a trend of moving the node deeper into the Devonian, with further implications of as yet poorly sampled crown-group chondrichthyan diversity throughout the subsequent Famennian.

Data accessibility. Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.40qc27m> [53].

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References

- Ginter M, Hampe O, Duffin CJ. 2010 Chondrichthyes: Paleozoic Elasmobranchii: teeth. In *Handbook of paleoichthyology*, vol. 3D (ed. H-P Schultze), p. 168, Munchen, Germany: Pfeil.
- Ginter M, Ivanov A. 1992 Devonian phoebodont shark teeth. *Acta Palaeontol. Pol.* **37**, 55–75.
- Long JA. 1990 Late Devonian chondrichthyans and other microvertebrate remains from northern Thailand. *J. Vert. Paleontol.* **10**, 59–71. (doi:10.1080/02724634.1990.10011790)
- Ginter M. 1990 Late Famennian shark teeth from the Holy Cross Mts, Central Poland. *Acta Geol. Pol.* **40**, 69–81.
- Ginter M, Ivanov A. 1995 Middle/Late Devonian Phoebodont-based ichthyolith zonation. [Zonation ichthyologique du Dévonien moyen/supérieur fondée sur les Phoebodontes]. *Geobios* **19**, 351–355. (doi:10.1016/S0016-6995(95)80137-5)
- Ivanov A. 1995 Late Devonian vertebrate fauna of the South Urals. *Geobios* **28**, 357–359. (doi:10.1016/S0016-6995(95)80138-3)
- Ginter M, Hairapetian V, Klug C. 2002 Famennian chondrichthyans from the shelves of North Gondwana. *Acta Geol. Pol.* **52**, 169–215.
- Ginter M, Turner S. 1999 The early Famennian recovery of phoebodont sharks. *Acta Geol. Pol.*, **49**, 105–117.
- Hairapetian V, Ginter M. 2009 Famennian chondrichthyan remains from the Chahrisheh section, central Iran. *Acta Geol. Pol.* **59**, 173–200.
- Hairapetian V, Ginter M. 2010 Pelagic chondrichthyan microremains from the Upper Devonian of the Kale Sardar section, eastern Iran. *Acta Geol. Pol.* **60**, 357–371.
- Grogan ED, Lund R. 2008 A basal elasmobranch, *Thrinacoselache gracia* n. gen & sp., (Thrinacodontidae, new family) from the Bear Gulch Limestone, Serpukhovian of Montana, USA. *J. Vertebr. Paleontol.* **28**, 970–988. (doi:10.1671/0272-4634-28.4.970)
- Ginter M, Turner S. 2010 The middle Paleozoic Selachian genus *Thrinacodus*. *J. Vertebr. Paleontol.* **30**, 1666–1672. (doi:10.1080/02724634.2010.520785)
- Williams ME. 1985 The “cladodont level” sharks of the Pennsylvanian Black Shales of central North America. *Palaontographica* **190**, 83–158.
- Ginter M. 2002 Taxonomic notes on ‘*Phoebodus heslerorum*’ and *Symmorium reniforme* (Chondrichthyes, Elasmobranchii). *Acta Palaeontol. Pol.* **47**, 547–555.
- Maisey JG. 2005 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. (doi:10.1206/0003-0090(2005)288<0001:BOTUDS>2.0.CO;2)
- Maisey JG. 2007 The braincase in Paleozoic symmoriiiform and cladoselachian sharks. *Bull. Am. Mus. Nat. Hist.* **307**, 1–122. (doi:10.1206/0003-0090(2007)307[1:TBIPSA]2.0.CO;2)
- Lane JA. 2010 Morphology of the braincase in the Cretaceous hybodont shark *Tribodus limae* (Chondrichthyes: Elasmobranchii), based on CT scanning. *Novitates* **3681**, 1–70. (doi:10.1206/681.1)
- Pradel A. 2010 Skull and brain anatomy of Late Carboniferous Sibirhynchidae (Chondrichthyes, Iniopterygia) from Kansas and Oklahoma (USA). *Geodiversitas* **32**, 595–661. (doi:10.5252/g2010n4a2)
- Pradel A, Maisey JG, Tafforeau P, Mapes RH, Mallatt JA. 2014 A Palaeozoic shark with osteichthyan-like branchial arches. *Nature* **509**, 608–611. (doi:10.1038/nature13195)
- Coates MJ, Gess RW, Finarelli JA, Criswell KE, Tietjen K. 2017 A symmoriiiform chondrichthyan braincase and the origin of chimaeroid fishes. *Nature*, **541**, 208. (doi:10.1038/nature20806)
- Coates MJ, Tietjen K. 2018 The neurocranium of the Lower Carboniferous shark *Tristychius arcuatus* (Agassiz, 1837). *Earth Environ. Sci. Trans. R. Soc. Edinb.* **108**, 19–35. (doi:10.1017/S1755691018000130)
- Dearden RP, Stockey C, Brazeau MD. 2019 The pharynx of the stem-chondrichthyan *Ptomacanthus* and the early evolution of the gnathostome gill skeleton. *Nat. Commun.*, **10**, 2050. (doi:10.1038/s41467-019-10032-3)
- Frey L, Rücklin M, Korn D, Klug C. 2018 Late Devonian and Early Carboniferous alpha diversity, ecospace occupation, vertebrate assemblages and bio-events of southeastern Morocco. *Palaogeogr. Palaeoclimatol. Palaeoecol.* **496**, 1–17. (doi:10.1016/j.palaeo.2017.12.028)
- Becker RT, House MR, Bockwinkel J, Ebbighausen V, Aboussalam ZS. 2002 Famennian ammonoid zones of the eastern Anti-Atlas (southern Morocco). *Münster. Forsch. Geol. Paläontol.* **93**, 159–205.
- Korn D, Klug C. 2015 Paleozoic ammonoid stratigraphy. In *Ammonoid paleobiology, volume II: from macroevolution to paleogeography*, vol. 44 (eds C Klug, D Korn, K De Baets, I Kruta, RH Mapes), *Topics in Geobiology*, pp. 299–328. Dordrecht, The Netherlands: Springer.
- Cignoni P, Callieri M, Corsini M, Dellepiane M, Ganovelli F, Ranzuglia G. 2008 MeshLab: an Open-Source Mesh Processing Tool. In *Sixth Eurographics Italian Chapter Conf.*, pp. 129–136.
- Swofford DL. 2003 *PAUP*: phylogenetic analysis using parsimony (*and other methods). version 4.0a147*. Sunderland, MA: Sinauer Associates.
- Huxley T. 1880 *A manual of the anatomy of vertebrated animals*, pp. 431. New York, NY: D-Appleton and Co.
- Bonaparte CLJL. 1838 *Iconografia della fauna italiana per le quattro classi degli animali vertebrati*. Tomo III: Pesci. pp. 266. (Salviucci), Roma.
- St. John O, Worthen AH. 1875 Description of fossil fishes. *Geol. Surv. Illinois*, **6**, 245–488.
- Schaeffer B. 1981 The xenacanth shark neurocranium, with comments on elasmobranch monophyly. *Bull. Am. Mus. Nat. Hist.* **169**, 1–66.
- Chaeffer B. 1975 Comments on the origin and basic radiation of the gnathostome fishes with particular reference to the feeding mechanism. In *Problèmes actuels de paléontologie, évolution des vertébrés*, vol. 218 (ed. J-P Lehman). *Colloque Int. Centre Nat. Rech. Sci.* pp. 101–109.
- Coates MJ, Tietjen K, Olsen AM, Finarelli JA. 2019 High-performance suction feeding in an early elasmobranch. *Sci. Adv.* **5**, eaax2742. (doi:10.1126/sciadv.aax2742)
- Maisey JG. 1981 Studies on the Paleozoic selachian genus *Ctenacanthus* Agassiz. No. 1. Historical review and revised diagnosis of *Ctenacanthus*, with a list of referred taxa. *Am. Mus. Novitates* **2718**, 1–22.
- Maisey JG. 1984 Chondrichthyan phylogeny: a look at the evidence. *J. Vertebr. Paleontol.* **4**, 359–371. (doi:10.1080/02724634.1984.10012015)
- Coates MJ, Finarelli JA, Sansom IJ, Andreev PS, Criswell KE, Tietjen K, Rivers ML, La Riviere PJ. 2018 An early chondrichthyan and the evolutionary assembly of a shark body plan. *Proc. R. Soc. B* **285**: 20172418. (doi:10.1098/rspb.2017.2418)
- Long JA, Burrow CJ, Ginter M, Maisey JG, Trinajstić KM, Coates MJ, Young GC, Senden TJ. 2015 First shark from the Late Devonian (Frasnian) Gogo Formation, Western Australia sheds new light on the development of tessellated calcified cartilage. *PLoS ONE* **10**, e0126066. (doi:10.1371/journal.pone.0126066)
- Ginter M. 2004 Devonian sharks and the origin of Xenacanthiformes. In *Recent advances in the origin and early radiation of vertebrates* (eds G Arratia, MVH Wilson, R Cloutier), pp. 473–486. München, Germany: Friedrich Pfeil.
- Anderson PS, Friedman M, Brazeau MD, Rayfield EJ. 2011 Initial radiation of jaws demonstrated stability despite faunal and environmental change. *Nature* **476**, 206–209. (doi:10.1038/nature10207)
- Lemberg J, Shubin NH, Westneat MW. 2019 Feeding kinematics and morphology of the alligator gar (*Atractosteus spatula*, Lacépède, 1803). Feeding mechanics of *Atractosteus spatula*. *bioRxiv preprint*, 70 pp. (doi:10.1101/561993)
- Dahl TW *et al.* 2010 Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish. *PNAS* **107**, 17 911–17 915. (doi:10.1073/pnas.1011287107)
- Werth AJ. 2006 Mandibular and dental variation and the evolution of suction feeding in odontoceti. *J. Mammal.* **87**, 579–588. (doi:10.1644/05-mamm-a-279r1.1)
- Smith BG. 1937 The anatomy of the frilled shark, *Chlamydoselachus anguineus* Garman. *Bashford Dean Memorial Volume: Archaic Fishes*, **6**, 333–506.
- Garman S. 1884 An extraordinary shark. *Bull. Essex Inst.* **16**, 47–55.

45. Ebert DA, Compagno LJV. 2009 *Chlamydoselachus africana*, a new species of frilled shark from southern Africa (Chondrichthyes, Hexanchiformes, Chlamydoselachidae). *Zootaxa* **2173**, 1–18. (doi:10.11646/zootaxa.2173.1.1)
46. Kubota T, Shiobara Y, Kubodera T. 1991 Food habits of the frilled shark *Chlamydoselachus anguineus* collected from Suruga Bay, Central Japan. *Nippon Suisan Gakk.* **57**, 15–20. (doi:10.2331/suisan.57.15)
47. Frey L, Pohle A, Rücklin M, Klug C. in press Fossil-Lagerstätten and preservation of vertebrates and invertebrates from the Devonian of Morocco (eastern Anti-Atlas). *Lethaia*.
48. Wendt J. 1985 Disintegration of the continental margin of northwestern Gondwana: Late Devonian of the eastern Anti-Atlas (Morocco). *Geology* **13**, 815–818. (doi:10.1130/0091-7613(1985)13<815:DOTCMO>2.0.CO;2)
49. Wendt J, Kaufmann B, Belka Z, Klug C, Lubeseder S. 2006 Sedimentary evolution of a Palaeozoic basin and ridge system: the Middle and Upper Devonian of the Ahnet and Mouydir (Algerian Sahara). *Geol. Mag.* **143**, 269–299. (doi:10.1017/S0016756806001737)
50. Lubeseder S, Rath J, Rücklin M, Messbacher R. 2010 Controls on Devonian hemi-pelagic limestone deposition analyzed on cephalopod ridge to slope sections, Eastern Anti-Atlas, Morocco. *Facies* **56**, 295–315. (doi:10.1007/s10347-009-0205-5)
51. Tessitore L, Naglik C, De Baets K, Galfetti T, Klug C. 2016 Neptunian dykes in the Devonian carbonate buildup Aferdou El Mrakib (eastern Anti-Atlas, Morocco) and implications for its growth. *Neues Jahrb. Geol. Paläontol.-Abh.* **281**, 247–266. (doi:10.1127/njgpa/2016/0598)
52. Cohen KM, Finney SC, Gibbard PL, Fan J-X. 2013 The ICS International Chronostratigraphic Chart. *Episodes*, **36**, 199–204. (doi:10.18814/epiiugs/2013/v36i3/002)
53. Frey L, Coates M, Ginter M, Hairapetian V, Rücklin M, Jerjen I, Klug C. Data from: The early elasmobranch *Phoebodus*: phylogenetic relationships, ecomorphology and a new time-scale for shark evolution. Dryad Digital Repository. (doi:10.5061/dryad.40q27m)