

## An enigmatic chondrichthyan spine from the Visean of Indiana, USA that resembles a median rostral cartilage of *Squaloraja* (Holocephali, Chimaeriformes)

Una enigmática espina de condriictio del Viseense de Indiana, Estados Unidos, parecida al cartílago rostral medio de *Squaloraja* (Holocephali, Chimaeriformes)

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**Abstract:** *Squaloraja* is a genus of chimaeriform fishes known from the Early Jurassic. It has a dorsoventrally flattened body and a long median rostral cartilage. Males have a lance-like tenaculum that articulates with a central groove on the dorsal face of the median rostral cartilage. The genus is the only member of the family Squalorajidae, itself the only family in the suborder Squalorajoidei of the order Chimaeriformes. Phylogenetic analyses suggest a divergence of the Squalorajoidei from other Chimaeriformes in the Mississippian, implying the existence of a ghost lineage of more than 130 My. A spine that resembles a median rostral cartilage of a male *Squaloraja* was found in the St. Louis Formation (Visean) of Indiana, USA. As in *Squaloraja*, the dorsal face has a long narrow groove that would have articulated with a long narrow tenaculum. The spine is designated as the holotype of *Sulcacanthus schachtii*, n. gen. et sp. *Sulcacanthus* is tentatively assigned to the Squalorajoidei based on morphology, but the possibility of convergence cannot be eliminated. A holocephalan tenaculum from the same locality might belong to the same taxon as the median rostral cartilage but could also belong to the suborder Myriacanthoidei.

**Resumen:** *Squaloraja* es un género de peces quimeriformes del Jurásico Inferior. Tiene un cuerpo aplanado y un cartílago rostral mediano largo. Los machos tienen un tenáculo en forma de lanza que se articula con un surco central en la cara dorsal del cartílago rostral mediano. Este género es el único miembro de la familia Squalorajidae, la única familia en el suborden Squalorajoidei del orden Chimaeriformes. Los análisis filogenéticos sugieren una divergencia de Squalorajoidei de otros Chimaeriformes en el Misisípico, lo que implica la existencia de un linaje fantasma de más de 130 Ma. En la Formación Caliza St. Louis (Viseense) de Indiana, Estados Unidos, se encontró una espina que se asemeja a un cartílago rostral mediano de un *Squaloraja* macho. En *Squaloraja*, la cara dorsal tiene un surco largo y estrecho que se habría articulado con un tenáculo largo y estrecho. La espina se designa como el holotipo de *Sulcacanthus schachtii*, n. gen. et sp. *Sulcacanthus* se asigna tentativamente a Squalorajoidei en función de la morfología, pero no se puede eliminar la posibilidad de convergencia. Un tenáculo holocéfalo de la misma localidad podría pertenecer al mismo taxón que el cartílago rostral medio, pero también podría pertenecer al suborden Myriacanthoidei.

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Squalorajidae

## INTRODUCTION

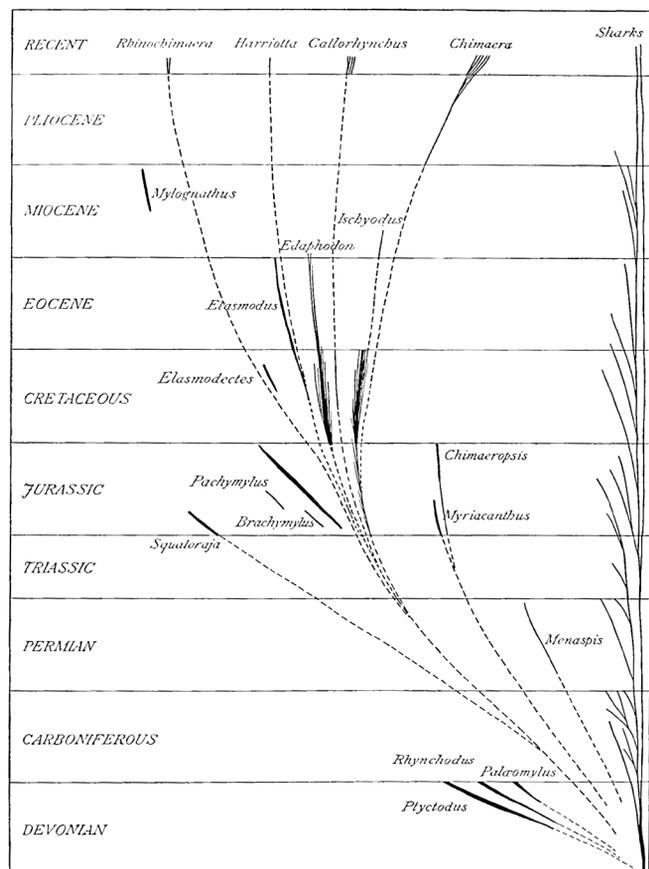
*Squaloraja* Riley, 1837 is a genus of Early Jurassic chimaeriform fishes first described from the ‘Lower Lias’ beds of Lyme Regis in Dorset, England. Unlike all other Mesozoic chimaeriforms, it has a depressiform, dorsoventrally flattened body morphology. The genus has also been described from the Sinemurian of Osteno (northern Italy) (Duffin & Patterson, 1993) and the Hettangian of Belgium (Delsate, 2005; Delsate *et al.*, 2002). Several quasi-complete skeletons are known. The relatively large head makes up around one third of the total body length. A large rostrum forms three

quarters of the total skull length and was supported in life by three main cartilages: a long median and two scimitar-shaped, broad-based lateral rostral cartilages. In males, the proximal two-thirds of the dorsal surface of the median rostral cartilage was opposed by a frontal clasper (tenaculum). This sexually dimorphic feature is largely parallel sided, with a rounded distal tip and a spatulate, expanded base proximally, articulating with the neurocranium. The length of the clasper cartilage sits in a shallow longitudinal groove on the dorsal surface of the median rostral cartilage.

The first known specimen of *Squaloraja* was found by Mary Anning (1799–1847) at Lyme Regis, Dorset, England, and comprised the anterior of the body. It was purchased by the Bristol Museum, but apparently was destroyed by German bombing during World War II. The tail section, which was found after the anterior portion, still exists and is in the Oxford University Museum with registration number OUMNH J.03097 (Sharpe, 2020). Henry Riley reported on the specimen at a meeting of the Geological Society of London on May 15, 1833, in which he classified it as a chondrichthyan fish with similarities both to rays and to sharks and named it *Squalo-raia dolichognathos*. Brief reports of this talk appeared soon thereafter (Riley, 1833, 1834), but the full report was not published until a few years later (Riley, 1837). Louis Agassiz examined the same specimen and published a brief description and two plates (Agassiz 1836a, p. 95, 1836b, pls. 42, 43), where he named the species *Spinacorhinus polyspondylus*. Later, he published a more complete description in which he used Riley's generic name (with a change in spelling), making the binomen *Squaloraja polyspondyla*, which is the one currently used (Agassiz, 1843, p. 379–381). He concurred with Riley that *Squaloraja* was a chondrichthyan and compared it to the extant sawshark *Pristiophorus*. Publication dates of individual parts of Agassiz's *Recherches sur les poissons fossiles* are given by Brown (1890) and by Quenstedt (1963). Classification of *Squaloraja* as a holocephalan, with affinities to Recent chimaeroids, was made by Howes (1890), based on the structure of the pectoral fin, and was confirmed by Traquair, quoted by Howes (1890), who found the skull to be of "autostylic structure". Patterson (1965) placed *Squaloraja* in its own suborder, Squalorajoidei, within the order Chimaeriformes. Current practice is to call the species originally called *Squalo-raia dolichognathus* *Squaloraja polyspondyla*, despite some nomenclatural problems with that choice (Duffin, 1983, p. 27).

Cladistic analyses including *Squaloraja* are not common. Of particular interest would be an indication of when the branch leading to the Squalorajoidei and *Squaloraja* diverged from other Chimaeriformes, including the Chimaeroidei, which includes all Recent holocephalans. Several cladograms that include both *Squaloraja* and crown group holocephalans (Grogan et al., 2012, fig. 1.1; Lund & Grogan, 1997; Lund et al., 2014, fig. 5(a); Stahl, 1999) differ somewhat in topology but all imply that such a divergence took place no later than the Serpukhovian (Late Mississippian), since it would have occurred prior to the appearance of *Echinochimaera*. *Echinochimaera* is known from the Serpukhovian Bear Gulch Lagerstätte of Montana, USA. The most recent cladistic analysis to include both *Squaloraja* and crown group holocephalans is that of Lebedev et al. (2021, fig. 17). This cladogram has less resolution than the others referred to here since it is based solely on dental characters. However, it implies

a divergence of the lineage leading to *Squaloraja* and the lineage leading to *Callorhynchus* no later than the earliest known appearance of *Protochimaera* Lebedev & Popov, 2021 in Lebedev et al. (2021) in the Middle Mississippian (Tulian substage of the Visean stage). As pointed out by Lebedev et al. (2021), this implies the existence of a 'ghost lineage' greater than 130 My from the earliest squalorajoid to *Squaloraja*. In this context, it is interesting to note the early phylogenetic tree of the holocephalans from Dean (1906) (Fig. 1). While it is obsolete in several aspects, such as the association of the early holocephalans with *Ptyctodus*, a placoderm, it is quite prescient in showing the divergence of the squalorajoids from the chimaeroids in the mid-Carboniferous, despite the lack of fossil evidence in 1906.



**Figure 1.** Graphical representation of the phylogeny of the Holocephali (Dean, 1906, fig. 144). Note the hypothesised divergence of the lineage leading to *Squaloraja* from that leading to Recent holocephalans in the mid-Carboniferous.

With regard to the paucity of fossil evidence for squalorajoids during the 130 My gap, it should be noted that *Squaloraja* is known only from a narrow time window in the Early Jurassic and that many of the fossils assigned to the genus are partial or complete skeletons. It is rarely recognised from disarticulated remains, other than frontal claspers or rostral cartilages. Many

fossil holocephalans are recognised from isolated tooth plates or finspines. Tooth plates of *Squaloraja* are small and delicate. If tooth plates of other squalorajoids shared these properties, they might be difficult to recognise in the fossil record. *Squaloraja* lacks finspines. A recently found spine from the Visean of Indiana, USA, displays a morphological similarity with the median rostral cartilage of a male *Squaloraja* and might shed some light on the nature of the 'ghost taxa' within the 130 My (or more) gap.

**Institutional abbreviations.** LFP, Lauer Foundation for Paleontology, Science and Education, Wheaton, Illinois, USA (<https://www.lauerfoundationpse.org>). The mission of the Lauer Foundation is to curate its fossil collection, providing the scientific community and other museums with permanent access for the purposes of exhibition, study and education. Public access to type and figured specimens, as well as specimens listed or cited in publications together with other scientifically important specimens is guaranteed; NHMUK, Natural History Museum, London, UK; OUMNH, Oxford University Museum of Natural History, Oxford, UK; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

## GEOLOGICAL AND STRATIGRAPHICAL SETTING

### Lyme Regis, Dorset, England

The specimens of *Squaloraja* that were examined for this study are all repositied in the collections of the NHMUK. All are labeled as "Lower Lias, Lyme Regis, Dorset, England". More detailed information is not available for individual specimens.

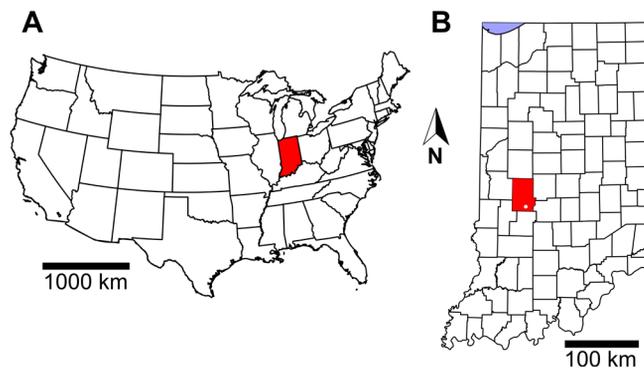
The lithostratigraphical and chronostratigraphical frameworks of the Lower Jurassic beds at Lyme Regis are discussed by Page (2010). The 'Lower Lias' at Lyme Regis comprises the Blue Lias Formation and the overlying Charmouth Mudstone Formation, which belong to the Hettangian, Sinemurian, and part of the lower Pliensbachian stages of the Lower Jurassic. According to Duffin (2010), *Squaloraja* occurs at Lyme Regis from, possibly, the late Hettangian, *angulata* chronozone to the late Sinemurian, possibly the *obtusum* chronozone. Index ammonites for these chronozones are *Schlotheimia angulata* (Schlotheim) and *Asteroceras obtusum* (J. Sowerby), respectively (Page, 2010). The range between these ammonite zones corresponds to a chronostratigraphical interval of ca. 200.2–195.2 My (Hesselbo *et al.*, 2020, fig. 26.10).

### Indiana, USA

The specimens from the St. Louis Formation examined for this study were found at 39° 32' 19" N, 86° 48' 12" W, in a limestone quarry near Cloverdale, Putnam County, Indiana, USA (Fig. 2). The bed lies within the St. Louis Limestone. In Indiana, the St. Louis Limestone is

conformably underlain by the Salem Limestone and is conformably overlain by the Ste. Genevieve Limestone (Carr, 1986).

The lower part of the St. Louis Limestone in Indiana is correlated by means of the corals *Lithostrotion proliferum*, *Lithostrotionella castelnaui*, and *Lithostrotionella hemisphaerica* with the type St. Louis Limestone and lies within the uppermost part of the *Taphrognathus varians*–*Apatognathus* conodont assemblage zone of Collinson *et al.* (1962, 1971). The upper part of the St. Louis Limestone corresponds to the *Apatognathus scalensis*–*Cavusgnathus* conodont assemblage zone of Collinson *et al.* (1971) = *Apatognathus geminus*–*Cavusgnathus* conodont assemblage zone of Collinson *et al.* (1962) and is correlated with the upper part of the type St. Louis Limestone (Carr, 1986). Details of these conodont assemblages in the Illinois Basin are given by Rexroad and Fraunfelder (1977). For comparison with other literature, it should be noted that the Valmeyeran regional stage of these authors corresponds to the combined Osagean (below) and Meramecian (above) stages as defined by others and that they place the Valmeyeran–Chesterian = Meramecian–Chesterian boundary at the base of the Ste. Genevieve Limestone. With the redefinition of the Meramecian–Chesterian North American regional stage boundary as the boundary between the foraminiferal zones 15 and 16i of the Mamet scheme (Mamet & Skipp, 1971), the boundary between the St. Louis Limestone and the overlying Ste. Genevieve Limestone coincides with the Meramecian–Chesterian boundary (Maples & Waters, 1987). While the bed in which the St. Louis Limestone specimens were found is not yet mapped with respect to its position within that formation, it clearly lies within the upper to uppermost Meramecian, ca. 337 My (Aretz *et al.*, 2020, fig. 23.5). This correlates with the Asbian substage of the British Isles (late Visean) (Lane & Brenckle, 2005, fig. 48; Lucas *et al.*, 2022, fig. 6).



**Figure 2.** A, Map of the United States, with the state of Indiana highlighted; B, map of Indiana with Putnam County highlighted. White dot within Putnam County indicates location where LF 5337 and LF 5338 were found.

## SYSTEMATIC PALAEOLOGY

Class CHONDRICHTHYES Huxley, 1880  
 Superorder HOLOCEPHALI Bonaparte, 1838  
 Order CHIMAERIFORMES Obruchev, 1953  
 Suborder SQUALORAJOIDEI Patterson, 1965

**Diagnosis.** Holocephalans with a dorsoventrally flattened body and head. Long, narrow median rostral cartilage with narrow, linear dorsal groove. In males, a lance-like frontal clasper articulates with the groove. Dorsal fin spine absent.

**Remarks.** One family (Squalorajidae) and one genus (*Squaloraja*). *Squaloraja* differs so much from other chimaeriforms that some place it in an order of its own (Lund & Grogan, 1997; Nelson *et al.*, 2016). The classification used here is consistent with that used by Stahl (1999).

Family SQUALORAJIDAE Woodward, 1886

**Diagnosis.** As for suborder.

Genus *Squaloraja* Riley, 1833

**Type-species.** *Spinacorhinus polyspondyla* Agassiz, 1836a. Early Jurassic; England, Belgium, and Italy.

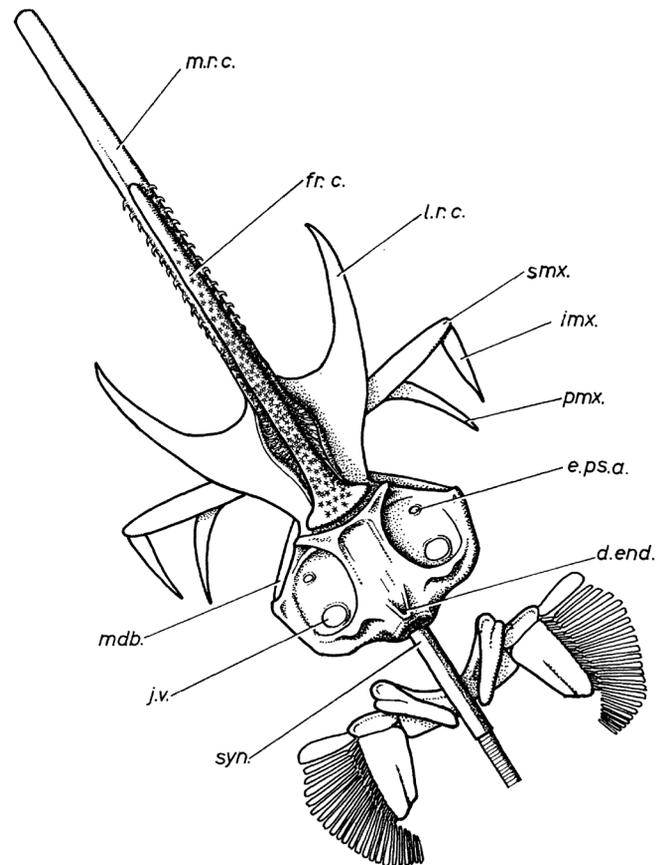
**Included species.** In addition to the type species, *Squaloraja tenuispina* Woodward, 1886, based on an isolated frontal clasper from Lower Lias, Lyme Regis, England.

**Diagnosis.** As for suborder.

*Squaloraja polyspondyla* (Agassiz, 1836a)

Figures 3–5

- 1833 *Squalo-raia dolichognathos*; Riley, p. 368–369.  
 1834 *Squalo-raia dolichognathos*; Riley, p. 483–484.  
 1836a *Spinacorhinus polyspondylus*; Agassiz, p. 95.  
 1836b *Spinacorhinus polyspondylus*; Agassiz, pls. 42, 43.  
 1837 *Squaloraia*; Riley, p. 83–88, pl. 4.  
 1843 *Squaloraja polyspondyla*; Agassiz, p. 379–381.  
 1872 *Squaloraia polyspondyla*; Davies, p. 145–150, pl. 4.  
 1885 *Squaloraja polyspondyla*; Hasse, p. 4, pl. 1, figs. 2, 3.  
 1886 *Squaloraja polyspondyla*; Woodward, p. 527–538, pl. 55.  
 1887 *Squaloraja*; Woodward, p. 481.  
 1890 *Squaloraja polyspondyla*; Howes, p. 687–688.  
 1891 *Squaloraja polyspondyla*; Woodward, p. 41–43, pl. 3, fig. 2.  
 1895 *Squaloraja polyspondyla*; Reis, p. 385–391, pl. 1, figs. 1, 2, 4–6.  
 1906 *Squaloraja polyspondyla*; Dean, p. 139–142, text-figs. 133, 137, 137A, 138, 139.  
 1922 *Squaloraja polyspondyla*; Leigh-Sharpe, p. 193–196, text-fig. 3.  
 1935 *Squaloraja*; De Beer & Moy-Thomas, p. 304–305, text-fig. 19.  
 1951 *Squaloraja polyspondyla*; Ørvig, p. 416, text-fig. 19.  
 1965 *Squaloraja polyspondyla*; Patterson, p. 116–127, 200, text-figs. 8–12, pl. 23, fig. 52, pl. 24, figs. 55, 56.  
 1983 *Squaloraja polyspondyla*; Duffin, p. 17–18, 26–28, text-fig. 7, pl. 5, fig. 2.



**Figure 3.** *Squaloraja polyspondyla*. Cranial region of male in dorsal view. **m.r.c.**, median rostral cartilage; **fr.c.**, frontal clasper; **l.r.c.**, lateral rostral cartilage; **smx.**, supramaxillary labial cartilage; **imx.**, inframaxillary labial cartilage; **pmx.**, premaxillary labial cartilage; **e.ps.a.**, foramen probably transmitting the efferent pseudobranchial artery; **d.end.**, opening of ductus endolymphaticus; **mdb.**, mandible; **j.v.**, foramen transmitting the jugular vein, orbital artery, and hyomandibular and palatine nerves; **syn.**, synarcual. After Patterson (1965, fig. 8). Copyright Royal Society, UK, used with permission.

- 1992 *Squaloraja polyspondyla*; Duffin, p. 294, fig. 1.  
 1992 *Squaloraja*; Patterson, p. 34, 37, 49, 50, 56, 58, 59.  
 1993 *Squaloraja polyspondyla*; Duffin & Patterson, p. 24–26, fig. 11.  
 1999 *Squaloraja polyspondyla*; Stahl, p. 108–112, figs. 104–107.  
 2002 *Squaloraja polyspondyla*; Delsate *et al.*, p. 25–26, text-figs. 21–23.  
 2005 *Squaloraja*; Delsate, p. 69, pl. 5, figs. 8–10.

**Holotype.** OUMNH J.03097, consisting of the tail portion of the specimen figured by Agassiz (1836b, pls. 42, 43). The anterior portions were destroyed in the German bombing of the Bristol Museum in 1940 (Sharpe, 2020).

**Material examined.** NHMUK PV OR 4999, OR 41353, OR 41354, OR 43307, OR 43970, OR 47402, OR 47018, P.2079, P.2081, P.2276, P.3184, P.3186, P.3187, P.3188, P.4323, P.4323a, P.4323b, P.4323c, P.4574, P.4880, P.6220, P.29375, P.65477. All from Lower Lias,

Lyme Regis, Dorset, England, except for NHMUK PV P.65477, from Marnes de Jamoigne (*Alsatites liasicus* zone, Hettangian, Early Jurassic), Fontenoille, near Luxembourg, Belgium.

**Remarks.** The specimens described and figured here come from a single locality: Lyme Regis, Dorset, England. Some of them have been described and figured by others (e.g., [Davies, 1872](#); [Patterson, 1965](#);



**Figure 4.** **A–B**, *Squaloraja polyspondyla*, Lower Lias, Lyme Regis, Dorset, England, NHMUK PV OR 47402. **A**, Cranial region of male in dorsal view; **B**, same specimen, frontal clasper set in dorsal groove of median rostral cartilage; **C**, *Squaloraja polyspondyla*, Lower Lias, Lyme Regis, Dorset, England. Median rostral cartilage of male in dorsal view, NHMUK PV OR 41354; **D**, *Squaloraja polyspondyla*. Frontal clasper of male in dorsal view, set in dorsal groove of median rostral cartilage, Lower Lias, Lyme Regis, Dorset, England, NHMUK PV P.2276. The prominent lateral denticles are attached to the median rostral cartilage, not to the frontal clasper; scale bars = 1 cm.



**Figure 5. A–C, *Squaloraja polyspondyla* male frontal claspers, Lower Lias, Lyme Regis, Dorset, England, all oriented with distal end to left. A, Dorsal view, NHMUK PV P.3187; B, ventral view, NHMUK PV P.3188; C, lateral view, dorsal face upward, NHMUK PV P.3186; scale bars = 2 cm; D–E, *Squaloraja polyspondyla*, Lower Lias, Lyme Regis, Dorset, England, NHMUK PV P.4574; D, anterior portion of male frontal clasper, dorsal view; E, detail of scales inside yellow rectangle of D; scale bar for D = 1 cm, E = 2 mm.**

Woodward, 1886). Emphasis here is given to cranial anatomy (Fig. 3) and, in particular, to the frontal clasper of the male and the median rostral cartilage with which it articulates, in order to compare these structures with the newly found specimens from the St. Louis Limestone of Indiana.

**Description.** In males, the proximal two-thirds of the dorsal surface of the median rostral cartilage was opposed by a frontal clasper. Females lack a frontal clasper. This sexually dimorphic feature (in males) is

largely parallel sided with a rounded distal tip and a spatulate, expanded base proximally, articulating with the neurocranium. The underside of the spatulate base possesses two symmetrical, roughly triangular hollows, separated by a thin vertical ridge and acting as points of insertion for the depressor musculature of the organ (Fig. 5B). The clasper itself is made up of densely calcified fibrocartilage whose grain runs longitudinally. The cross-section is slightly flattened and sub-oval. The dorsal surface and lateral flanks of the clasper cartilage are populated by a series of distinctive scales. These

each possess a stellate base with villiform lateral projections, surmounted by a stout, robust single denticle whose apex is generally directed anteriorly (Fig. 5E). The length of the clasper cartilage sits in a shallow longitudinal groove on the dorsal surface of the median rostral cartilage, and whose base is lined with a bed of tesserae which are differentiated from those of the remainder of the cartilage.

The placement of the male frontal clasper in the dorsal groove of the median rostral cartilage is shown in Figure 4A, 4B. The total extent of the median rostral cartilage is not clear, but it certainly exceeds the length of the frontal clasper. A dorsal view of a male median rostral cartilage with the frontal clasper removed is shown in Figure 4C. Figure 4D shows a dorsal view of a male frontal clasper set in place in the dorsal groove of the median rostral cartilage. Lateral denticles, hair-like proximally, hook-like distally, are visible and are attached to the sides of the median rostral cartilage (Fig. 4D). Views of three male frontal claspers are shown in Figure 5A–5C. Figure 5A (dorsal) shows stellate denticles, arranged irregularly on the dorsal surface. Figure 5B (ventral) displays the muscle attachment areas at the proximal end of the frontal clasper. No denticles are visible on the ventral surface. Possibly the absence of denticles on the ventral face of this specimen is an artefact of poor preservation, as another frontal clasper of *Squaloraja polyspondyla*, SMNS 9443, displays numerous low denticles on its ventral surface (Duffin, 1983, pl. 5, fig. 2). Figure 5C (lateral) displays a gentle curvature dorsally. Though this curvature is not observed in some other specimens, it might be that those specimens are dorsoventrally flattened by post-mortem compression. The curvature is considered to be real, since it is also observed in specimens NHMUK PV P.3186 and P.6220. The spine in Figure 5C displays some lateral denticles, proximally.

**Geographic and stratigraphic distribution.** Known from Lyme Regis, Dorset, England; near Luxembourg, Belgium; Osteno, Italy. Hettangian to Sinemurian (Early Jurassic).

Suborder SQUALORAJOIDEI

Family *incertae sedis*

Genus *Sulcacanthus* Itano & Duffin, n. gen.

**Type-species.** *Sulcacanthus schachti* Itano & Duffin n. sp.

**Included species.** Only the type species.

**Derivatio nominis.** From Latin *sulcus* = furrow, ancient Greek ἄκανθα (*acantha*) = spine.

**Diagnosis.** Known only from a rostral cartilage, which is long and narrow, gradually tapering distally. Dorsal surface with a narrow groove, which continues nearly to the distal end of the rostral cartilage. Approximately evenly spaced lateral denticles, which appear to be fused to the rostral cartilage.

**Geographic and stratigraphic distribution.** Indiana, USA. Meramecian North American regional stage (Mississippian, Visean).

*Sulcacanthus schachti* Itano & Duffin, n. sp.

Figure 6

**Derivatio nominis.** After the collector of the holotype, Mr. Robert Schacht, of Indiana, USA.

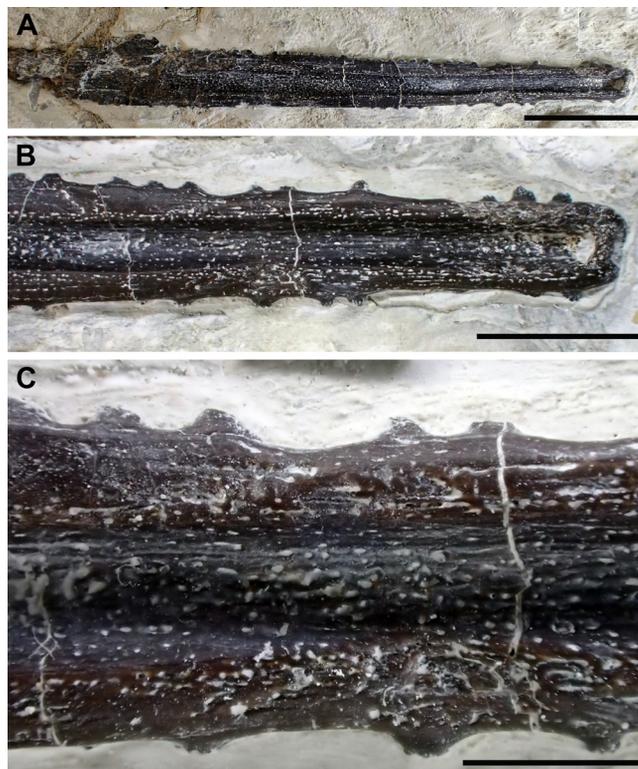
**Holotype.** A chondrichthyan rostral cartilage, LF 5338.

**Type locality.** A limestone quarry near Cloverdale, Putnam County, Indiana, USA, 39° 32' 19" N, 86° 48' 12" W.

**Type horizon.** Upper to uppermost Meramecian North American regional stage (Mississippian, Visean) = Asbian regional substage of the British Isles.

**Diagnosis.** As for genus.

**Description.** The holotype and only known specimen is interpreted as a rostral cartilage of a holocephalan fish, which is similar to the median rostral cartilage of *Squaloraja*. The preserved length is 62 mm, and the maximum width is 6 mm. The longitudinal groove on the presumed dorsal face resembles



**Figure 6.** Holotype of *Sulcacanthus schachti* Itano & Duffin, n. sp. Rostral cartilage in dorsal view, LF 5338, St. Louis Limestone, Mississippian (Visean), near Cloverdale, Putnam County, Indiana, USA. **A**, Entire preserved rostral cartilage; scale bar = 1 cm; **B**, distal tip of same; scale bar = 5 mm; **C**, midsection; scale bar = 2 mm.

the corresponding groove on the median rostral cartilage of *Squaloraja*, which articulates (in males) with the frontal clasper. Unlike in *Squaloraja*, the groove seems to continue nearly to the distal end. As in *Squaloraja*, there is a single row of denticles on each lateral edge. These denticles have a maximum base length of 0.5 mm and maximum height of 0.3 mm. Their attitude is normal to the long axis of the cartilage. Some of the denticles show weak striations, but others are unornamented. The bases expand but are not flattened and are not villiform. Unlike in *Squaloraja*, the denticles appear to be fused to the surface. The corresponding denticles on the median rostral cartilage of *Squaloraja* are attached to the main structure but not fused (Fig. 4D). Superficially, the denticles resemble those on the posterior face of a ctenacanthiform or hybodontiform dorsal fin spine, however, they have a different orientation, since they project mainly laterally and slightly ventrally. If a shark fin spine were placed in the equivalent orientation, with its posterior face orientated in the same way as the presumed dorsal face of the *Sulcacanthus* rostral cartilage, the denticles would project in the dorsal direction, as defined by the *Sulcacanthus* rostral cartilage. The *Sulcacanthus* rostral cartilage appears to be made up of fibrocartilage, indicated by the dominantly longitudinal surface markings (Fig. 6C). The proximal end of the rostral cartilage is damaged, showing no sign of the spatulate arrangement present in *Squaloraja*, which articulates with the frontal clasper. That structure, if originally present, might have been lost by postmortem damage.

Suborder, family, genus, species *incertae sedis*

Holocephalan frontal clasper

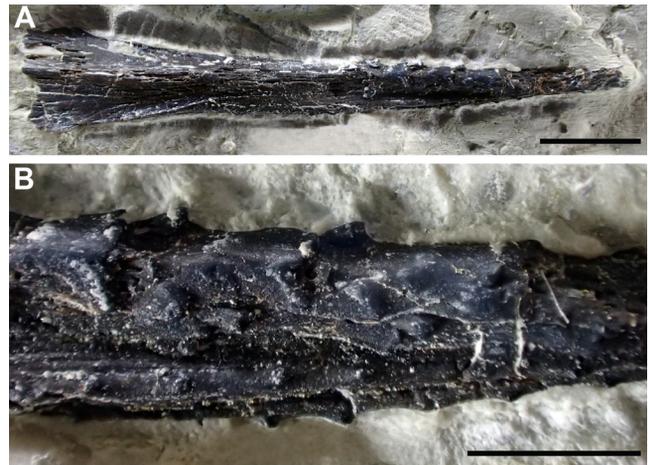
Figure 7

**Material.** LF 5337.

**Locality.** A limestone quarry near Cloverdale, Putnam County, Indiana, USA, 39° 32' 19" N, 86° 48' 12" W.

**Horizon.** Upper to uppermost Meramecian North American regional stage (Mississippian, Visean) = Asbian regional substage of the British Isles.

**Description.** The unique specimen has a long, narrow shape that is similar to that of the frontal clasper of *Squaloraja*. The preserved length is 31 mm, and the maximum preserved width is 5.5 mm. It does, however, taper distally more rapidly than the frontal clasper of *Squaloraja*. The proximal end flares laterally and has a median ridge flanked by triangular depressed areas on each side, presumably for muscle attachment (Fig. 7A). This structure is similar to the corresponding ones on the frontal claspers of *Squaloraja* and some myriacanthoids, such as *Halonodon warneri* (Duffin, 1984, fig. 4A). The presence of the muscle attachment areas indicates that this specimen displays the ventral face. The surface is covered with low-crowned denticles



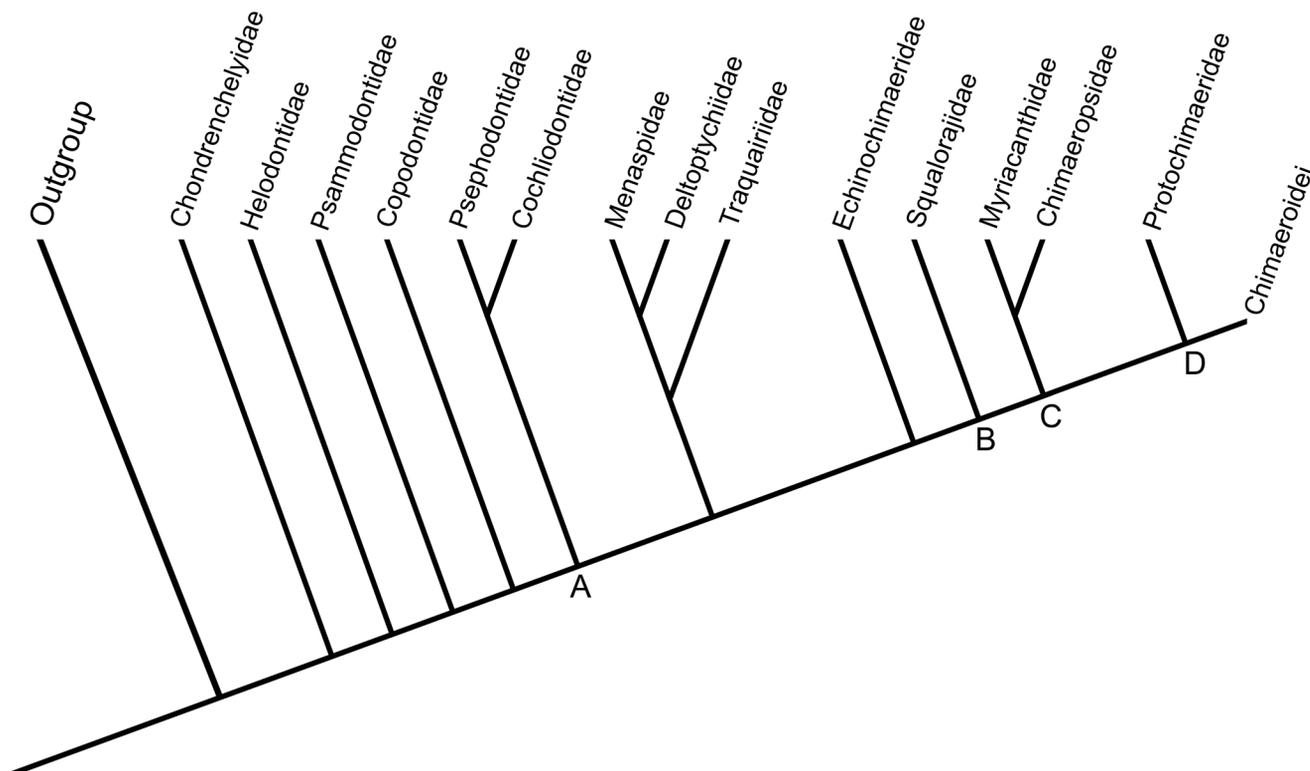
**Figure 7.** Holocephalan frontal clasper in ventral view, LF 5337, St. Louis Limestone, Mississippian (Visean), near Cloverdale, Putnam County, Indiana, USA. **A**, Entire preserved specimen; scale bar = 5 mm; **B**, distal part of same; scale bar = 2 mm.

arranged in several longitudinal rows (Fig. 7B), giving the surface a corrugated appearance similar to that of a frontal clasper of *Squaloraja polyspondyla* figured by Duffin (1983, pl. 5, fig. 2). Apices of the denticles are blunt and inclined anteriorly. Base margins are not villiform as in *Squaloraja*.

## DISCUSSION

While phylogenetic evidence suggests that the squalorajoids diverged from other chimaeriforms in the Carboniferous (Lebedev *et al.*, 2021), up to now, no pre-Jurassic squalorajoid remains have been identified. *Sulcacanthus schachtii*, represented by a rostral cartilage from the Visean that resembles that of *Squaloraja*, might help to fill that gap. The resemblance could also represent convergence. The shapes of the median rostral cartilage and of the frontal clasper of *Squaloraja* might be adaptations to having a dorsoventrally flattened body, which itself might be an adaptation to a benthic mode of life. In that case, the morphology of *Sulcacanthus* could be due to having a similar environment and mode of life compared to *Squaloraja* and not to a close phylogenetic relationship. Without more fossil evidence, it is not possible to rule out convergence. If the morphological resemblance between *Sulcacanthus* and *Squaloraja* is not due to convergence, then *Sulcacanthus schachtii* is the earliest known squalorajoid by *ca.* 130 My.

The morphology of the holocephalan frontal clasper (LF 5337) indicates that it could possibly belong to *Sulcacanthus*, since it could fit into the dorsal groove of the rostral cartilage of that taxon. However, holocephalans other than *Squaloraja* are known that also have long, narrow frontal claspers, including myriacanthoids such as *Metopacanthus granulatus* (Agassiz, 1837) or *Halonodon warneri* Duffin, 1984. A Visean myriacanthoid



**Figure 8.** Cladogram of the Holocephali, based on [Stahl \(1999\)](#) and [Lebedev et al. \(2021\)](#). Labels A–D indicate nodes where new information on their minimum ages has recently become available.

would be of great interest, since the oldest currently known myriacanthoids are from the Late Triassic ([Popov et al., 2009](#)), but cladistic analyses suggest that myriacanthoids had diverged from other chimaeriforms at least by the Visean ([Lebedev et al., 2021](#)). In this regard, we note that an unnamed holocephalan from the Late Pennsylvanian (Kasimovian) Kinney Brick Quarry Konservat-Lagerstätte of New Mexico, USA is thought to be a myriacanthoid ([Hodnett & Lucas, 2021](#), p. 369; Hodnett, pers. commun., 2022).

Figure 8 is a cladogram of the Holocephali *sensu* [Stahl \(1999\)](#), based on [Stahl \(1999\)](#), tab. 2), with the interpolation of the Protochimaeridae between the Myriacanthidae and the Chimaeroidei ([Lebedev et al., 2021](#), fig. 17). Labels A–D indicate nodes where information on minimum ages has recently become available. The origin of the Psephodontidae (node A) is now known to be no later than the Late Devonian (Famennian) due to the identification of *Psephodus* sp. from the Dyer Formation of Colorado ([Schultze et al., 2021](#)). Previous reports of *Psephodus* prior to the Carboniferous are doubtful ([Itano, 2022](#)). If the cladogram (Fig. 8) is correct, then the Chondrenchelyiiformes, the Helodontiformes, the Psammodontiformes, and the Copodontiformes also have their origins prior to the Carboniferous. The Visean age of *Protochimaera mirabilis* (node D) ([Lebedev et al., 2021](#)) implies origins for the Echinochimaeroidei, the Squalorajoidei (here tentatively identified from the Visean) (node B), and the Myria-

canthoidei (now tentatively known from the Kasimovian) (node C) no later than the Visean. This suggests that myriacanthoids 30 My older than the one identified from the Kinney Brick Quarry Konservat-Lagerstätte exist but are yet to be identified.

The cladogram of Figure 8, together with the known fossil record, implies that three holocephalan clades survived the end-Permian extinction: the Myriacanthoidei, the Squalorajoidei, and a clade comprising the Protochimaeroidei and the Chimaeroidei. This implies considerable gaps in the fossil record for all three clades. As documented here, there is a gap in the fossil record of the Squalorajoidei from the Carboniferous (Visean) to the Early Jurassic (Hettangian). There are gaps in the fossil record of the Myriacanthoidei from the Carboniferous (Kasimovian) to the Late Triassic (Norian), and of the Protochimaeroidei + Chimaeroidei from the Carboniferous (Serpukhovian) to the Late Triassic (Norian). The Norian occurrences of a callorhynchid chimaeroid, cf. *Eomanodon* sp. and of Myriacanthoidei indet. are both from the Franz Josef Land archipelago ([Popov et al., 2009](#)). Remarkably, [Dean \(1906\)](#) (Fig. 1) hypothesised a Palaeozoic origin for all three clades, even though pre-Jurassic fossils of members of those clades were unknown in 1906.

## CONCLUSIONS

Evidence for one or two new holocephalan taxa from the Visean of North America is presented, based on (1) a rostral cartilage and (2) a frontal clasper. The specimens are from the same location and horizon. The morphology of the rostral cartilage suggests that it resides within the *Squalorajoidei*. The morphology of the frontal clasper suggests placement in either the *Squalorajoidei* or the *Myriacanthoidei*.

**Supplementary Information.** New taxonomic names proposed in this paper, and the nomenclatural acts it contains, have been registered in ZooBank, the online registration system for the ICZN: <https://zoobank.org/References/87DBE3CB-C9F4-41D7-B7A1-A5A75D45C834>

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