Squaloraja Riley 1833 (Holocephala: Squalorajidae) from the Lower Jurassic of Osteno Konservat-Lagerstätte (Como, NW Italy)

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Abstract - A remarkable, complete specimen of a squalorajid holocephalian is described for the first time from the Lower Jurassic (lower Sinemurian) rocks of Osteno (Como, NW Italy). It is the only such specimen known from the locality and belongs to a (possibly juvenile) female. The Italian specimen is assigned to *Squaloraja* sp., and has a large dorsoventrally flattened head, long rostrum, a single mandibular tooth plate on each lower jaw, a well-developed synarcual, thick notochordal sheath calcifications, and only slightly reduced squamation comprising distinctive placoid scales with stellate bases. There is no ethmoid canal, dorsal fin or fin spine. The Lower Jurassic succession ('Lower Lias') of Lyme Regis (Dorset, UK) has yielded only two incomplete purported female specimens of the type species of the genus, *Squaloraja polyspondyla*, thus restricting potential comparison with the Italian specimen. This new record of the genus expands the known palaeogeographical distribution of this rare holocephalian.

Key words: Chimaeriformes, Elasmobranchii, *Squaloraja*, taxonomy.

Riassunto - *Squaloraja* Riley 1833 (Holocephala: Squalorajidae) del Giurassico inferiore di Osteno (Como, NO Italia).

Un esemplare completo e perfettamente conservato di olocefalo squaloraide è descritto per la prima volta, rinvenuto nel Giurassico inferiore (Sinemuriano inferiore) di Osteno (Como, NO Italia). Rappresenta il solo esemplare finora conosciuto di olocefalo squaloraide rinvenuto in questa località appartenente ad un individuo di sesso femminile (probabilmente uno stadio giovanile). L'esemplare di Osteno è assegnato a *Squaloraja* sp. e possiede una larga testa appiattita dorsoventralmente, un lungo rostro, una singola piastra dentale su ciascuna delle mandibole inferiori, un sinarcuale ben sviluppato, spesse calcificazioni della guaina notocordale e una ridotta ornamentazione formata da squame placoidi a base stellata. L'esemplare non presenta il canale etmoide, pinna dorsale o spina. Nella successione del Giurassico inferiore ('Lias inferiore') di Lyme Regis (Dorset, Inghilterra) sono stati rinvenuti solo due esemplari femminili incompleti della specie tipo del genere, *Squaloraja polyspondyla*, che non permettono un potenziale confronto con l'esemplare di Osteno. Il rinvenimento di *Squaloraja* a Osteno estende la distribuzione paleogeografica di questo raro olocefalo.

Parole chiave: Chimaeriformes, Elasmobranchii, *Squaloraja*, tassonomia.

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HISTORICAL BACKGROUND

The first ever specimen of *Squaloraja* was found by the famous fossil collector from Lyme Regis, Mary Anning (1799-1847) in or before 1829. The subsequent history of the specimen has been unravelled in some detail by Taylor & Torrens (1987). Earning her living by the rather precarious process of the commercial sale of fossils, M. Anning wrote to the great and the good of the British geological world, offering the item for sale. She specifically targeted the Bristol Institution (now the Bristol City Museum and Art Gallery). The specimen aroused considerable interest amongst contemporary geologists, but by 1831 the fossil still had not been sold for in a letter dated 11 February of that year, M. Anning offered it together with other Liassic fossils to A. Sedgwick (1785-1873), then Professor of Geology at the University of Cambridge. M. Anning included a rough sketch of the specimen in her letter (Taylor & Torrens, 1987: fig. 1). She further distributed a hand-written notice of the specimen, known from surviving examples in the papers of G.B. Greenough (1778-1855) and the Buckland papers at the Oxford University Museum (Fig. 1). In this circular, she noted the distinct characters of the specimen – 'the head does not bear an analogy to anything yet discovered' – and drew attention to the ray-like dermal denticles embedded in the skin, wing-like fins and simple pectoral and pelvic girdles (Taylor & Torrens, 1987: 137).

In the event, M. Anning's specimen of *Squaloraja* was purchased by J.N. Sanders (c. 1777-20-1870), who then deposited it in the collections of the Bristol Institution. The surgeon Dr H. Riley (1797-1848), a Bristolian by birth, a keen amateur geologist and a founder member of the Bristol Institution, provided the first description of the specimen in a paper read to the Geological Society on 15 May 1833 and published in the Proceedings of the Society

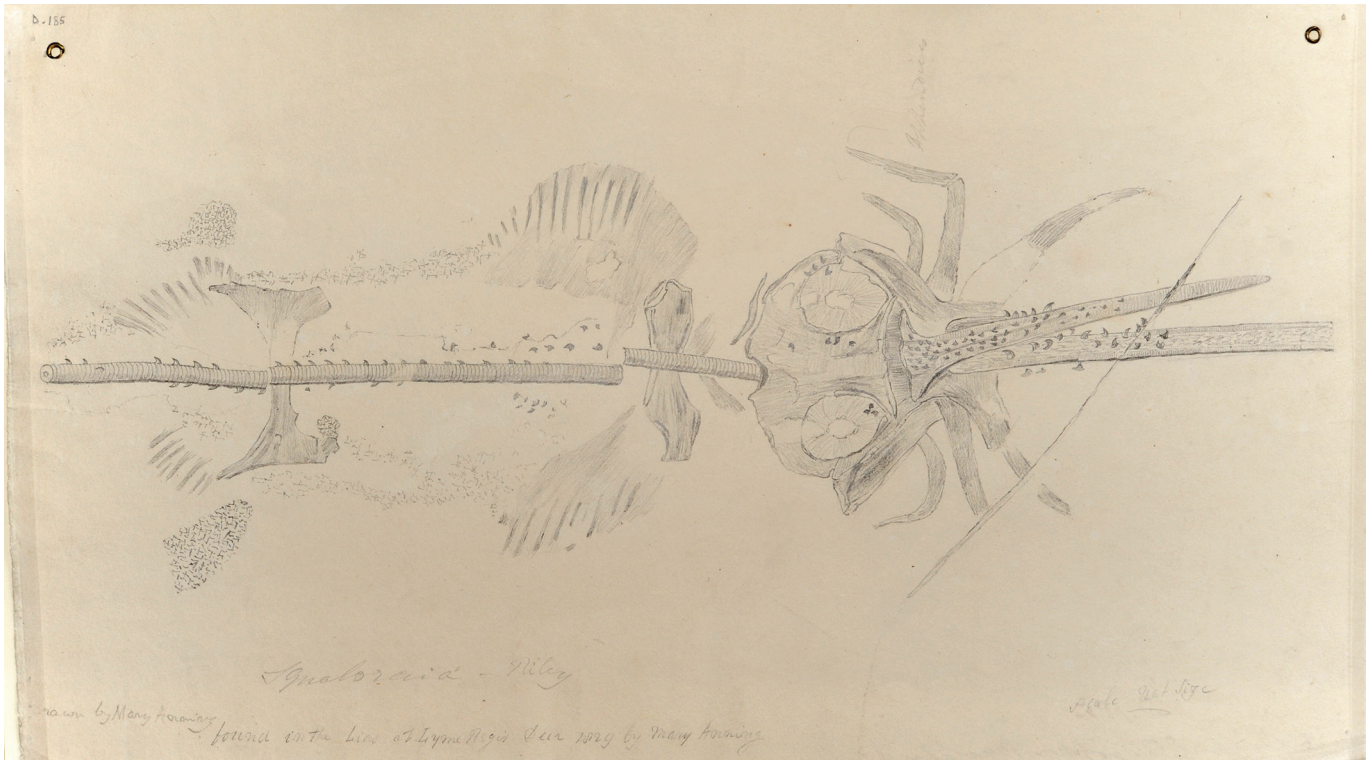


Fig. 1 - OUMNH WB/C/D/185: A careful pencil drawing of 'Squaloraia' [a fish]. Riley. Drawn by Mary Anning; found in the Lias at Lyme Regis. Dec. 1829 by Mary Anning. (48x28 cm). / OUMNH WB/C/D/185: Un accurato disegno a matita dello 'Squaloraia'[un pesce]. Riley. Eseguito da Mary Anning; rinvenuto nel Lias di Lyme Regis. Dicembre 1829, Mary Anning. (48x28 cm). (Photo by / Foto di: OUMNH).

the following year (Riley, 1833a), and reprinted in other journals (Riley, 1833b). Opinion was divided as to the affinities of the specimen – it was suggested to belong to a reptile and even a bird (Taylor & Torrens, 1987: 142; Sharpe, 2020: 101). Riley (1833a), however, claimed it belonged to a cartilaginous fish, as is obvious in the construction of the scientific name which he gave it – *Squalo-raia dolichognathus* or 'shark-ray intermediate with long jaws'.

Agassiz (1807-1873) visited Bristol in 1834, studied their specimen of *Squaloraja*, and included a description in his monumental pioneering work on fossil fishes, *Recherches sur les Poissons Fossiles* (Agassiz, 1833-1843; Fig. 2A, B), announcing it to be a ray and one of the most interesting fossils he had ever seen. Preparing the Bristol specimen a little further, Agassiz was able to refine some details lacking in Riley's description but was at a loss to give a definitive announcement as to its relationships, other than indicating that it was a chondrichthyan. Davies (1872) recognised the frontal clasper as being analogous with the sexually dimorphic feature restricted to males in extant chimaeroids, but both he and Woodward (1886) retained the genus in the selachians. The chimaeriform identity of *Squaloraja* was recognised when a new specimen of the genus was purchased by the Edinburgh Museum in 1887 (Taylor & Torrens, 1987: 143). Possessing a rather better preserved and exposed skull and jaws than previous specimens, this one revealed that the upper jaws were fused to the neurocranium. This led Traquair in Howes (1890) and Woodward (1891) to place the genus in the Holocephali, the sister group of the sharks, skates, and rays. Revisionary work by De Beer & Moy-Thomas (1935) confirmed this assignment and Patterson (1965) showed its distinctive nature by placing it within its own monotypic Suborder, the Squalorajoidei.

The specimen purchased by the Bristol Institution comprised the anterior part of the fish only. M. Anning promised to send them the tail if it was ever discovered. In the event, the tail ended up in the collection of the Philpot sisters, friends of M. Anning living in Lyme Regis. Approaches to them for the purchase of the tail portion of the specimen were unsuccessful, and the specimen was eventually donated to the Oxford University Museum (Fig. 3). The Bristol Museum suffered considerable damage and the loss of parts of its collection during an air raid on the night of 24/25 November 1940, and the *Squaloraja* is believed to have been amongst the casualties. This means that OUMNH J.03097 is the only surviving part of the genoholotype. Whilst its affinities are clear, unfortunately the tail region holds few characters of value in making comparisons and defining species.

OBJECTIVES

The purpose of this study is to provide a comprehensive and accurate description of the specimen of *Squaloraja* from Osteno in order to check its main morphological characters and its possible systematic assignment. The studied specimen was collected from the Osteno Konservat-Lagerstätte, where a roughly 10-metre-thick stratum of fossiliferous rock, formed by fine sediments

Fig. 2 - Illustrations of Mary Anning's specimen of *Squaloraja*, originally housed in the Bristol Institution, and figured in Agassiz (1836: tom. 3, pl. 42) (A) and the tail portion (OUMNH J.03097) in Agassiz (1836: tom. 3, pl. 43) (B). / Illustrazioni dell'esemplare di *Squaloraja* rinvenuto da Mary Anning, originariamente conservato presso la Bristol Institution e raffigurato in Agassiz (1836: atlante volume 3, tavola 42) (A) e della porzione di coda (OUMNH J.03097), in Agassiz (1836: atlante volume 3, tavola 43) (B).

Fig. 3 - Philpot sisters' specimen housed in Oxford University Museum, OUMNH J.03097, genoholotype, preserving just the tail portion (x 0.6). / Esemplare delle sorelle Philpot conservato presso l'Oxford University Museum, OUMNH J.03097, geno-olotipo, che conserva solo la porzione caudale. (x 0,6). (Photo by: / Foto di: OUMNH).

deposited during the Lower Jurassic (lower Sinemurian) in a deep-sea basin, crop out. The fossiliferous Konservat-Lagerstätte is located near to the Porto Franco (Crotto del Doglio) locality on the left northern shore of Lake Lugano (or Lake Ceresio), around 3 kilometres west of the hamlet of Osteno (Como, Lombardy, NW Italy) (Fig. 4). The first formal record of fossiliferous material was reported by Pinna (1967). Later, Pinna (1968, 1969) described the first decapod crustaceans from Osteno and the interest in the locality and its fossils by palaeontologists at the Museo di Storia Naturale di Milano (MSNM) increased during the 1970s thanks both to private donations of additional specimens, and notably the results of controlled excavations by the staff of the MSNM at "Porto Franco" quarry during the 1980s and 1990s. The excavations at the Osteno outcrop enriched the MSNM collections by hundreds of specimens, expanding our knowledge of the faunal palaeodiversity of the Osteno Konservat-Lagerstätte. The field prospection works ended in 2002, and the outcrop was definitively abandoned.

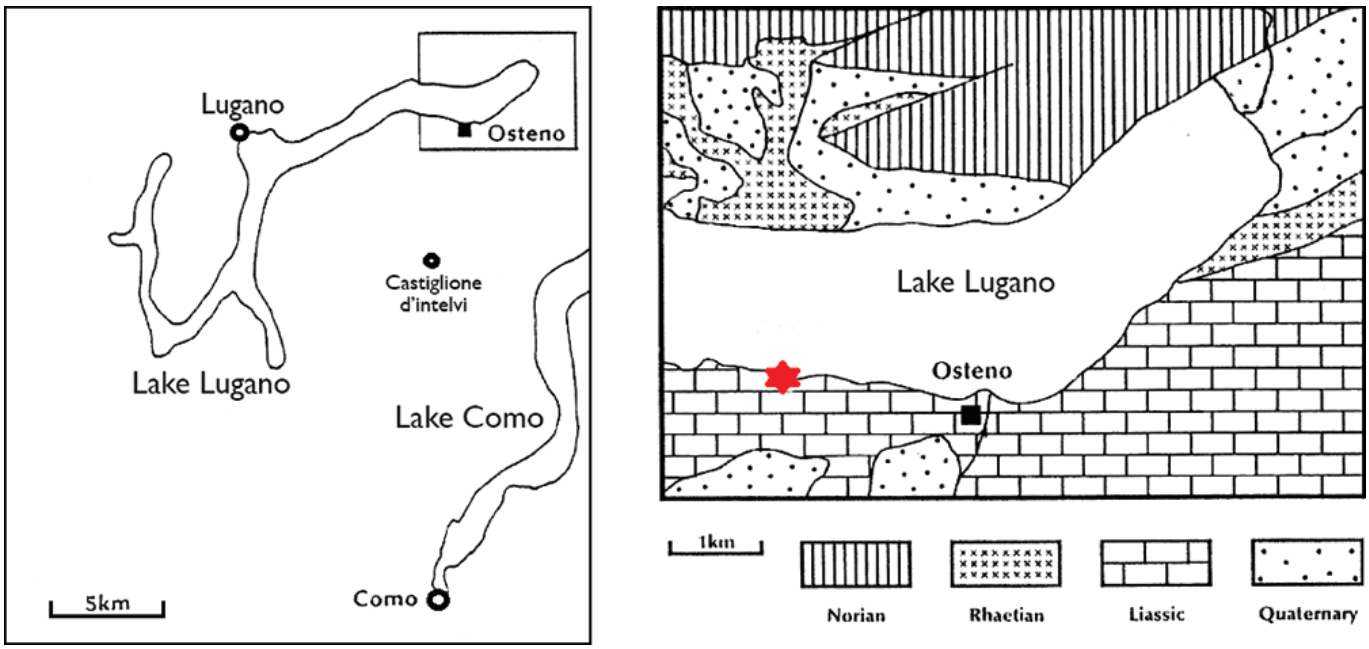


Fig. 4 - Geographic map of the north part of Lake Lugano with the ubication (*) of Porto Franco outcrop close to the hamlet of Osteno (Como, Lombardy, NW Italy) (modified after Duffin & Patterson, 1993). / Mappa geografica della parte settentrionale del Lago di Lugano con l'ubicazione (*) dell'affioramento di Porto Franco vicino alla frazione di Osteno (Como, Lombardia, Italia nordoccidentale) (modificata da Duffin & Patterson, 1993).

GEOLOGICAL SETTING AND FOSSIL PRESERVATION

The fossiliferous Osteno "lens" is a roughly 10-metre-thick stratum of rock, grey-white on the exposed surface and bluish-grey when fractured, formed by fine sediments and rich in siliceous sponge spicules. The exact three-dimensional shape of this "lens" of fossiliferous rock is unknown. It lies within the Moltrasio Limestone Formation, a very thick formation rich in flint nodules and well developed in the Como and Lugano areas (NW Italy). The sediments were deposited in a deep-sea basin during the Lower Jurassic, and form part of a complex of sediments 3,000 to 4,000 meters thick at the deepest point in the basin. The presence of synsedimentary faults, caused by landslides of the muddy deposits, provides evidence of density currents laden with sediment (turbidites). The Moltrasio Limestone is generally poorly fossiliferous, but the belemnites, ammonites, and brachiopods that have been found within it have enabled it to be dated to between the Hettangian (201 million years ago) and the lower Pliensbachian (Carixian, 190 million years ago). The Osteno "lens" was probably formed under special conditions in a very localised area of the basin. However, since it is impossible to follow its lateral development and, therefore, its relationship with more characteristic Moltrasio Limestone sediments, it is difficult to understand exactly what conditions were at the time (Pinna, 1985). In thin section, the rock usually presents as finely layered and rich in fragments of calcareous organisms and spicules from siliceous sponges (Garassino & Teruzzi, 2015). The attribution of the lens and its contents to the lower Sinemurian, *Arietites bucklandi* zone, was based on the discovery of the ammonite *Coroniceras bisulcatum* (Bruguière, 1789) in association with *Eoctocentrites* Canavari, 1888 and *Sulciferites* Spath, 1922 (Pinna, 1967; Arduini *et al.*, 1982). The fossils are very compressed and flattened, often with superimposed structures, which make their reconstruction difficult. Soft body parts are preserved mostly as thin films of grey or blackish kerogen, a substance of organic origin whose mechanism of formation at Osteno still remains to be clarified. Among the invertebrates, the best-preserved remains belong to arthropods, marine worms, and coleoid cephalopods. The reason for this particular preservation appears to be that those organisms had phosphate-rich structures – such as the chitinous exoskeleton of the arthropods – that, during the *post-mortem* decomposition phase, provided a saline component essential for bacteria covering the soft tissues (e.g. muscles) to quickly preserve their morphology allowing, for example, the preservation of individual muscle fibres (Wilby & Briggs, 1997). Several hypotheses have been put forward to explain the formation of the fossiliferous Osteno "lens", but so far none have proved to be entirely satisfactory or sufficiently confirmed either by the sedimentological data or by the analysis of the fossilized remains. The sediments do not show traces of bioturbation – the activity of organisms living on or inside the bottom, such as tunnel digging in search of food or shelter – so it is very probable that the organisms that were entirely or partially linked to life on the sea bottom were transported there from a certain distance away. The fossils are often preserved almost intact, with their structures in anatomical connection: decapod crustaceans especially retain all appendages, even the most delicate ones (Briggs & Kear, 1994; Hof & Briggs, 1997). Thus, transport of organic remains over relatively short distances, followed by rapid burial in a milieu that was strongly reducing, oxygen-free and lacking scavengers may have been the principal factors favouring the peculiar state of preservation of most of the fauna from the Osteno Konservat-Lagerstätte.

The Osteno outcrop contains mainly the remains of marine organisms (invertebrates and fish) (see Lamsdell *et al.*, 2021 for a detailed description and Tang, 2002 for an overview). The vertebrate fauna represents a minor component of the Osteno faunal assemblage, including chondrichthyan (holocephalian and selachian) and actinopterygian fish (Duffin & Patterson, 1993). The chondrichthyan component of the fish fauna includes a synechodontiform shark, *Synechodus pinnai* (Duffin 1987), and a neoselachian shark of obscure affinities – *Ostenoselache stenosoma* Duffin 1998 (Duffin, 1987, 1998). Two holocephalians have been recovered to date: one is an un-named myriacanthid (Duffin, 1992) and the other specimen, the subject of this study, was listed informally as *Squaloraja polyspondyla* (Duffin & Patterson, 1993: 24; Duffin, 1998: 5; Stahl, 1999: 111; Garassino & Teruzzi, 2015: 41-43) and figured three times (Duffin & Patterson, 1993: fig. 11; Stahl, 1999: fig. 107; Tang, 2002: fig. 14.6), but never described.

MATERIAL

One complete specimen, exceptionally well preserved in part and counterpart (lacking tail), exposed in dorsal view. Photographs were taken under natural and UV lights and the specimen was alcohol-impregnated to increase contrast between the body and the surrounding matrix, thereby helping to highlight the morphological details present. The specimen is housed in the palaeontological collections of the Museo di Storia Naturale di Milano (MSNM).

Abbreviations. *Institutional* – NHMUK PV P: Fossil Fish (Pisces), Vertebrate Palaeontology Collection, The Natural History Museum, London (UK); OUMNH: Oxford University Museum, Oxford (UK); SMNS: State Museum of Natural History Stuttgart (Germany). *Anatomical* – 1. Dimensions: hl: head length; mw: head maximum width; nl: neucrocranium length; nw: neurocranium width; pgw: pelvic girdle width; rl: rostral length; sgw: scapular girdle width; trl: trunk length; tl: tail length; TL: total body length. 2. Lateral line sensory canals: AC: angular canal; AVRC: anterior ventral rostral canal; CRC: central rostral canal; DRC: dorsal rostral canal; HC: hyomandibular or preopercular canal; IOC: infraorbital canal; LSC: lateral line sensory canal of the trunk; OC: occipital canal; ORC: oral canal; OTC: otic canal; PRVC: posterior rostral ventral canal; SC: supratemporal canal; SOC: supraorbital canal.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley 1880
Subclass Euchondrocephalia Lund & Grogan 1997
Superorder Holocephali Bonaparte 1838
Order Chimaeriformes Obruchev 1953
Suborder Squalorajoidei Patterson 1965
Family Squalorajidae Woodward 1886

Remarks: The family includes the single genus *Squaloraja* Riley 1833, with two nominal species, both from the Lower Lias (*bucklandi* zone to basal *semicostatum* zone in the lower Sinemurian; Paul Davis pers. comm., 2021) of Lyme Regis, Dorset (UK): the type species *S. polyspondyla* (Agassiz 1836) (for full discussion on authorship assignment see Patterson, 1965: 117) and *S. tenuispina* Woodward 1886. The latter species is known from a single isolated frontal clasper only (NHMUK PV P.2081, Egerton Coll.; Woodward, 1886: 529, pl. 55, fig. 6) (Fig. 5A). However, Smith & Patterson (1988: 182) have pointed out that "two species of *Squaloraja* have been named but they cannot be distinguished", considering *S. tenuispina* apparently conspecific with the other Lyme Regis specimens. A comprehensive review of the squalorajid frontal claspers, both isolated and on articulated specimens at the NHMUK leads us to support Smith & Patterson's statement. The two characters used by Woodward (1886) to define *S. tenuispina* and distinguish it from the claspers of *S. polyspondyla* were the slender nature of the trunk of the clasper and the presence of an acuminate, pointed distal tip. The first thing to note is that the holotype of *S. tenuispina* is complete and measures 105 mm from the base to the distal tip. This makes it one of the shortest frontal claspers in the NHMUK collection. NHMUK PV OR 47402 is an articulated skull with an 82 mm long frontal clasper preserved in life position (Fig. 5B). Like the 112 mm long, virtually complete clasper in NHMUK PV OR 43307 (Fig. 5C), the structure is slender and although the tip is not sharply pointed, neither is it blunt or rounded. We conclude that the isolated clasper represented by *S. tenuispina* falls within an accepted range of morphological variation for *S. polyspondyla* and that *S. tenuispina* should therefore be considered its junior synonym.

Genus *Squaloraja* Riley 1833

Type species: *Spinacorhinus polyspondylus* Agassiz 1836 by monotypy.

Fossil records of *Squaloraja*

The specimen presented herein fits well within the diagnostic characters of the Squalorajidae Woodward 1886 as summarised by Patterson (1965: 116). These characters include dorso-ventrally flattened head; one pair of toothplates in the lower jaw; crown made up of alternating parallel bands of osteonal and interosteonal dentine; rostrum very large; no ethmoid canal; no dermal plates on the head; synarcual present, notochordal calcifications very thick; no dorsal fin spine, first dorsal fin absent; and scales placoid, squamation not much reduced.

Squaloraja is known by two nominal species. *Squaloraja polyspondyla* is represented (see Remarks) by a half a dozen almost complete skeletons from Lyme Regis, Dorset (UK) (Patterson, 1965: 117) and has been studied by several authors (Riley, 1833a, 1833b; Agassiz, 1833-1844; Davies, 1872; Woodward, 1886, 1891; Reis, 1895; Dean, 1906). The pectoral girdle and fin were figured by Leigh-Sharpe (1922), the skull was restored and discussed by De Beer & Moy-Thomas (1935), and a single frontal clasper in ventral view (SMNS 9443) was described by Duffin (1983). Moreover, Patterson (1965) provided a general description of the animal and discussed its phylogeny. Stahl (1999: 108) summarized all previously reported data and provided an updated reconstruction of the skeleton based on Patterson's earlier figure (1965, fig. 8). *Squaloraja tenuispina,* based on a single isolated frontal clasper, also from Lyme Regis, was raised by Woodward (1886) and is here considered to be a junior synonym of *S. polyspondyla* (see above). Finally, Delsate *et al.* (2002: 25) reported two incomplete tooth plates and some loose scales from the middle Hettangian (Lower Jurassic) of southern Belgium assigned to *S. polyspondyla*, whereas some isolated elements were generically referred to *Squaloraja* sp., both representing the oldest record to date for the genus.

A recent cladistic analysis of the main holocephalian taxa produced a consensus tree which placed *Squaloraja* 'in a polytomy with other holocephalian taxa (including chondrenchelyiforms, cochliodontiforms and menaspidiforms), far removed from the clade Myriacanthoidei + Protochimaera + Chimaeroidei' (Lebedev *et al.*, 2021: 840). This implied squalorajoid origins during the Carboniferous, with an effective ghost lineage of around 130 million years. Itano & Duffin (2022) have noted the presence of a rostral cartilage, with structural similarities to that of *Squaloraja*, from the St Louis Formation of Indiana (Viséan of the USA).

Squaloraja sp.
Figs. 6, 8-11

Note: Although the studied specimen was previously reported and partially figured in several papers as *Squaloraja polyspondyla* (Arduini *et al.*, 1982: pl. 8, fig. 1; Duffin & Patterson, 1993: fig. 11; Stahl, 1999: figs. 34 H, 106B, 107; Tang, 2002: fig. 14.6; Garassino & Teruzzi, 2015: figs. 64-66), nobody has never formally described the specimen (Figs. 6, 8). Based upon the short diagnosis provided by Patterson (1965) (focused on the male clasper shape only), it is impossible to assign the studied specimen to *S. polyspondyla*. The only specimen reasonably confidently identified as pertaining to a female is that housed in the NHMUK (Woodward, 1886: 529, pl. 55, figs. 3, 7; catalogue number NHMUK PV P.3184; Fig. 7A), but it is too incomplete to allow a close comparison with the studied specimen. Woodward (1886: 529) suggested that a second, previously unfig-

Fig. 5 - Frontal claspers of male specimens of *Squaloraja*. A) NHMUK PV P.2081, holotype and only known specimen of *Squaloraja tenuispina* Woodward, 1886 from the Lower Lias of Lyme Regis (x 1.4). B) NHMUK PV 47402, detail of the skull of *S. polyspondyla* (x 1.06). C) NHMUK PV 43307, detail of the skull of *S. polyspondyla* (x 1.02). / Clasper cefalici di esemplari maschili di *Squaloraja*. A) NHMUK PV P.2081, olotipo e unico esemplare noto di *Squaloraja tenuispina* Woodward 1886 del Lias inferiore di Lyme Regis (x 1,4). B) NHMUK PV OR 47402, particolare del cranio di *S. polyspondyla* (x 1,06). C) NHMUK PV OR 43307, particolare del cranio di *S. polyspondyla*. (x 1,02). (Photo by: / Foto di: C.J. Duffin).

ured (apart from a section through a vertebra; Woodward 1886 pl. LV fig. 8) specimen might belong to a female. The specimen in question is NHMUK PV P.2079 and, as Woodward observed, belongs to an older individual. Whilst it is perfectly possible that the specimen does belong to a female, unfortunately the rostrum is missing and the cartilage fragments anterior to the dentition are badly preserved (Fig. 7B); it is possible that if a frontal clasper was present it might have been lost together with the anterior cartilages of the head.

Material and measurements: One complete articulated specimen, preserved in part and counterpart, in dorsal view.

MSNM V665 – hl: 91 mm; hw: 56 mm; nl: 25 mm; nw: 28 mm (excluding mandibles); pgw: 17 mm (excluding rays); rl: 66.5 mm; sgw: 30 mm (excluding rays); trl: 44 mm; tl: 9.5 mm (as preserved); TL: *c*. 220 mm.

Description: *Head* - Broad elongate head (over 1/3 of the total body length), rhomboid in outline, flattened dorsoventrally, widest at the supramaxillary lateral cartilages; dorso-ventrally flattened rostrum elongate and sub-rectangular with smooth lateral margins, relatively wide base and tapering anteriorly; rostral tip unsupported by cartilage and slightly tapering; rostrum supported by five sets of cartilage – single median rostral cartilage (mrc), paired lateral rostral cartilages (lrc) anteriorly, paired supramaxillary cartilages (smc) plus inframaxillary (imc) cartilages, and paired premaxillary cartilages (pmc) laterally; mrc lance-like, slightly flattened, gradually tapering distally, with wide proximal base overlying nasal capsules and distal tip bifurcating with a deep, concave distal margin; dorsal surface of mrc differentiated from tessellated cartilage into evenly distributed coarse granulations (Fig. 9A) which do not contact each other; lrc each extending half way down full length of rostrum, curved and roughly triangular in shape, flaring anterolaterally, distally pointed with base fused to preorbital region of neurocranium; proximal posterior margin of lrc incomplete, exposing underlying symphysis and mandibular dentition; smc project laterally at roughly 40° to midline and are slightly curved, with slight distal tapering; short, medially-directed transverse cartilage strut (?pre-labial cartilage) seems to connect the anterior mid-point of the smc to the lrc; imc short, distally pointed, posteriorly-directed extends from tip of each smc; pmc each scimitar-like, distally pointed and posteriorly-directed with base obscured by overlying smc (Fig. 9C).

Neurocranium - Neurocranium compressed dorsoventrally, partially crushed, with poorly preserved braincase and orbital margins; wide sub-pentagonal neurocranium with rounded lateral margins; neurocranium laterally constricted, slightly elevated in the orbital region, lacking evidence of preorbital lateral projections; neurocranium extended anteriorly by fusion with the elongate rostral cartilages; orbits wide, sub-ovoid and dorsolaterally positioned; occipital margin wide, slightly convex medially and poorly preserved (Fig. 9B).

Dentition - Lower dentition exposed in occlusal view; strong mandibular arc gently convex, converging mesially to the symphyseal cartilage and extending to form a short protruding and bluntly rounded point; each mandible bears a single elongate tooth plate; the occlusal surface is crossed by bands of hypermineralised tissue which are roughly parallel to the labial margin of the tooth plate; the hypermineralised tissue is exposed by antemortem wear in transverse strips angled away from the mesial angle in symphyseal view, revealing laminated development of the tritural tissue (Fig. 9D).

Postcranial skeleton - Vertebral column reinforced by closely-set thick calcified rings, slightly tapering posteriorly to the narrow elongate tail; calcifications in the sheath of the notochord continue in the occipital region of the neurocranium where the notochord was enclosed; synarcual made of calcified cartilage present just behind occiput enclosing anterior distal section of notochord; no dorsal fin spine or dorsal fin present (Fig. 10A).

Pectoral girdle and fins - Pectoral girdle close to the posterior occipital margin, arc-like in form with large scapular process and moderately broad coracoid; wide metapterygium with 26 distinct radials segmented distally produced in a broad wing-like fin (Fig. 10B).

Pelvic girdle and fins - The two halves of the pelvic girdle are not fused; curved halves arcuate posteriorly, lacking an anterior process; single metapterygium with 18 articulated segmented radials; pelvic fins smaller than pectoral fins at only half their width (Fig. 10C).

Dorsal and caudal fins - Despite the exceptional detailed preservation of the specimen, there is no direct evidence or trace of any structure suggesting the presence of dorsal median and caudal fins; a flattened epichordal lobe could be present in the terminal half of the narrow tail, but evidence of supporting radials is lacking.

Body scales - Squamation comprises placoid scales distributed over the whole body except the rostrum; scales small and scattered around the orbits; dorsal and lateral trunk scales wider and coarser with different shape; scales between pectoral and pelvic girdles and in various locations on the proximal part of the tail have rounded crown margins produced into elongate, radially directed unequal rays; hooked-shape scales ranged in a pair of parallel rows dorsally unite to form a single row towards the distal part of the tail; hooked-shape scales situated along the inferior margin of each side of the tail, decreasing in size towards the tail tip (Fig. 10D).

Mechanosensory canals [the nomenclature for the different elements of the lateral line sensory system used herein follows that used in Patterson (1965) and Didier (2004)] (Fig. 11). – The mechanoreceptive lateral line system forms a pattern of grooves or tubes on the snout and head regions; they are exceptionally well preserved; the lateral line canals are supported by c-shaped cartilaginous rings which are open to the external surface; the trajectories of the different components of the lateral line sensory canal system can be traced through the survival of minimally disarticulated lengths of such cartilaginous rings on the specimen; the lateral line sensory canal (LSC) of the trunk passes down the length of the body on the flanks of either side; both left and right trunk canals can be clearly seen extending from a point just posterior to the base of the pelvic fin to the tip of the tail.

Fig. 6 - *Squaloraja* sp., MSNM V655, complete specimen (part & counterpart) (x ca. 0.84). / *Squaloraja* sp., MSNM V655, esemplare completo (impronta e controimpronta) (x ca. 0,84). (Photo by: / Foto di: R. Sigismondo).

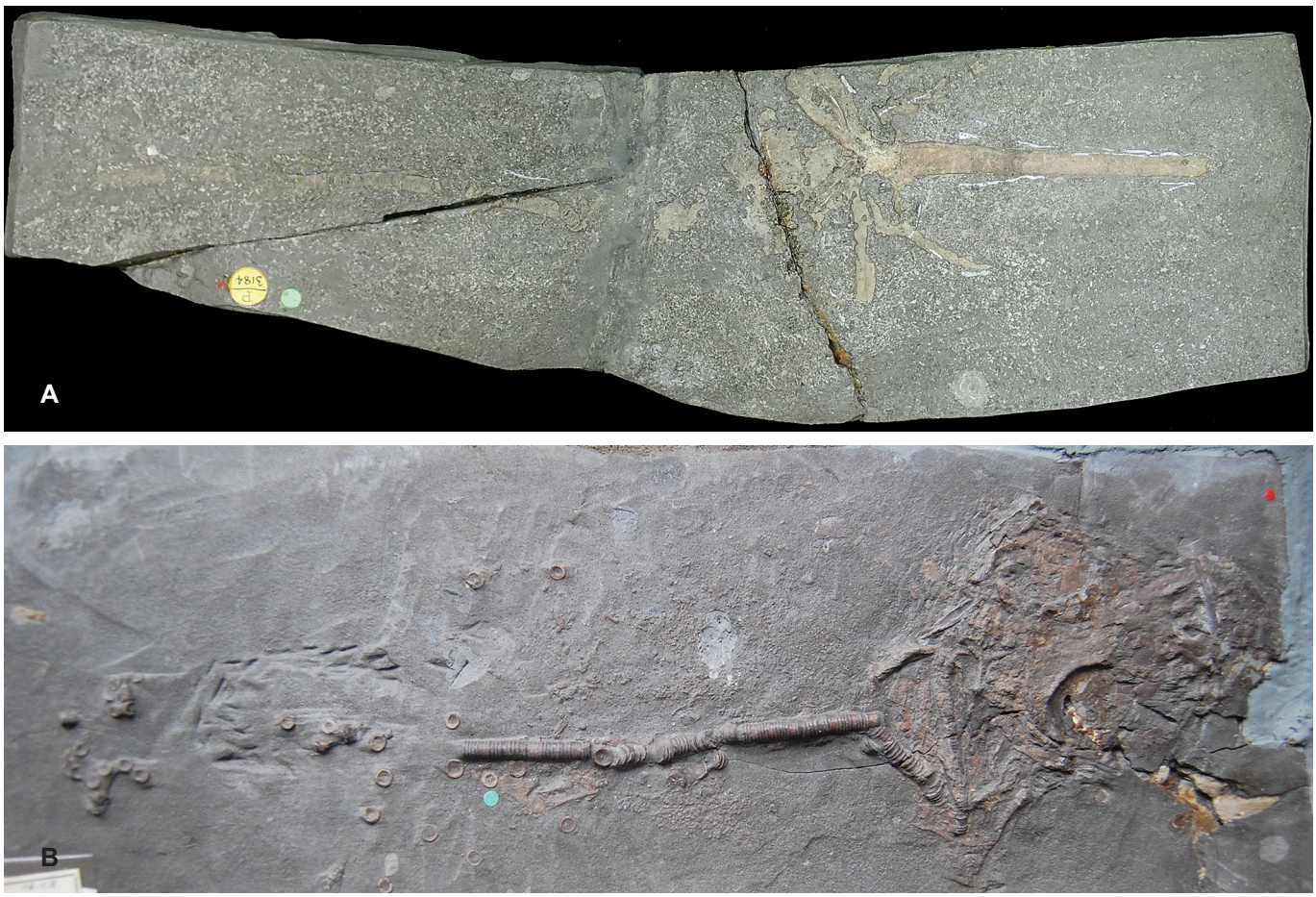


Fig. 7 - *Squaloraja polyspondyla*. A) NHMUK PV P.3184, incomplete female specimen from Lyme Regis (UK) (x 0.62). B) NHMUK PV P.2079, a mature specimen from Lyme Regis (UK) (x 0.51). / *Squaloraja polyspondyla*. A) NHMUK PV P.3184, esemplare femminile incompleto proveniente da Lyme Regis (Regno Unito) (x 0,62). B) NHMUK PV P.2079, esemplare adulto proveniente da Lyme Regis (Regno Unito) (x 0,51). (Photo by: / Foto di: C.J. Duffin).

Preservation of the specimen in dorsal view means that it is sometimes difficult to discern more subtle changes in the three-dimensional trajectory of individual canals; nevertheless, a slight kink in the pathway of the trunk canals approximately 15 mm from the tip of the tail marks a change in position from the upper flanks to the lower flanks in that region, a characteristic feature of all extant chimaeroids and all Mesozoic holocephalians in which the tail region is known.

In the skull region, the sensory canal system is best preserved around the anterior part of the neurocranium and the rostrum. A supratemporal canal (SC) ascends the postero-dorsal surface of the head, joining to form a commissural structure crossing the dorsal surface of the neurocranium (this canal is visible in the counterpart of MSNM V665); the trunk canal (LSC) is connected to the base of the supratemporal canal by a short occipital canal (OC), again visible in the counterpart; the base of the left supraorbital canal (SOC) is just discernible at the OC/SC junction in the counterpart, and some indistinct lengths of c-shaped rings indicate the presence of the supraorbital canal extending to a point just anterior to the orbit. An otic canal (OTC) branches from the SC/OC junction and swings down to a position ventral to the orbit; at an antero-ventral point to the orbit it branches at a complex junction; the most posterior branch is what is interpreted herein as the hyomandibular or preopercular canal (HC), but note that this canal is in a much more anterior position than in extant chimaeroids, with the exception of *Callorhincus* (Didier, 1995: figs. 8, 10). A second, shorter branch descends to the tissues of the lower jaw and is the oral canal (ORC); this branch is succeeded anteriorly by a bifurcation; the lower of these two branches is the angular canal (AC) which extends forwards to a point approximately half way along the rostrum; here, it loops beneath the lateral rostral cartilage; the upper branch is the infraorbital canal (IOC) which runs forward over the rostrum in front of the orbit to a bifurcation point in front of the anteriormost extent of the AC; from here, an anterior branch, the dorsal rostral canal (DRC) runs over the tip of the rostrum and then loops back to a point just less than half-way back to the mouth close to the midline; a posterior branch, the central rostral canal (CRC) flanks the medial border of the lateral rostral cartilage extending posteriorly to meet the anterior ventral rostral cartilage (AVRC), which itself runs anteriorly until ending blindly about two thirds of the way along the underside of the rostrum; thus, the distal parts of the DRC and the AVRC

have a reasonably extensive overlap on the underside of the distal part of the rostrum; a second branch, the posterior ventral rostral canal (PVRC) runs posteriorly toward the mouth; terminating near the rostrum base, it seems to have at least one and possibly two branches, the proximal rostral canals leading to the underside of the proximal part of the rostrum.

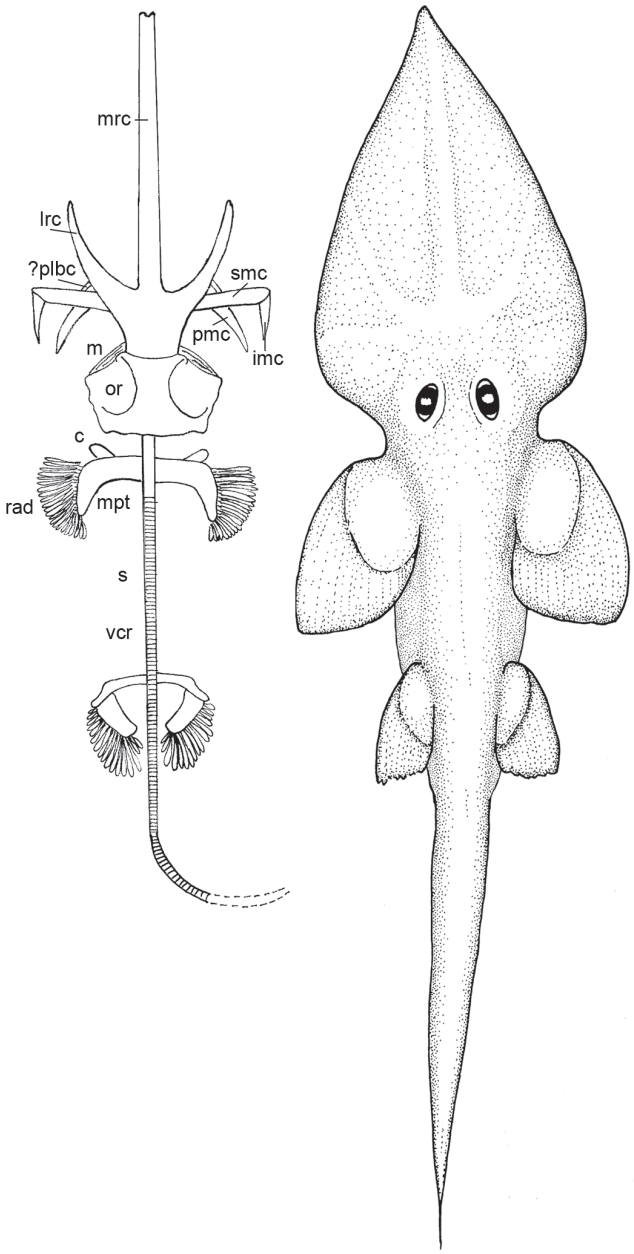


Fig. 8 - *Squaloraja* sp., MSNM V655. A) Line drawing of the skeleton. Abbreviations - c: coracoid; imc: inframaxillary cartilagine; lrc: lateral rostral cartilage; m: mandible; mpt: metapterygium; mrc: median rostral cartilagine; or: orbit; ?plbc: pre-labial cartilage; pmc: premaxillary cartilagine; rad: radials; s: synarcual; smc: supramaxillary cartilagine; vcr: vertebral column rings. B) hypothetical reconstruction (not to scale). / *Squaloraja* sp., MSNM V655. A) Disegno al tratto dello scheletro. Abbreviazioni - c: coracoide; imc: cartilagine inframascellare; lrc: cartilagine rostrale laterale; m: mandibola; mpt: metapterigio; mrc: cartilagine rostral mediana; or: orbita; ?plbc: cartilagine prelabiale; pmc: cartilagine premascellare; rad: radiali; s: sinarcali; smc: cartilagine sopramascellare; rcr: anelli della colonna vertebrale. B) ricostruzione ipotetica (non in scala).

Discussion: According to Didier (2004), the mature males in extant chimaeroids have distinctive secondary sexual dimorphic characters, such as an elongate frontal clasper which opposes the rostrum, and paired pre-pelvic tenaculae and claspers, characters shared in all the best-preserved specimens of *Squaloraja polyspondyla* from Lyme Regis (UK). However, these characters are clearly absent in the specimen described here, allowing us to exclude that it represents a mature male. Possible female specimens of *S. polyspondyla* include NHMUK PV P.3184 from the Enniskillen collection in NHMUK, and NHMUK PV P.2079 (see discussion above), both reported by Woodward (1886: 527) (Figs. 7A, B). Whilst the Lyme Regis specimens are both only partial, the Italian specimen is represented by a complete and articulated body in both part and counterpart and in a state of exceptional preservation. The diagnostic characters revealed in the specimen, such as the absence of the frontal clasper, pre-pelvic tenaculae and pelvic clasper cartilages indicates that the specimen belongs to a female *Squaloraja*, and possibly a juvenile or immature individual. The latter conclusion is supported by the following considerations: 1) the poor degree of calcification in juvenile tissues might mean that the true outline of the rostral tip (bifurcating in the Italian specimen *vs*. rounded in *S. polyspondyla* from the UK) is missing or not developed yet; 2) the granular surface of the rostral cartilage might represent a condition in which juvenile tesserae have not achieved their full geometric shape and size, as in all known specimens of *S. polyspondyla*; 3) the lack of dorsal and epichordal fin radials (partially observed in *S. polyspondyla*) might also indicate that these elements might not yet be calcified (= a juvenile condition). Finally, the shorter body length compared to all specimens of *S. polyspondyla*, although not considered to be a valid distinctive character, could be an additional datum, suggesting juvenile/immature status for MSNM V665.

Despite the excellent state of preservation, we prefer to leave the studied specimen in open nomenclature for the following reasons: 1) as previously pointed out, the diagnosis and description of *S. polyspondyla* are based on several male specimens (plus a single, poorly preserved, and incomplete female); as result all the main distinctive characters of the type species are based on the description of masculine features, precluding any comparison with the studied specimen; 2) there are too few morphological characters to allow adequate comparison with the type species or to establish a confident diagnosis of a new taxon within the genus *Squaloraja*; 3) it is impossible to judge if some morphological characters in the studied specimen, such as the different number of radials in both fins compared to those of the type species could be related to sexual dimorphism or could be considered a specific character, since specimens of the type species lack preserved fin radials in the supposed female examples; this question is still unresolved due to the lack of appropriate data from extant and fossil holocephalians.

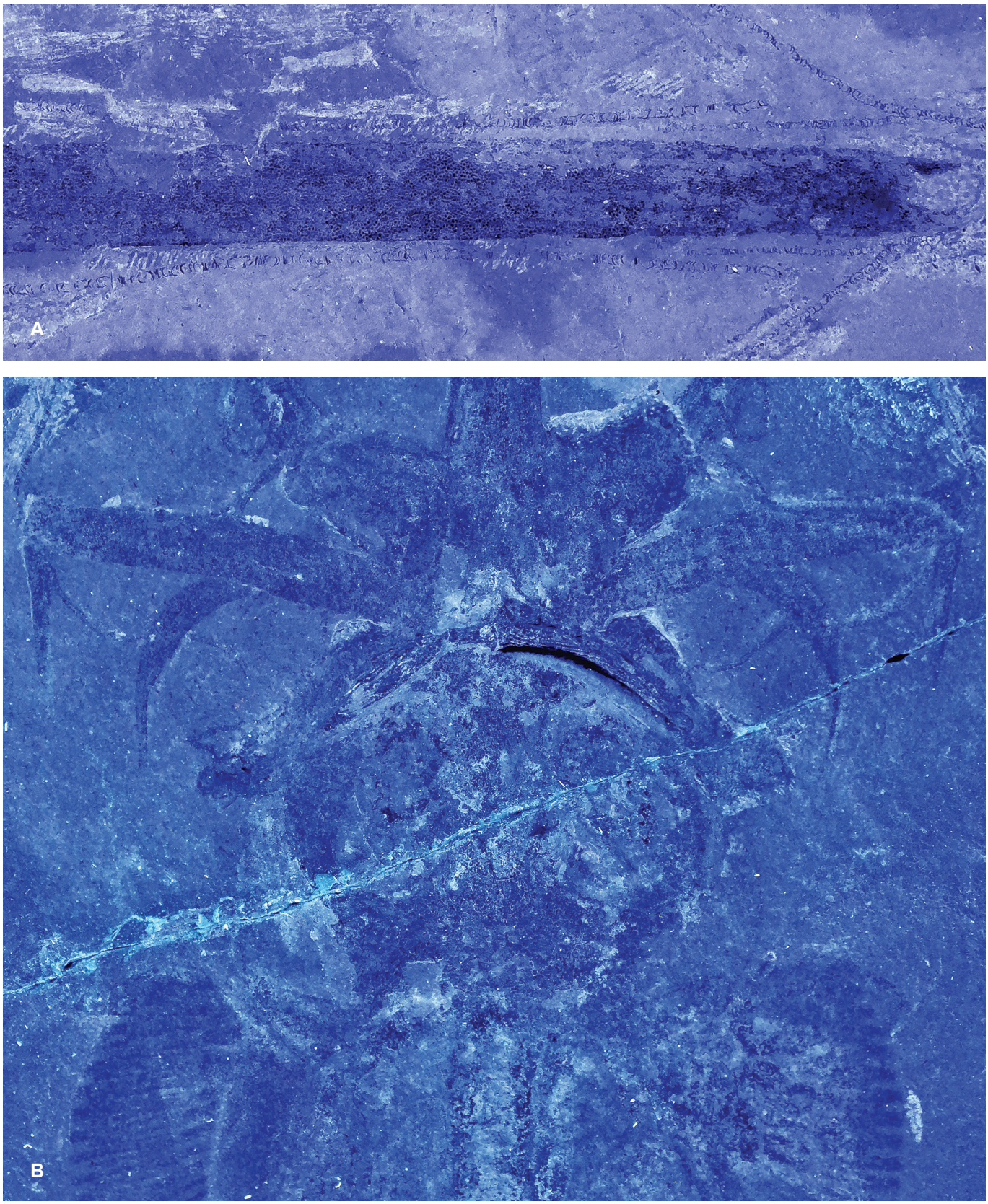
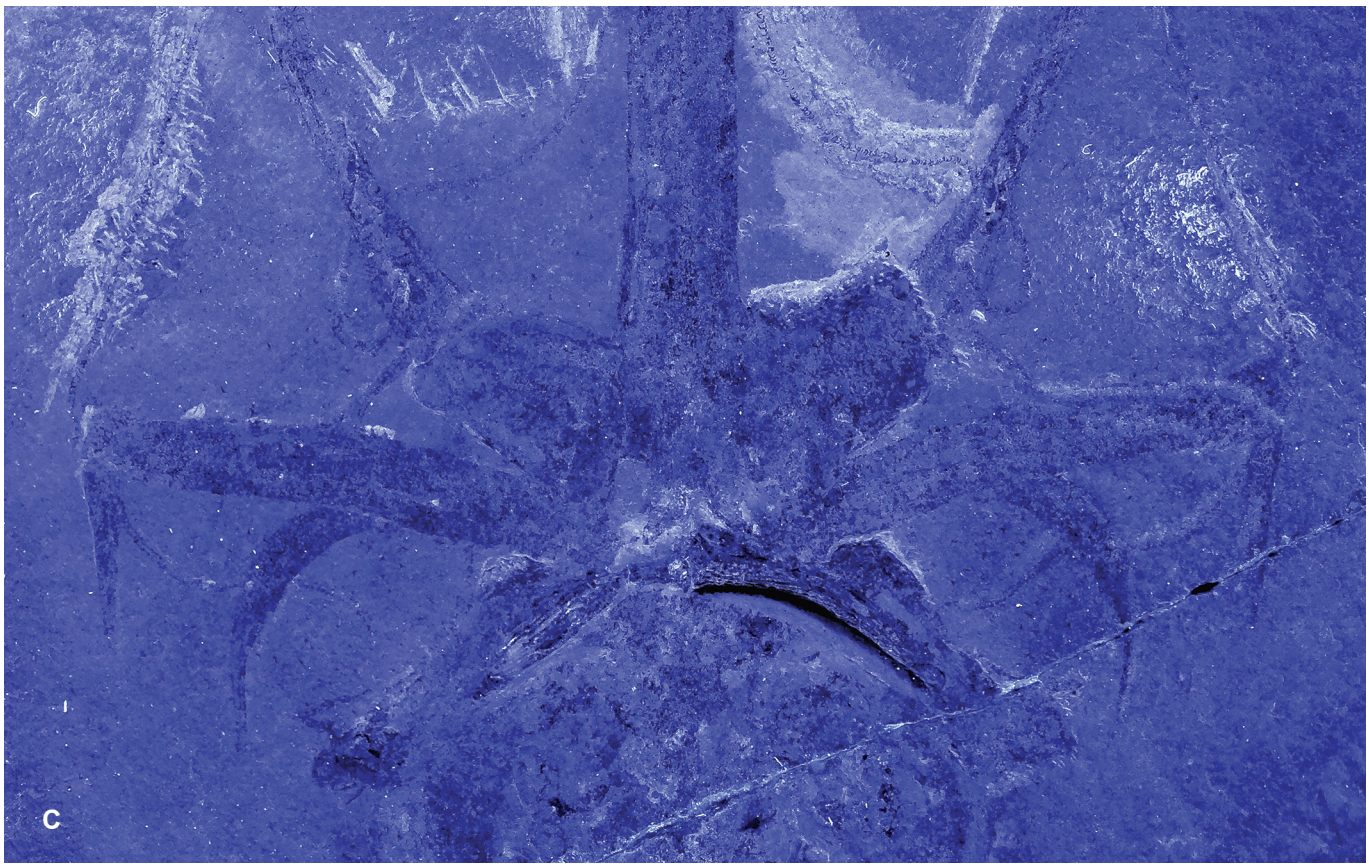


Fig. 9 - *Squaloraja* sp., MSNM V655. A) Close-up of the median rostral cartilage covered with granulations, UV light (part) (x ca. 5). B) Close-up of the neurocranium, UV light (part) (x ca. 2.75).C) Close-up of the supramaxillary, premaxillary, and ?pre-labial bars, UV light (part) (x ca. 2.6). D) Close-up of the strong mandibular arc, UV light (part) (x ca. 5.2). / *Squaloraja* sp., MSNM V655. A) Dettaglio della cartilagine rostrale mediana ricoperta di granulazioni, luce UV (impronta) (x ca. 5). B) Dettaglio del neurocranio, luce UV (impronta) (x ca. 2,75). C) Dettaglio delle barre sopramascellari, premascellari e prelabiali, luce UV (impronta) (x ca. 2,6). D) Dettaglio del robusto arco mandibolare, luce UV (impronta) (x ca. 5,2). (Photo by: / Foto di: R. Sigismondo).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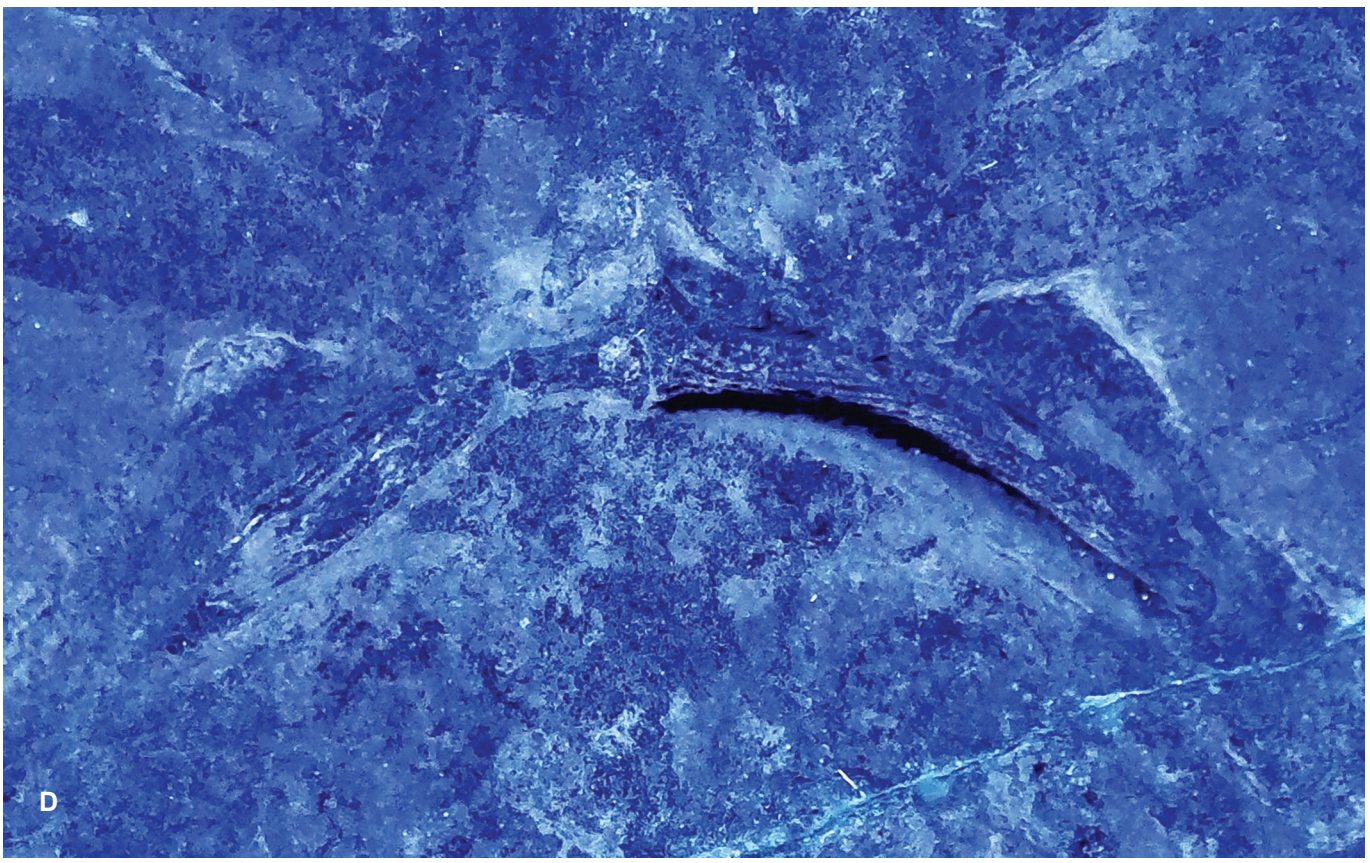
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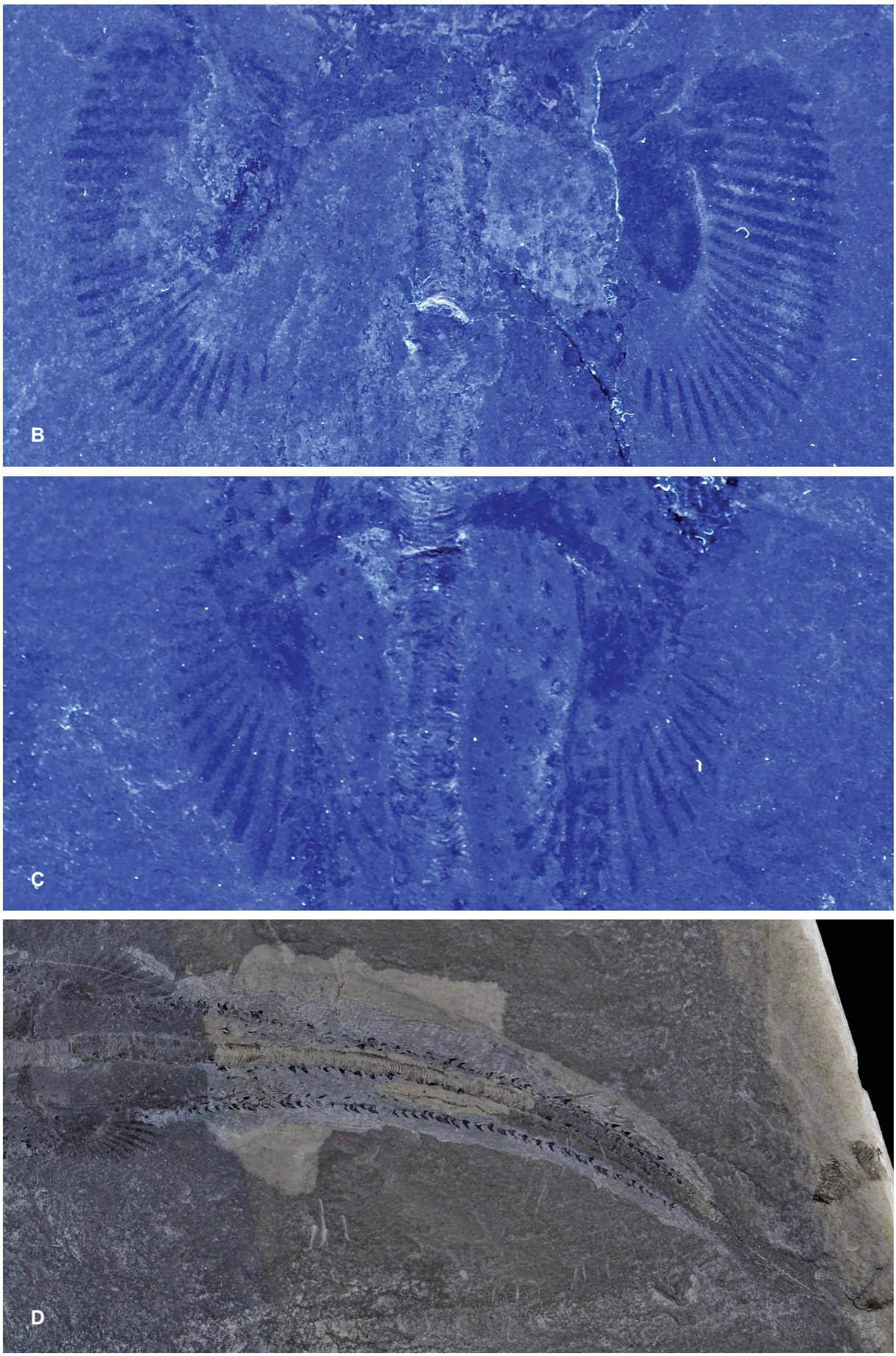
Fig. 10 - *Squaloraja* sp., MSNM V655. A) Close-up of the vertebral column with placoid scales, natural light (counterpart) (x 2.5). B) Close-up of the pectoral girdle and fins, UV light (counterpart) (x ca. 2.65). C) Close-up of the pelvic girdle and fins, UV light (counterpart) (x ca. 2.65). D) Close-up of the tail with hooked-shape scales ranged in a pair of parallel rows dorsally and hooked-shape scales ranged along the inferior margin of each side, natural light (part) (x ca. 1.4). / *Squaloraja* sp., MSNM V655. A) Dettaglio della colonna vertebrale con scaglie placoidi, luce naturale (controimpronta) (x 2,5). B) Dettaglio del cinto pettorale e delle pinne, luce UV (controimpronta) (x ca. 2,65). C) Dettaglio del cinto pelvico e delle pinne, luce UV (controimpronta) (x ca. 2,65). D) Dettaglio delle scaglie dorso caudali uncinate disposte su due file parallele e delle scaglie uncinate latero caudali disposte lungo i margini inferiori, luce naturale (impronta) (x ca. 1,4). (Photo by: / Foto di: R. Sigismondo).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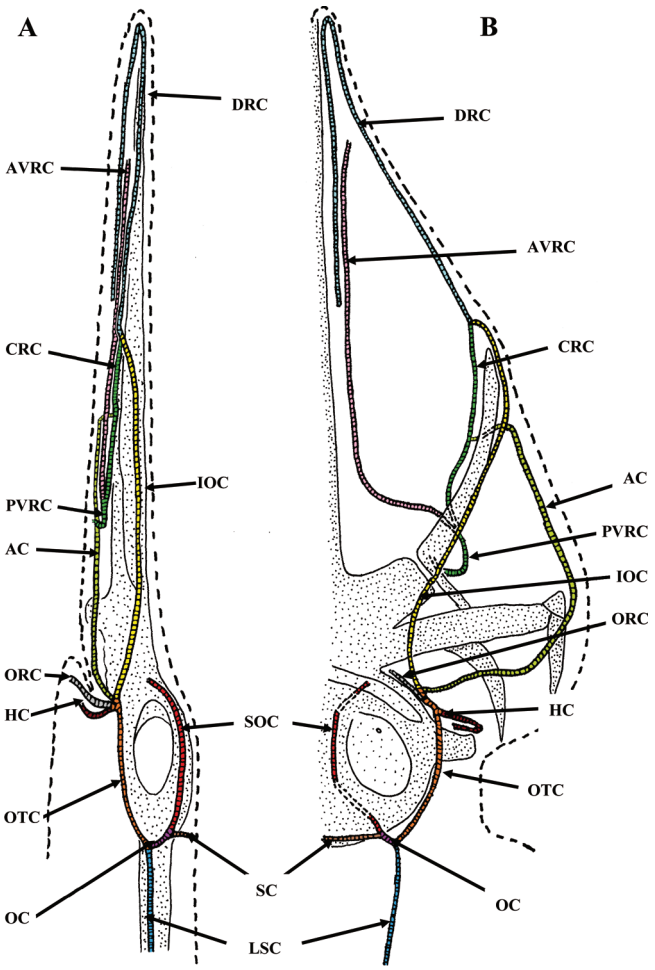

Fig. 11 - *Squaloraja* sp., MSNM V655. Scheme of mechanosensory canals. Abbreviations - AC: angular canal (yellow); AVRC: anterior ventral rostral canal (light blue); CRC: central rostral canal (bright green); DRC: dorsal rostral canal (light blue); LSC: lateral line sensory canal of the trunk (dark blue); OC: occipital canal (purple); ORC: oral canal (grey); OTC: otic canal (orange); PRVC: posterior ventral rostral canal (pink); SC: supratemporal canal (dark red); SOC: supraorbital canal (red). / *Squaloraja* sp., MSNM V655. Schema dei canali sensoriali. Abbreviazioni - AC: canale angolare (giallo); AVRC: canale rostrale ventrale anteriore (azzurro); CRC: canale rostrale centrale (verde brillante); DRC: canale rostrale dorsale (azzurro); LSC: canale sensoriale della linea laterale del tronco (blu scuro); OC: canale occipitale (viola); ORC: canale orale (grigio); OTC: canale otico (arancione); PRVC: canale rostrale ventrale posteriore (rosa); SC: canale sopratemporale (rosso scuro); SOC: canale sovraorbitale (rosso).

PALAEOECOLOGICAL EVIDENCE

According to Page (2003: 28), during the Hettangian-Sinemurian (Lower Jurassic) "no direct Boreal links existed in Europe, so a simple pattern of a northern Northwest European Province and a southern and deeper water Mediterranean Province is recognisable", as supported for instance by the ammonoid taxa showing distinct differences, with a "Sinemurian ammonoid provincialism, with a broad Northwest European Province over much of Europe, and a Mediterranean Province in south-easternmost areas" (Page, 2003: 32). Indeed, there are substantial differences between the marine fossil taxa from the north-western Europe and those of the southern Mediterranean Provinces.

The palaeogeographic position of the Osteno basin during the Sinemurian (Lower Jurassic), located at the northern boundary of the Tethyan faunas, just at the limit of the deep water sediments of the Western Tethys Sea and surrounded by shallow waters and emergent land masses, outlines an environmental scenario unfavourable to a possible migration/distribution within the two faunal Provinces for a species considered to have a benthic deep water to bathyal style of life.

Based on these considerations, we cannot exclude *a priori* that the studied specimen might represent a new taxon within *Squaloraja*, a hypothesis that can only be verified and supported by the discovery of other specimens, especially adult males.

CONCLUSIONS

1. MSNM V655, a complete, articulated specimen represented by part and counterpart and previously reported from the Osteno lens Konservat Lagertätte in the Moltrasio Limestone (*Arietites bucklandi* zone, lower Sinemurian, Lower Jurassic) of Osteno, NW Italy, is confirmed as belonging to a squalorajoid holocephalian.
2. The specimen is described in detail for the first time. Its salient features are a large dorsoventrally flattened head, elongate rostrum, a single mandibular tooth plate on each ramus of the lower jaw, a well-developed synarcual, thick notochordal sheath calcifications, and only slightly reduced squamation comprising distinctive placoid scales with stellate bases. There is no ethmoid canal, dorsal fin or fin spine.
3. Based on its size (in comparison to specimens of *S. polyspondyla* from the Lower Jurassic of the UK), the granular (rather than tesselated) structure of the rostral cartilage, and potentially poorly calcified cartilages elsewhere in the rostral and post-cranial skeleton, the specimen is believed to belong to an immature, juvenile individual.
4. The lack of a frontal clasper cartilage and prepelvic tenaculae together with their accompanying revetments of specialised scales indicates that the specimen is a female.
5. Following a comparison with specimens in the NHMUK, and bearing in mind (3) and (4) above, MSNM V655 is left in open nomenclature as *Squaloraja* sp. The discovery of further specimens, including those of mature individuals, is needed for further clarification of the taxonomic status of the Osteno squalorajoid, especially considering the palaeogeographic separation between the Italian and UK holocephalian faunas.

6 *Squaloraja tenuispina* Woodward 1886 based upon an isolated slender frontal clasper from the Lower Jurassic of Lyme Regis, is concluded to be a junior synonym of *S. polyspondyla* Agassiz 1836.

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