Taxonomic revision of the genus Ichthyosarcolites Demarest, 1812, and description of a new canaliculate rudist from the Cenomanian of Slovenia: Oryxia sulcata gen. et sp. nov. (Bivalvia, Hippuritida)

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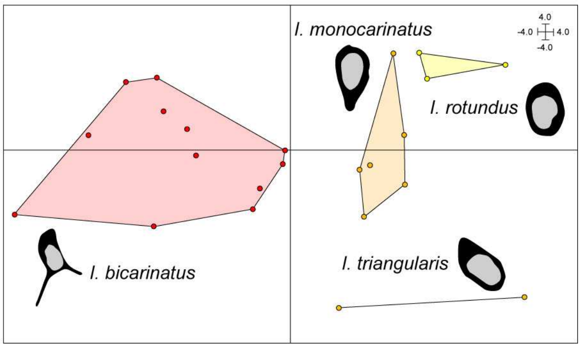
I. monocarinatus
4.0
-4.0
4.0
-4.0
I. rotundus
I. bicarinatus
I. triangularis

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Taxonomic revision of the genus *Ichthyosarcolites* Desmarest, 1812, and description of *Oryxia sulcata* gen. et sp. nov. (Bivalvia, Hippuritida), a new canaliculate rudist from the Cenomanian of Slovenia:

Abstract

Ichthyosarcolites was amongst the first rudist genera to be described. Nineteen species have been assigned to this genus since its introduction in 1812, all from shallow-marine tropical carbonates of Albian and Cenomanian age (mid-Cretaceous). Almost all nominal species suffer from vague original descriptions, and some forms were inaccurately assigned to the genus. Several species were defined on the basis of the number of flanges along the shell, such as *Ichthyosarcolites rotundus*, *I. monocarinatus*, *I. triangularis*, *I. bicarinatus*, *I. tricarinatus*, *I. alatus* and *I. polycarinatus*. An analysis of the relative position of the flanges on the shell by hierarchical clustering helps with taxon definition. Two species with a single flange are here recognised, one with a dorsal flange (*I. monocarinatus*), the other with a ventral one (*I. triangularis*). There is no consistency in flange distribution on the shells whatever their number is, i.e., two or more, and homology of individual flanges cannot be demonstrated. Morphometric analysis finds a link between the shape of the general cavity and flange number and distribution. Out of the nineteen species named in the literature, only four can be retained after our thorough morphological analyses, namely *Ichthyosarcolites rotundus* (defined by a circular shell that lacks flanges), *I. triangularis* (defined by a single dorsal flange), *I. monocarinatus* (defined by a single ventral flange) and *I. bicarinatus* (defined by two flanges or more). Flanges have very variable morphological features among *I. bicarinatus*. In addition, we here erect *Oryxia sulcata* nov. gen. et sp., a new form based on specimens previously identified as *I. bicarinatus*, *I. poljaki* and *I. tricarinatus*. This new taxon is defined by the presence of a ligament groove, this in contrast to *Ichthyosarcolites* which never shows any trace of ligament. *Oryxia* nov. gen. may be the sister group of a clade of canaliculated forms that lost contact between the ligament support and the shell exterior and includes antillocaprinids, trechmannellids or ichthyosarcolitids.

Keywords:

Rudist bivalves

Ichthyosarcolitidae

Morphological analysis

Species delimitation

Mid-Cretaceous

Ligament evolution

1. Introduction

Ichthyosarcolites ranks amongst the oldest named genera of rudist bivalves, having been erected by Desmarest (1812) on the basis of internal moulds found in Cenomanian strata of Charentes, western France, although the first mention of these fossils in the literature can be found in Guettard (1786), who referred to them as “Cucroïdes” and “corps marins fossiles” with the morphology of “cercles pierreux” (Fig. 1A). Desmarest (1812, 1817) considered these fossils to be a link between “*hippurites*” and “*orthoceratites*” (interpreted at the time as cephalopods), on account of a structure that was interpreted as a sipho (Fig. 1B). Later, d’Orbigny (1850) showed that the structure that had been assumed to be a sipho by Desmarest was in fact a small cavity filled by tabulations, without communication between the chambers. D’Orbigny (1850) erected the genus *Caprinella* (= *Ichthyosarcolites*) within the group of rudists that were close to *Caprina* because of similar shell coiling and the presence of canals in the shell. With the discovery of novel forms of rudists during the nineteenth century and a better understanding of rudist anatomy, the affinities of *Ichthyosarcolites* became more difficult to assess. The hinge of *Ichthyosarcolites* shares similarities with that of radiolitids (Skelton and Smith, 2000) and shell canals occur also in caprinuloideids and antillocaprinids (Skelton, 2013a, fig. 2). Douvillé (1887) erected the family Ichthyosarcolitidae, which remained monogeneric until the description of *Curtocaprina clabaughikinsorum* (Mitchell, 2013a). *Ichthyosarcolites* had been continuously enriched with new species names, now numbering nineteen, the latest addition being

Ichthyosarcolites alatus from central America, as described by Filkorn (2002).

The fossil record of *Ichthyosarcolites* is rich, with shells found in abundance across carbonate platforms of Cenomanian age. The state of preservation of specimens usually is poor, being found either as internal moulds or encased in indurated limestones. Specimens have traditionally been studied on the basis of thin sections. The genus *Ichthyosarcolites* can be recognised on the basis of the notable development of its narrow right valve that can attain nearly a metre in length, but overall shell shape development demonstrates a wide range of variation which leads to problems of species delimitation.

Here we reassess the morphology of the genus *Ichthyosarcolites* using specimens from institutional collections and newly collected shells from the presumed type locality in Charentes. These specimens were compared with descriptions in the literature. We also discuss the relevance of the current taxonomic framework for species of the genus, mainly based on the number of flanges and general shell shape in cross section. An analysis of flange positions is used to compare specimens and to test homologies amongst shells. We also performed a discriminant analysis to see if any correlation or dependence existed between internal anatomy and external flange locations. Based on morphological character combinations that minimise information redundancy, a new taxonomic framework is proposed that provides higher phylogenetic significance.

2. Material and methods

2.1. Material studied

Investigations are based on a literature survey, access to specimens in the AMU, MNHN, SB and NMNH collections (abbreviations, see below), complemented with pictures of collection or field specimens for a number of European countries and Mexico. Fieldwork in Charentes focused on middle and upper Cenomanian levels in which *Ichthyosarcolites* is common as internal moulds. *Ichthyosarcolites* are found on the northern part of Île Madame (45°96'N 1°12'W) in two distinct stratigraphical levels, i.e., units C1 and C2 of the Cenomanian series (Moreau, 1993; Videt, 2003). *Ichthyosarcolites triangularis* co-occurs with *Sphaerulites foliaceus* in grey wackestones and packstones of middle Cenomanian age that represent subtidal, quiet environments. The aragonitic shell layer is dissolved but frequently encrusted with oysters and other epibionts that preserved shell outlines. At Pointe de Chaucre on the west coast of Île d'Oléron (45°98'N 1°39'W), the rocky shore exposes largely units B3 to C3 in which rudists (*Caprina adversa*, *I. triangularis* and *S. foliaceus*) are found in high density of individuals (Chéreau et al., 1997). The rudists occur in carbonate deposits together with oysters (*Rhynchostreon suborbiculatum* and *Rastellum carinatum*), nerineid gastropods, chaetetid sponges and diverse benthic foraminifera depending on initial environmental conditions. At Pointe de Chaucre, a biostrome of large *C. adversa* and *I. triangularis* develops in beds representing high-energy environment and shallow-marine, sandy bottoms, whereas quiet environments associate more often *I. triangularis* with *S. foliaceus*. Amongst rudists, *Ichthyosarcolites* is the most widely distributed form, occurring in a range of sedimentary environments, from shallow-marine carbonate sands to circa-littoral offshore muds. The genus is interpreted to have been environmentally tolerant, being the first rudist to settle on shallow-marine mobile and soft sediments (Chéreau et al., 1997).

D'Orbigny (1850) provided good descriptions and illustrations of *Ichthyosarcolites* among which two figured specimens of *I. triangularis* are from Charras (Charente-Maritime, France; MNHN.F.R08003; Fig. 1C). An additional specimen of *I. triangularis* from Charras is available in the Sorbonne University collections. The d'Orbigny Collection includes additional specimens from Île Madame (MNHN.F.6517-B). One fragment of *I. triangularis* from an unpublished plate of material in the Guéranger Collection (MV.2003.1.10900; Le Mans, France) shows its three-dimensionally preserved shape, along with the syntype of *Ichthyosarcolites bicarinatus* (MGUP.021.2-110; Fig. 3C). The lectotype of *Ichthyosarcolites doublieri* from Martigues (Bouches-du-Rhône, France) was also accessed (MNHN.F.R07971; Fig. 3F). One specimen of *Ichthyosarcolites rotundus* from Roquefort-la-Bédoule is available at Aix-Marseille University (AMU.ICH1; Fig. 4A). M. Floquet provided field photographs of other *Ichthyosarcolites* specimens from Roquefort-la-Bédoule, while six thin-sliced specimens of *I. bicarinatus* (AMU-HBES 84a–b) and one thin-sliced specimen of *I. tricarinatus* (AMU-HBES 85a; Fig. 4C) from Jebel Selloum (Tunisia) can be found in the Bessaïs Collection (Aix-Marseille University). The collection of J. Philip houses two thin slices (AMU-PCC 41a) of *Ichthyosarcolites* *poljaki* from Koulovate (Greece). Several additional species are analysed from photographs taken at Aquismon Ciudad Valles, Canon de la Servilleta (Tamaulipas), San Joaquin Queretaro and Paso del Rio (Mexico) by Javier Aguilar-Perez (Fig. 4D–E), inclusive of the holotype of *Ichthyosarcolites alatus* (Figs. 2A, 3E), from Istria (Croatia) and Bosnia Herzegovina, including the types of *Ichthyosarcolites monocarinatus* and *Ichthyosarcolites polycarinatus* by Alceo Tarlao (MB.3470, MB.3482, MB.4197 (3); see Fig. 3B, D) and from Hrušica (Slovenia) by Bogdan Jurkovšek (BJ1901, BJ1914, BJ1942). Two small pieces of probable myophoral parts of a specimen labelled "*Ichthyosarcolites cornutus*" and several unidentifiable specimens from USA, labelled *Ichthyosarcolites* sp. (YPM 24697, 24694 and 24696), were also considered and compared to Old World specimens, completed by photographs of a Canadian specimen of *Ichthyosarcolites coraloidea* (GMUS.Mp 1; see Fig. 4F; Caldwell and Evans, 1963).

Abbreviations. AMNH, American Museum of Natural History, New York; AMU, Aix-Marseille University, Centre Européen de Recherche et d'Enseignement des Géosciences de l'Environnement; BJ, palaeontological collection of Drs Bogdan Jurkovšek and Tea Kolar-Jurkovšek, Ministry of Culture of Republic of Slovenia and the Natural History Museum of Slovenia, Ljubljana; GMUS, Geological Museum of the University of Saskatchewan, Saskatoon, Canada; LGPZ, Laboratory of Geology and Paleontology of the Faculty of Science of Zagreb, Croatia; MB, Zemaljski Muzej BiH, Sarajevo, Bosnia and Herzegovina; MGUP, Museo Geologico G.G. Gemmellaro della R. Università degli Studi di Palermo, Italy; MNHN, Muséum National d'Histoire Naturelle, Paris; MV, Musée Vert, Muséum d'Histoire Naturelle du Mans, France;

NMNH, National Museum of Natural History (Washington DC, USA); SB, Sorbonne Université, Paris, France; UNAM, Universidad Nacional Autónoma de México, Mexico; YPM, Yale Peabody Museum, New Haven, USA.

2.2. Morphological analysis

Only very few three-dimensionally preserved shells of *Ichthyosarcolites* are available. Fossils usually are internal molds of the general cavity or recrystallised shells observed in cross sections. The distinction of *Ichthyosarcolites* species in the literature is based on external features: occurrence of external flanges along the shell (Figs. 2–3), shape of the internal cavity (Figs. 3–4) and development of internal tabulae (Figs. 4, 5A–D). All of these features were reappraised and analysed using morphometry and statistical tools to improve species definitions (Table 1) and taken into account as Least Inclusive Taxonomic Units or LITU (e.g., minimal taxonomic unit; Pleijel and Rouse, 2000).

Several species have been defined by the number of flanges (see Polšak, 1967). However, the relative position of flanges around the shell has received very limited attention, whereas the location and growth patterns of flanges or other shell ornament often support homologies in molluscs (Merle, 2005). The anatomical position of a flange is not recognisable unless the shell can be properly oriented. We quantify the position of a flange by its angle, measured from the central tooth of the right valve or the central tooth socket, between the anterior and posterior teeth of the left valve (Fig. 6A). This method requires thin slices that are parallel to the growth lines of the shell (parallel to the commissural plane for uncoiled shells). Thin slices that deviated too strongly were not used in the present study (specimens such as number 21 – SOM 1 – are used because shell coiling affects only part of the dorsal outline). The method also requires to place a landmark at the centre of the general cavity that we approximate as the centre of the smaller circle including the general cavity. This procedure allows comparisons of shells of different sizes with flanges of different sizes, morphologies and directions. The posterior and anterior sides on the left valve can be identified with the help of the posterior myophore which is always shorter than the anterior one. On the right valve, a small cavity lies at the anterior side of the shell. The angle is always measured from the dorsal to the posterior part of the shell. All measurements were done on pictures of thin-sliced specimens using ImageJ 1.48v (Rasband, 1997). Measurements proved possible only on 20 shells, yielding a total of 58 measurements of angles. The angles are plotted in Figure 6B using R (R Development Core Team, 2008) to summarise the data set. A hierarchical clustering using Ward's method was made on the basis of angular positions of flanges (Fig. 6C) in order to test for homologous flange positions.

We carried out an analysis using geometric morphometry on the shape of the internal cavity. Only specimens with clear orientation and no trace of taphonomic compaction were chosen. Twenty-three shells were considered; those used for analysis of flange orientation, plus three shells lacking flanges. The general cavities are described by ten landmarks equally distributed on the outline. Landmark co-ordinates are digitised from photographs using the website PhyloNimbus (SOM 1). The procruste-fitted landmark data set were converted to procruste residuals by subtracting the mean shape using Past 3.15 (Hammer et al., 2001). A principal component analysis (PCA) was implemented from the Procruste residuals (Harper, 2008). The ten principal components from the PCA were used as uncorrelated variables for a linear discriminant analysis (LDA; Fig. 7). An LDA is especially suited for maximising inter-group separation and minimising intra-group separation for predefined groups (McLachlan, 2004). The LDA is used here to check if the clusters constructed with the data of flange positions are congruent with the analysis of internal anatomy.

3. Morphology

3.1. Pallial canals

The canals are often missing due to the generally poor preservation of fossils (Fig. 4). Whenever preserved, the patterns of pallial canal distribution are similar on the two valves. There is always a single outer row of small palisading canals, the rest of the aragonitic shell being filled by capillary canals of variable diameter (1 mm on average), rounded to polygonal in cross section. Some Mexican specimens exhibit irregular rows of enlarged round canals inside the flanges (Fig. 3E). Canals generally increase in diameter and number with shell size. The specimen from Jordan illustrated as *I. bicarinatus* by Chikhi-Aouimeur (2010, fig. 4B) exhibits exceptionally large, round to polygonal canals. This larger canal size leads to an accentuated polygonal shape of the canals and a relative reduction of shell material between the canals. Canal size and distribution patterns are linked to ontogeny and flange development. However, the high inter-individual variability does not support the recognition of any distinct pattern that could be used to support any of the nominal species.

3.2. Tabulae

Tabulae are thin skeletal walls produced during shell growth that represent successive floors of the internal shell cavities. The species of *Ichthyosarcolites* are described with tabulae grossly parallel to the commissural plane, except for *I. obliquus* that is defined by obliquely oriented tabulation and for *I. doublieri* which lacks tabulations. The tabulae are very thin, fragile aragonitic structures that may disappear easily through taphonomic and diagenetic processes. The tabulations usually are recrystallised or appear as dissolution voids in internal moulds. Under best-preservation conditions, tabulae are to be found in the general cavity, the sockets and the posterior myophoral cavity (Figs. 4D, 5A). In practice, traces of tabulae are often erased (Figs. 3F, 5E–F). In Figure 6B, the tabulae of the lower shell are well visible on the left side, but disappear nearly completely on the right side. The partial preservation of tabulae suggests incomplete dissolution prior to lithification. The lack of tabulae in the holotype of *I. doublieri* (Fig. 3F) is probably due to complete dissolution of the tabulae during early diagenesis.

In fossils, tabulae may appear parallel with or strongly oblique to the commissural plane (Fig. 5). Oblique tabulae have the shape of a three-quarter cornet with a downward-pointing dorsal attachment, and an open rounded ventral attachment to the front wall of the general cavity. The obliqueness of the tabulae can be seen only in dorsoventral view (Fig. 5C, F). The obliqueness of tabulae appears highly variable amongst specimens within a local assemblage and may reflect the tilting of individuals during their life span. In *I. triangularis* from Charentes, the expression of tabulae varies gradually among individual shells from parallel with the commissure to strongly oblique (Fig. 5A, D). The high variation in tabulae expressed in *I. triangularis* includes the typical morphology of *I. obliquus*, which challenges the reliability of *I. obliquus* as a distinct species.

3.3. Shell coiling

There is a wide range of variation amongst coiling patterns in shells of *Ichthyosarcolites*. Some species have been described as completely uncoiled, others as simply curved or coiled. The coiling is always in a spiral plane, with loose to tight whorls (Figs. 1C, 5E). The torsion of the flanges in Figure 3C suggests twisting in the coiling plane, probably in response to substrate irregularities. Shells are never straight along their entire development. In Figure 5F, the uncoiled shell begins from a coil at its right apex. The uncoiling seems to appear during the animal's life in relation with environmental constraints. A wide range of coiling pattern can be encountered at any given location.

3.4. Ligament

The ligament is totally missing in typical *Ichthyosarcolites* (Fig. 2) along with associated structures (ligament groove, ligament cavity). Amongst specimens from Slovenia, described as *I. poljaki*, *I. bicarinatus* and *I. tricarinatus* by Pleničar & Jurkovšek (1999), few shells exhibit a small dorsal protrusion that was considered a flange by those authors. This dorsal protrusion is bordered by a ligament groove. This protrusion should be understood as a bulge of shell stranded posteriorly to the ligament groove, not homologous to a flange. The groove of the shells sinks to the anterior tooth socket and ends with a tiny shell bulb. Similar dorsal ligamentary bulges are also recognised in some forms from Istria (Croatia) illustrated by Polšak (1967), even if the inside of the shell does not permit to see a ligament groove due to poor preservation. Ligament structures are of critical importance in the phylogeny of rudists (Yonge, 1967; Skelton and Smith, 2000). Four evolutionary stages are recognised: (1) the ligament follows the commissure dorsally (e.g., *Diceras*); (2) the verticalised ligament is perpendicular to the commissure plane (e.g., *Valletia*, monopleurids); (3) the ligament structures are internalised and only a ligament cavity remains that loses contact with the exterior (e.g., trechmannellids); (4) the ligament disappears completely, including ligament cavity and groove (e.g., Titanosarcolitinae, Parasarcolitinae). *Ichthyosarcolites* represents the fourth stage. However, the ligament groove found in the Slovenian shells would place them in the second stage, out of the genus *Ichthyosarcolites*.

3.5. Flanges

Flanges, ribs, carinae and ridges are local thickenings of the shell (Fig. 2A–B), appearing in differential growth patterns. Even if the expression of shell thickenings in *Ichthyosarcolites* varies from low rounded bulges or ribs to high and thin, blade-like ridges (Figs. 3–4), all have a similar structure and likely appear following the same developmental processes. If the number and positions of flanges are consistent amongst individuals, we can assume homology and use them to define species. Few attempts were made to homologise flanges, by giving each flange a number or a letter based on its relative position on the shell (Polšak, 1967; Carbone et al., 1971). However, only the number of flanges have been listed in diagnoses of species of *Ichthyosarcolites*, but not their positions. *Ichthyosarcolites rotundus* is defined by the absence of flanges. A single flange occurs both in *I. monocarinatus* and *I. triangularis*, two are seen in *I. bicarinatus*, three in *I. tricarinatus*, three to six in *I. alatus* (Filkorn, 2002; Aguilar-Pérez, 2008) and seven in *I. polycarinatus*. Flange morphology can vary in multiple ways: location, orientation and relative development, which can be quantified using the length to width ratio of the flange in cross section. The recognition of flanges may become difficult when these are weakly developed. Filkorn (2002) illustrated adults of *I. alatus* with either four, five or six flanges, but small juveniles with only three flanges were also assigned to *I. alatus* (see Fig. 3E), suggesting variation of flange number during ontogeny.

A consistent test of homology for the flanges would be to detect consistency in their positions. Flanges of same positions are more likely to be homologous. Among the species described with a single flange, *I. monocarinatus* can be defined by the presence of a ventral one and *I. triangularis* by a dorsal one. This variation in flange position is corroborated by the main two clusters (Fig. 6C) in the hierarchical classification. The position of the flange could perfectly support the definition of these two species considering that the uniqueness of the flange is not homologous.

On shells with more than one flange, groups of the hierarchical clustering may provide evidence of patterns of flange distribution homologies. In the case of two flanges, homology is assumed if the two flanges consistently, or never, fall within the same cluster. The cluster analyses fail to recognise consistent patterns of flange distribution among two-flanged or three-flanged shells. It is not possible to distinguish consistently homologous flanges among shells. The plasticity of flange distribution pattern and number of flanges is not reliable from an evolutionary point of view. The definition of a species on the basis of the number of flanges must be avoided in future.

Ichthyosarcolites is a recumbent form (Skelton, 1976) that lay on sandy to muddy substrates. This ecotype constrains the development of flanges around the shell. Our primary hypothesis was that no flange is likely to have developed on the side of the shell that lay on the sea floor, and that we can expect the flattest side of any *Ichthyosarcolites* shell to be in contact with the substrate. The hierarchical classification of flanges separates ventral flanges from dorsal ones well, with a rare occurrence of flanges on the anterior side (Fig. 6B). Most species of *Ichthyosarcolites* likely lay on their anterior side, with usually a stabilising flange in ventral or dorsal position. This is consistent with the anterior attachment of the juvenile spiprogyrate right valve (Skelton, 1974).

3.6. General cavity

Some species of *Ichthyosarcolites* were defined solely on the basis of shell cross sections. The character descriptions focused on external features including bulges, flanges, relative shell thickness and outline of the general cavity. For example, *I. triangularis* is characterised by a triangular shape in cross section. As observed in many molluscs, external shell features reflect the shape of internal structures such as the general cavity. Because flange number and general cavity shape are the two main features used to erect species of *Ichthyosarcolites*, we tested whether the groups defined by flange distribution could also be recognised in general cavity outline.

Following the results of the hierarchical classification on flanges, a discriminant analysis was performed on cavity outline descriptors, assuming two kinds of single-flanged *Ichthyosarcolites* (*I. triangularis* and *I. monocarinatus*), the flange-lacking *I. rotundus* and a last cluster with all shells with two or more flanges. The results show a clear partition of *I. triangularis, I. monocarinatus, I. rotundus* and the multi-flanged *Ichthyosarcolites* in the morphospace (Fig. 7). The congruence between the number and position of flanges and the internal cavity outline suggests geometric constraints on shell development. Addition of flanges leads to a more or less polygonal cavity.

The Mexican populations of *Ichthyosarcolites* demonstrate an important variability in the number of flanges amongst adults (4–7) and also ontogenetic variation, with juveniles of *I. alatus* bearing a smaller number of flanges (3–4) than adults (4–5) (Filkorn, 2002; Aguilar-Pérez, 2008). A similar plasticity in the expression of flanges number is understood as intraspecific variability in antillocaprinids (e.g., *Parasarcolites atkinsoni*; Mitchell and Gunter, 2006), a group close to Ichthyosarcolitidae (Skelton and Smith, 2000). The shells with two or more flanges in our cluster analysis always have both a ventral and a dorsal flange. For specimens possessing more than one flange, flanges are located more randomly. For these reasons, we retain a single species of *Ichthyosarcolites* bearing two flanges or more.

4. Systematic palaeontology

Our analyses lead us to retain four species that are characterised by a unique combination of homologous parts (Wheeler and Platnick, 2000): one with a single ventral flange, one with a single dorsal flange, one with at least two flanges one without any flange. The systematic arrangement of the Bivalvia used here follows Carter et al. (2011) and Skelton (2013a–b).

Class Bivalvia Linnaeus, 1758

Infraclass Heteroconchia Gray, 1854

Order Hippuritida Newell, 1965

Suborder Hippuritidina Newell, 1965

Superfamily Caprinoidea d’Orbigny, 1850

Family Ichthyosarcolitidae Douvillé, 1887

Genus *Ichthyosarcolites* Desmarest, 1812

Type species. *Ichthyosarcolites triangularis* Desmarest, 1812, by monotypy.

Diagnosis. Rudist with small left valve and extremely strongly developed right valve. Both valves loosely coiled with non-contiguous whorls that may uncoil during shell growth. Presence of none to seven longitudinal flanges along the shell. The relative size and shape of the flanges vary from rounded costae to prominent ridges. Aragonitic shell layer filled with capillary canals (Fig. 2). Tabulae fill all cavities of the two valves and the pallial canals. No ligament groove, nor cavity. The two anterior and posterior sockets of the right valve are of equal size, small and rounded. Small posterior accessory cavity (PAC; Fig. 2C–D). The two myophores are similar to those of radiolitids, forming blades attached to the ventral side of the teeth on the left valve. The myophores of the left valve insert directly in the wall of the general cavity of the right valve.

Remarks. The monogeneric family Ichthyosarcolitidae was created by Douvillé (1887) to reflect the high differentiation of *Ichthyosarcolites* from all other rudists. *Ichthyosarcolites* possesses such specific features that confusion with other genera can be ruled out. *Stellacaprina gunteri* shows a similar morphology but the species has two additional toothlets, i.e., the diagnostic feature of the Antillocaprinidae (Mitchell, 2013b). *Curtocaprina clabaughikinsorum* is the only other member of the Ichthyosarcolitidae, following Mitchell (2013a). That species utterly differs from *Ichthyosarcolites* in the structure of its dentition, size and shell shape (right and left valves of same size, approximately 20 mm, a single ventral flange). If all *Ichthyosarcolites* identified to species are dated as Cenomanian, a specifically indeterminate *Ichthyosarcolites* was recorded from the Albian of Sinai, Egypt (Zakhera, 2010). The map (Fig. 8) shows the geographical location of all specimens, making use of the following references and collection specimens: Mexico (Filkorn, 2002; Aguilar-Pérez, 2008), USA (YPM 24697, 24694, 24696), Cuba (Rojas, 2004), Portugal

(Berthou, 1973), Spain (Troya García, 2015), France (Desmarest, 1812), Italia (MGUP.021.2-110; Gemmellaro, 1865), Slovenia (Pleničar, 1965; Pleničar and Jurkovšek, 1999), Croatia (Polšak, 1967), Bosnia and Herzegovina (Slišković, 1968**)**, Czech Republic (Počta, 1887), Greece (AMU-PCC 41a), Bulgaria (Paquier, 1905), Turkey (Özer, 1998), Algeria (Van de Fliert, 1952), Tunisia (Toucas, 1908; Razgallah et al., 1994), Libya (Parona, 1921), Tanzania (Hennig, 1916), Egypt (Bauer et al., 2001; Zakhera, 2010), Jordan (Chiki-Aouimeur, 2010), Afghanistan (Berizzi Quarto di Palo, 1970) and China (Lan and Wei, 1995).

Ichthyosarcolites is a recumbent form that has been recorded from peri-reefal and fore-reef environments with a high water-energy (Korbar et al., 2001; Filkorn, 2002) to calm mudflats, where it played a pioneer role (Videt, 2003).

Ichthyosarcolites triangularis Desmarest, 1812

Figs. 1C, 2E.

Selected synonymy

1786 Cucroïdes; Guettard, p. 552, pl. 28, fig. 2.

1812 *Ichthyosarcolites triangularis* Desmarest, p. 321.

1817 *Ichthyosarcolites triangularis*; Desmarest, p. 50, pl. 2, figs 9–10.

1821 Glossopètres; Defrance, p. 72.

1821 Ichthyosarcolite; Defrance, p. 549.

1825 *Ichthyosarcolites triangularis*, Desmarest; Deshayes, p. 501.

1825 *Rhabdites triangularis* De Haan, pp. 41–42, 52–53, 57, 160.

1826 *Ichthyosarcolites*, Desmarest; d'Orbigny, p. 167.

1827 Ichthyosarcolite; Ducrotay de Blainville, pl. 11, fig. 2.

1846 *Ichthyosarcolithus* A.G. Desmarest 1817; Herrmannsen, p. 554.

1849 *Caprinella triangularis*, d'Orb., 1847; d'Orbigny, pl. 542.

1850 *Caprinella triangularis*, d'Orb., 1847; d'Orbigny, p. 192.

1854 *Ichthiosarcolites quadrangularis* Tuomey, p. 172.

1855 *Caprinella triangularis* Desm.; Woodward, pp. 52–53, figs 25–27.

1887 *Ichthyosarcolites marginatus* Počta, p. 207.

1887 *Ichthyosarcolithus triangularis* Desmarest; Douvillé, p. 791, figs 15–17.

1887 *Ichthyosarcolites triangularis* Desmarest; Fischer, p. 1057, fig. 804.

1888 *Ichthyosarcolithes*; Douvillé, pp. 706, 728–729.

1889 *Ichthyosarcolites marginatus* Poč.; Počta, p. 87, pl. 6, figs 6–7.

?1905 *Ichthyosarcolites triangularis* Desmarest 1817; Paquier, p. 94, pl. 9, figs 7–9.

?1916 *Ichthyosarcolites triangularis*; Hennig, p. 461.

1921 *Ichthyosarcolites triangularis* Desm.; Parona, p. 10, pl. 1, figs 1a–b, 9.

1930 *Caprinella triangularis*; Repelin, p. 61, pl. 7, fig. 5.

1937 *Ichthyosarcolites triangularis* Desmarest; MacGillavry, p. 47.

1968 *Ichthyosarcolites triangularis*; Damestoy, pp. 2-6, figs 1–3.

1969 *Ichthyosarcolites triangularis*; Dechaseaux, p. N795, fig. 4a–b.

1970 *Ichthyosarcolites triangularis* Desmarest; Berizzi Quarto di Palo, p. 107, pl. 15, fig. 1.

2000 *Ichthyosarcolites triangularis* Desmarest; Skelton and Smith, pp. 110–111, 117, 123, fig. 4c–d.

2010 *Ichthyosarcolites triangularis* Desmarest; Chikhi-Aouimeur, p, 96, fig. 87.1.

2015 *Ichthyosarcolites triangularis* Desmarest; Troya García, pp. 248–254, 267, 271, figs 139–141.

Type material. The type specimen illustrated by Desmarest (1817) has been lost (see Fig. 1B). Here we designate specimen MNHN.F.R08003 (Fig. 1C) as neotype of *Ichthyosarcolites triangularis* Desmarest, 1812, from the Cenomanian at Charras (Charentes, France).

Diagnosis. Species of *Ichthyosarcolites* with small left valve and extremely strongly developed right valve. Both valves loosely coiled with non-contiguous whorls. Presence of a unique dorsal flange somewhat triangular in cross section.

Description. Shell markedly inequivalve; left valve very small (approximately one tenth of length of right valve) and slightly coiled. Right valve narrowly tubular, extremely strongly developed and ventrally coiled (dorsal external side) with non-contiguous whorls (Fig. 1C). Planispiral growth of the shell (Figs. 1C, 5E). Left valve loosely ventrally coiled and very small compared to the right valve. Shape of right valve highly variable, ranging from 0.5 to 2 coils, the space between two coils ranging from a distance of 30 to 500 mm for completely coiled specimens (Figs. 1C, 5E). Both valves of equal diameter. General cavity of both valves of equal diameter, between 10 and 80 mm for adults (e.g., Figs. 1C, 4E, respectively), flange not included. A unique flange is present, always in dorsal position (Fig. 1C), of triangular shape, of equal width and height. Flange straight with a rounded external margin. External aspect of shell completely smooth or with presence of small tightened costae of approximately 0,1 mm in height and 1 mm in width. Shell composed of an outer calcitic layer of approximately 0,5 mm and an inner aragonitic shell layer with a thickness of approximately 15 per cent of the diameter of the body cavity in transverse section, flange not included. The aragonitic shell layer is densely canaliculated with close-set, small capillary canals (approximately 1 mm in diameter), round to slightly ovoid (occasionally honey combed) except for the myophores and the anterior and posterior teeth. The external side of the aragonitic shell layer is bordered with a single row of subrectangular/pallisading canals of same width as capillary canals. Tabulae present on both valves with highly variable thickness and surface orientation in the general cavity, pallial canals, sockets and the PAC. Tabulae flat to highly curved dorsally. When highly oblique, presence of a horizontal part in the middle of the tabulae in dorsoventral axis (Fig. 1C). Tabulae within the pallial canals; tabulae of a canal are regularly spaced and independent of other canals. Single other ovoid PAC present posteroventrally on the right valve, slightly larger than sockets and filled with tabulae (Fig. 5A). No ligament groove, nor cavity.

Left valve myocardinal apparatus. Inverse dentition, composed on the left valve of an anterior and a posterior conical tooth of similar shape and size, separated by a central tooth socket that is never observable as a distinct cavity. Thin vertical, wall-like myophore ventrally adjoined to each tooth. The two myophores constitute a U-shaped myophoral arcade, attached to the teeth, protruding directly into the general cavity of the right valve. Development of vertical myophores generates a space between them and the inner shell, looking like a cavity that may be filled with a few thin, oblique tabulae arranged along an anteroposterior axis. Whole myocardinal apparatus is U-shaped and extends itself to make a connection with the ventral edge of the shell.

Right valve myocardinal apparatus. Central tooth shape unknown, probably reduced, filled with pallial canals. Presence of two ovoid anterior and posterior tooth sockets only separated from the general cavity by a thin wall devoid of canals and elongated along an anteroposterior axis. Sockets always very close to each other (approximately 2 mm separation space). Myophores undifferentiated from the inner shell, no known muscle scars.

Remarks. The type species of the genus, primarily based on internal moulds of the general cavity and sockets segmented by tabulae, was first described by Desmarest (1812) as « Coquille droite et épaisse, presque triangulaire, munie intérieurement de cloisons obliques en forme de mi-cônes ou cornets, et d'un sinus ou siphon longitudinal et latéral ». *Ichthyosarcolites triangularis* was illustrated for the first time by Desmarest (1817) (see Fig. 1B). The main distinctive feature was the triangular shell shape. The type locality of Desmarest's species remained unknown to himself, but it is certain that it originated from Charentes in western France. The dorsal thickening of the aragonitic shell layer was correctly represented in d'Orbigny's illustration (see Fig. 1C).

With a single dorsal flange, *I. marginatus* (Počta, 1887), described as having external longitudinal ribs, completely falls within the range of variation of *I.*

triangularis. Specimens described by Hennig (1916) belong probably to *Ichthyosarcolites* and constitute southernmost known specimens of the genus, from continental Tanzania. However, their attribution to *I. triangularis* is doubtful as the fossils lack diagnostic features.

Occurrences. Exclusively Cenomanian and typical of tropical shallow waters on carbonate platforms along northern and southern Tethyan margins. More precisely, *I. triangularis* has so far been recorded from France (Charentes, western France and Provence, southeastern France), northern Spain, Croatia, Greece, the Czech Republic, Italy, Tunisia, northwest Turkey, Poland and Libya (Fig. 8; Table 1).

Ichthyosarcolites rotundus Polšak, 1967

Figs. 3A, 4A

Selected synonyms

*1967 *Ichthyosarcolites rotundus* Polšak, pp. 80–81, 187, pl. 6, fig. 2; pl. 9, figs. 2–3.

1971 *Ichthyosarcolites rotundus* Polšak; Carbone et al., p. 147, fig. 16.

1998 *Ichthyosarcolites monocarinatus* Sliškovic; Cestari et al., p. 70, figs 1–2.

1998 *Ichthyosarcolites rotundus* Polšak; Özer, p. 240, figs 6–7.

1999 *Ichthyosarcolites rotundus* Polšak; Özer, p. 69, pl. 1, fig. 4.

2001 *Ichthyosarcolites rotundus* Polšak; Özer et al., p. 860, figs 10–11.

2015 *Ichthyosarcolites monocarinatus* Desmarest; Troya García, p. 260, figs 145–147.

Type material. The holotype of *I. rotundus* (Fig. 3A) is housed at the Laboratory of Geology and Paleontology of the Faculty of Science at Zagreb (collection number 778); it is from the Cenomanian of Fontanela Bay (Istria, Croatia).

Diagnosis. Species of *Ichthyosarcolites* with very loosely coiled right valve. Complete absence of flange or thickening of the shell. Cross section of shell and of general cavity ovoid with a longer dorsoventral diameter. Presence of a distinct PAC on the right valve, slightly larger than sockets. PAC occasionally cannot be observed (Fig. 3A). Aragonitic shell layer filled with capillary canals and an external row of palisading canals.

Description. Left valve unknown. Right valve narrowly tubular and nearly straight; length unknown. Section circular (35 to 150 mm in diameter) to elliptical along dorsoventral axis (length/width: 60/45 mm). Shell thickness constant on all shell for approximately one third to one quarter of diameter. Aragonitic shell layer of the right valve densely canaliculated with close-set, very small, round to slightly ovoid capillary canals, sometimes honey combed (diameter 0.5 to 3 mm). The external side of the aragonitic shell layer is bordered with a single row of radial pallisading canals of same width as capillary canals, but subrectangular in cross section. Outer calcitic shell layer unknown. Ovoid cavity (length/width: 7/10 mm) present posteroventrally, of equal size as sockets (PAC; Fig. 4A) on the right valve. Very thin tabulae occurring in general cavity, canals, sockets and PAC. The blade between this cavity and general cavity is so thin that it contains no canal, as the blades separating sockets from the general cavity. No ligament groove, nor cavity.

Right valve myocardinal apparatus. Rudist with inverse dentition. Central tooth shape unknown, filled with canals of variable size, ranging between less than 1 to 10 mm in diameter. Anterior and posterior tooth sockets directly connected to the general cavity. Anterior tooth socket size (length/width) between 5/5 mm and 15/5 mm, posterior tooth socket between 12/5 mm and 15/5 mm. Sockets always very close to each other (distance of 1 to 7 mm). Posterior socket occasionally subpentagonal with two small faces on anterior side (Fig. 4A) making it stranded on the anteroposterior axis. The socket outline presents five angles: a right angle on its posterodorsal side, two acute angles on the posteroventral and anterior sides and two open angles on the anterodorsal and anteroventral sides. Anterior of the posterior tooth socket of similar size. Myophores undifferentiated.

Remarks. The species *I. rotundus* was so named in view of the circular right valve in transverse section, without any flange. Cestari et al. (1998) suggested that *I. rotundus* was synonymous with *I. monocarinatus*, assuming that the flange and shell outline were eroded in specimens assigned to the former. Our examination of samples from La Bédoule, southeastern France (Fig. 4A), refutes this; there is a continuous row of pallisading canals in cross section alongside the shell outline, while it should be discontinuous if a (now abraded) flange had been present.

Occurrences. Exclusively Cenomanian, occurring in shallow tropical waters of the western Tethys, with records from western (Charentes) and southeastern France (Provence) and Italy (Sicily) (Fig. 8; Table 1).

Ichthyosarcolites monocarinatus Slišković, 1966

Fig. 3B

Selected synonyms

*1966 *Ichthyosarcolites monocarinatus* Slišković, p. 177, fig. 1.

1967 *Ichthyosarcolites monocarinatus* Slišković; Polšak, pp. 80, 186, pl. 6, fig. 1; pl. 8, figs 1–5, pl. 9, fig. 1.

1968 *Ichthyosarcolites iokungensis* Bobkova, pp. 289–290, pl. 68.

1976 *Ichthyosarcolites monocarinatus* Slišković; Praturlon and Sirna, pp. 90–100, pl. 1, fig. 18.

1983 *Ichthyosarcolites monocarinatus major* Slišković; Slišković, pp. 19–21, fig. 1.

1992 *Ichthyosarcolites monocarinatus* Slišković; Turnšek et al., p. 220, pl. 14, fig. 2.

1998 *Ichthyosarcolites monocarinatus* Slišković; Cestari et al., pp. 70–72, figs 1, 2/1–6.

?1999 *Ichthyosarcolites monocarinatus* Slišković; Pleničar and Jurkovšek, p. 77, pl. 11, fig. 3a–b.

2005 *Ichthyosarcolites* cf. *monocarinatus* Slišković; Pleničar, p. 34, pl. 5, fig. 1.

2015 *Ichthyosarcolites monocarinatus* Desmarest; Troya García, pp. 260–264, 269, figs 145–147.

Type material. The holotype, MB370, is housed at the Geological-Paleontological Collection of the National Museum at Sarajevo; there is a single paratype, MB 4197(3); both from the Cenomanian of the Dinaric Alps.

Diagnosis. Species of *Ichthyosarcolites* with loosely coiled shell. A unique ventral flange of variable size, from short, triangular in cross section (10/10 mm) to thin and of similar size to the general cavity. General cavity ovoid in dorsoventral axis.

Description. Left valve unknown. Right valve planispiral, known only from a 400-mm-long, butt-shaped fragment, rotating 90 degrees over 200 mm, followed by 200 mm of substraight shell. Elliptical section in dorsoventral axis: 30/40(+ 3) mm, 110/130(+ 20) mm, 40/44(+ 10) mm, these three values representing individual specimen length/width and flange length. Shell thickness approximately constant on all shell for one half to one fifth of diameter. Presence of a unique flange, in anteroventral position. Flange shaped as a little bulge rounded and protruding only 5 mm to a more developed one forming an isosceles triangle of 20 mm in length with a largely rounded end (Fig. 3B). Because of this flange, the cylindrical shell presents a flat ventral side. The aragonitic shell layer of the right valve is densely canaliculated with close-set, very small capillary canals, round to slightly ovoid (diameter approximately of 1 mm). Outer calcitic shell layer unknown. A single other ovoid cavity 4/10 mm is present posteroventrally in the right valve, of equal size to slightly more important than sockets and PAC. Very thin tabulae present on the general cavity, canals, sockets and the PAC. Blade between PAC and the general cavity so thin that it contains no canal, with blades separating sockets from the general cavity. No ligament groove, nor cavity.

Right valve myocardinal apparatus. Rudist with inverse dentition. Central tooth of unknown shape, filled with canals. Diameter between 2 to 6 mm. Presence of two ovoid (approximately 4/8 mm) to polygonal very close anterior and posterior tooth sockets directly connected to the general cavity. One is generally slightly more elongate than the other in the anteroposterior axis. Myophores undifferentiated from the inner shell.

Remarks. Ichthyosarcolites monocarinatus was first described with a single flange and an ovoid general cavity. A subspecies, *I. monocarinatus major*, was erected to accommodate forms with a "highly developed longitudinal edge" (Slišković, 1983, p. 22). *Ichthyosarcolites iokungensis* was assumed to differ from *I. triangularis* by an ovoid section of the general cavity, an absence of costae and a poorly developed ventral flange (Bobkova, 1968). Both the descriptions of *I. monocarinatus* and *I. iokungensis* match the definition of the former, assuming variability in the expression of flange development, which is why they are here synonymised.

Occurrences. Exclusively Cenomanian, occurring in tropical, shallow-water carbonate platforms of the European Tethyan margins, with records from Slovenia, Italy (Abruzzo, Lazio, Sicily), Croatia, Bosnia Herzegovina and Turkey (Denizli).

Ichthyosarcolites bicarinatus Gemmellaro, 1865

Figs. 3C–D, 4B–E, 6A

Selected synonyms

*1865 *Caprinella bicarinata* Gemmellaro, pp. 236–237, pl. 4, figs 5–6.

1898 *Caprinella bicarinata*; Douvillé, p. 150.

1914 *Ichthyosarcolites bicarinatus* Gemmellaro; Parona, p. 21.

1921 *Ichthyosarcolites bicarinatus* (Gemm); Parona, p. 12, pl. 2, figs 1, 7, 10.

1921 *Ichthyosarcolites tricarinatus* Parona, p. 13, pl. 2, figs. 2, 8, 11.

1937 *Ichthyosarcolites bicarinatus* (Gemmellaro); MacGillavry, pp. 49, 51, 54–56.

1937 *Ichthyosarcolites tricarinatus* Parona; MacGillavry, pp. 49, 54–56.

1964 *Ichthyosarcolites poljaki* Polšak, p. 66.

1965 *Ichthyosarcolites rogi* Pleničar, pp. 97–98, 100–101, figs 8–10.

1966 *Ichthyosarcolites polycarinatus* Slišković, p. 178, fig. 2.

1967 *Ichthyosarcolites bicarinatus* Gemmellaro; Polšak, p. 186, pl. 5, fig. 1B–C.

?1967 *Ichthyosarcolites bicarinatus* Gemmellaro; Polšak, p. 186, fig. 21, pl. 5, fig. 2A.

1967 *Ichthyosarcolites tricarinatus* Parona; Polšak, pp. 76, 185, fig. 19, pl. 4, figs 5, 7; pl. 5, fig. 2.

1967 *Ichthyosarcolites poljaki* Polšak; Polšak, pp. 77, 185, pl. 4, fig. 6; pl. 5, fig. 1.

1971 *Ichthyosarcolites bicarinatus* (Gemm.); Carbone et al., p. 146, fig. 14.

1971 *Ichthyosarcolites poljaki* (Gemm.); Carbone et al., p. 147, fig. 15.

1971 *Ichthyosarcolites tricarinatus* Parona; Carbone et al., p. 147, fig. 17.

1982 *Ichthyosarcolites bicarinatus* (Gemmellaro); Sirna, p. 84, fig. 7, pl. 1, fig. f.

1988 *Ichthyosarcolites bicarinatus* Gemmellaro; Accordi et al., p. 139, fig. 5, pl. 1, fig. 7.

1988 *Ichthyosarcolites bicarinatus* Gemmellaro; Accordi et al., p. 165, pl. 2, fig. 7.

1993 *Ichthyosarcolites bicarinatus* (Gemmellaro); Cherchi et al., p. 93, fig. 2, pl. 4, fig. 5.

1998 *Ichthyosarcolites bicarinatus* Gemmellaro; Özer, p. 240, fig. 6-5.

1998 *Ichthyosarcolites tricarinatus* Polšak; Özer, p. 240, fig. 6-6.

1998 *Ichthyosarcolites poljaki* Polšak; Özer, p. 240, fig. 6-4.

?1999 *Ichthyosarcolites poljaki* Polšak, 1967; Pleničar and Jurkovšek, p. 75, pl. 7, fig. 2b.

*non*1999 *Ichthyosarcolites bicarinatus* (Gemmellaro); Pleničar and Jurkovšek, p. 75, pl. 8, fig. 2a–b; pl. 11, fig. 2.

*non*1999 *Ichthyosarcolites tricarinatus* (Gemmellaro); Pleničar and Jurkovšek, p. 76, pl. 5, figs 1b, 3; pl. 8, fig. 3; pl. 9, figs 1-6; pl. 10, figs 1a–b, 2; pl. 11, figs 1a–b.

2001 *Ichthyosarcolites tricarinatus* Parona; Özer et al., p. 860, figs. 10, 11-4.

2002 *Mexicaprina alata* Filkorn, pp. 681–686, figs 4–7.

2008 *Ichthyosarcolites alatus* (Filkorn 2002); Aguilar-Pérez, pp. 113–116, fig. 64/1–4.

2009 *Ichthyosarcolites bicarinatus* (Gemmellaro); Sarı and Özer, p. 367, fig. 9a.

2010 *Ichthyosarcolites bicarinatus* (Gemmellaro, 1865); Chikhi-Aouimeur, p. 96, fig. 87/2–4.

2010 *Ichthyosarcolites tricarinatus* (Gemmellaro, 1865); Chikhi-Aouimeur, p. 97, fig. 88/2–3.

2013b *Ichthyosarcolites alatus* (Filkorn); Mitchell, pp. 85–87, fig. 1/f–g.

2015 *Ichthyosarcolites tricarinatus* Parona; Troya García, pp. 254–260, 269–271, figs 142–143, 148, 150

Type material. In view of the fact that Gemmellaro failed to designate a type specimen, we here designate specimen MGUP-021.2-110 (from the original paper) lectotype of *I. bicarinatus* and MGUP-021.2-111 paralectotype. Both are housed in the Museo Geologico G.G. Gemmellaro della R. Università degli Studi di Palermo and are from the Cenomanian of Piemonte (Italy).

*Diagnosis.*Species of *Ichthyosarcolites* with two to seven flanges, rarely more. The flange number probably increases during ontogeny. Flanges highly plastic in their position and shape, generally distributed all around the shell, varying in shape from small bulges to very thin and narrow blades that can exceed shell diameter in size. Orientation of flanges variable, generally perpendicular to shell margin. General cavity ovoid, quadrangular or polygonal. Aragonitic shell layer filled with capillary canals and an external row of pallisading or pyriform canals.

Description. Left and right valves of similar diameters (6/5 to 25/45 mm, flange not included). Relative length between valves unknown. Coiling pattern unknown. Always a minimum of two flanges and a maximum of up to seven. Shell cross section varying in shape from grossly rounded to polygonal (triangular or quadrate) according to the number of flanges. When two flanges occur they usually appear at two contiguous vertices of a square (Fig. 4B). Shape section appearing grossly triangular in case of three flanges (Fig. 4C), more quadrate with four flanges (Fig. 4D–E). When flange number increases, shell sides change from convex to flat or even concave (Fig. 3E); distribution of flanges globally equidistant when four or more flanges are present (Fig. 3E). Flange development highly variable among individuals and among flanges of single individuals. Flanges regularly extend to a size larger than the diameter of the shell. Flanges usually narrow, parallel sided and reaching a large size, occasionally short, triangular with rounded extremity. End of a flange always rounded, keel like, occasionally with enlarged margin. Number of flanges increases during shell growth. Flanges generally oriented perpendicularly to shell at their base, but can make an angle of 70–120° with shell surface. Outer calcitic layer unknown. Inner aragonitic shell layer thickness varying between 6 and 25 per cent of diameter of the body cavity. Aragonitic shell layer densely canaliculated with tiny, round to honeycomb capillary canals (diameter of approximately 1 mm), except in myophores, posterior and anterior teeth. External side of aragonitic shell layer bordered by a single row of radial canals of same diameter as capillary canals, but subrectangular to pyriform in cross section. Single row of enlarged rounded canals in the middle of large flanges. Ovoid PAC on the posteroventral side on the right valve, slightly larger than sockets and filled with tabulae. Tabulae present on both valves in the general cavity, the pallial canals, the sockets and the PAC.

Left valve myocardinal apparatus. Anterior and posterior conical teeth of similar shape and size (Fig. 3E). Wall-like myophore ventrally adjoined to each tooth. Thin vertical myophores attached to the teeth, making a U-shape myophoral apparatus protruding in the general cavity of the right valve. Development of vertical myophores generating a space between the stem of the protruding myophores and the inner shell margin occupied by thin curved tabulae. This myophoral "space" near the anterior myophore stem can develop itself in a diverticulum dorsally to the anterior tooth. Myophoral cavity of the posterior tooth always smaller. Anterior myophore extending itself to make a connection with the ventral edge of the shell. Posterior myophore twice shorter, connected to the posterior shell wall of the general cavity by an open angle.

Right valve myocardinal apparatus. Central tooth shape unknown, probably very reduced and filled with pallial canals. Presence of two ovoid anterior and posterior tooth sockets directly connected to the general cavity, elongated in an anteroposterior axis. Myophores undifferentiated from the inner shell, no known muscle scars (Fig. 4E).

Remarks. Several species names were introduced on the basis of the number of flanges superior to or equal to two and a particular shape of the internal cavity, two elements that we have shown to be correlated according to clustering and discriminant analysis.

Ichthyosarcolites bicarinatus was the first species with multiple flanges to be formally described and thus has taxonomic priority. Several fossils from Hrušica

(Slovenia) assigned in the literature to *I. bicarinatus* (Pleničar and Jurkovšek, 1999) exhibit a ligament groove connected to a very thin cavity that ends near to the posterior tooth socket. Specimens bearing a ligament groove are excluded here from *Ichthyosarcolites*.

Ichthyosarcolites tricarinatus Parona, 1921 was based on the combination of three flanges and a quadrangular general cavity. Some specimens described from Hrušica (Slovenia) by Pleničar and Jurkovšek (1999) must be excluded from *Ichthyosarcolites* because of the presence of a ligament groove.

Ichthyosarcolites poljaki Polšak, 1964 from the Cenomanian of southern Istria (Croatia) was not described, nor illustrated in Polšak (1964) and must be considered a *nomen nudum*. Pleničar (1965) considered specimens in the Polšak Collection to be conspecific with material that he described as a new species, *I. rogi*.

Ichthyosarcolites rogi Pleničar, 1965 from the upper Cenomanian at Kočevski Rog (Slovenia) was described as a variety of *I. triangularis*, with three “narrow and well-marked ribs”, but without the typical triangular cross section. That form differs from *I. bicarinatus* solely by addition of a flange; this is here considered to be an expression of intraspecific variation.

Ichthyosarcolites polycarinatus Slišković, 1966 from the upper Cenomanian of the Dinaric Alps was based on a single specimen with seven flanges and a rounded general cavity in cross section. Following our analyses, all the available specimens of *I. polycarinatus* match our new definition of *I. bicarinatus*.

Of *Ichthyosarcolites alatus* (Filkorn, 2002) from the lower Cenomanian of Guerrero (Mexico), originally placed in *Mexicaprina* but later transferred to *Ichthyosarcolites* by Aguilar-Pérez (2008), individual shells are characterised by the presence of three, four or five, mostly highly developed flanges. This form cannot be differentiated from *I. polycarinatus*, both being characterised by "several" flanges. In Mexico, *I. alatus* occurs in strata of Albian and Cenomanian age.

Occurrences. Albian to Cenomanian (Aguilar-Pérez, 2008) and widespread in tropical shallow-marine waters along the Tethyan margins and central Atlantic; *I. bicarinatus* has been recorded from Mexico (Tamaulipas, Guerrero, San Luis Potosí, Querétaro y Colima), France (Provence), northern Spain, Croatia, Greece, the Czech Republic, Italia, Tunisia, Algeria, northwest Turkey, Libya and China (Xinjiang) (Fig. 8; Table 1).

***Incertae sedis* species**

The following names (according to the original definitions) cannot be linked to distinct species because descriptions are insufficient to assign them to taxa assignable to *Ichthyosarcolites*. Moreover, a specimen identified as *I. coraloidea* by Caldwell and Evans (1963) is an antillocaprinid and *I. ensis* is not a species of *Ichthyosarcolites* because it bears features of Caprinuloideidae and, in fact, lacks characters required for a definitive taxonomic assignment.

1825 *Ichthyosarcolites obliqua* Deshayes, p. 501.

1937 *Ichthyosarcolites obliquus* Deshayes 1825; MacGillavry, p. 52.

Ichthyosarcolites obliquus Deshayes, 1825 from the Cenomanian of Charentes (France): Deshayes was the first to understand that filaments accreted to the moulds of *Ichthyosarcolites* were an integral part of the shell and thus had to be understood as pallial canals. He also found that another species must be separated from *I. triangularis* on the basis of the morphology of its which way is more oblique. He erected the species *I. obliqua* but, unfortunately, failed to present an illustration. This species is a synonym of *I. triangularis* that already shows oblique tabulae (Fig. 1C) with highly variable shapes in local assemblages such as the ones from Île d'Oléron (Fig. 5A–D).

1850 *Caprinella doublieri*, d'Orb., 1847; d'Orbigny, p. 191, pl. 541.

1967 *Ichthyosarcolithes doublieri* (d'Orb); Philip, p. 498.

1973 *Caprinula doublieri* d'Orbigny; Berthou, p. 97, pls 57–58.

2007 *Caprinula doublieri* d'Orbigny; Macé-Bordy, p. 173.

Ichthyosarcolites doublieri d'Orbigny, 1847 from the upper Cenomanian of Martigues (Bouches-du-Rhône, France) was first described as a species of *Ichthyosarcolites* without any tabulae. There are records from Charentes (Fig. 3F), Provence (Philip, 1967) and Portugal (Berthou, 1973), invariably occurring as internal moulds. The number of flanges is unknown in *I. doublieri*. The tabulae are fragile and very thin structures (Fig. 3D). On the internal mould in Figure 5B, at the bottom of the mould the presence of tabulae can be seen; these progressively disappear in the same individual. The thickness and development of tabulae varies among specimens (Figs 4D, 5A), some specimens showing tabulae at variable preservational states, some disappearing partially or completely, while they are entirely lost in other shells. It is likely that *I. doublieri* corresponds to a preservational state of another congener in which tabulae dissolved. Due to the unilobate form of the internal moulds, *I. doublieri* cannot be assigned to the genus *Caprinula* (bilobate because of the strong development of CTS in relation to the general cavity), contrary to what Berthou (1973) and Macé-Bordy (2007) noted.

1854 *Ichthiosarcolites loricatis* Tuomey, p. 172.

1854 *Ichthiosarcolites cornutis* Tuomey, p. 172.

1854 *Ichthiosarcolites quadrangularis* Tuomey, p. 172.

These three taxa, from Noxubie County (Mississipi, USA), were never formally describe; their age is unknown. Tuomey based them on the shape of the aperture (and, by extension, on general shell shape), while all other characters are similar to *I. triangularis*. In *I. quadrangularis*, the aperture is “[…] terminating obliquely and rather abruptely”; in *I. loricatis*, it is “[…] somewhat oval, irregular, obtusely rounded at the base, giving the cast an imbricated appearance”. Finally, *I. cornutis* was “distinguished from the preceding [*I. loricatis*] by the more distant and regular septa, and in the greater regularity of the curvature of the shell” (Tuomey, 1854). The coiling and tabulae can be highly variable in a single population of *Ichthyosarcolites*, meaning that Tuomey’s forms do not present sufficiently different features to support the definition of new taxa. Key features are unknown, but they might be assignable to the family Antillocaprinidae (Stephenson, 1938).

1855 *Caprinella coraloidea* Hall and Meek, p. 380, pl. 2, fig. 3a–f.

Ichthyosarcolites coraloidea from the upper Campanian of Sage Creek (South Dakota, USA) was differentiated from *I. triangularis* by “being curved not exactly in the same plane, in increasing much more rapidly in size from the apex, and in having the fibrous portion of the shell so thick upon the inner side of the volution as to bring the sides in contact if continued a single turn” (Hall and Meek, 1855). Shell coiling is variable enough not to be considered as a valuable criterion for species definition. Desmarest originally described *I. triangularis* on the basis of straight internal molds, but 30 years later, d’Orbigny (1850) illustrated a highly coiled right valve as *I. triangularis* (see Fig. 1C). The large shells from Charentes show that coiling pattern can change during ontogeny (Fig. 5F). In southeastern France, other specimens can be seen to be completely coiled up to large sizes (Fig. 5E). In *I. coraloidea*, “The septa are also much more irregular than in the European species, those which are distinct upon the back of the shell often converging so that two unite in a single one on the inner side of the volution” (Hall and Meek, 1855). The diversity of forms, expressed only in populations of Charentes, shows the diversity of tabulae obliqueness, some of them occasionally converging (Fig. 5C). The number of flanges is unknown in *I. coraloidea* and pending description of new, complementary material, the species name should be considered *incertae sedis*. The unique specimen described as *I. coraloidea* by Caldwell and Evans (1963) is related to antillocaprinids and not to *Ichthyosarcolites*. This specimen has its sockets and myophoral cavities filled with pallial canals, a characteristic feature of Titanosarcolitinae and Parasarcolitinae.

1887 *Ichthyosarcolites ensis* Počta, p. 207.

Ichthyosarcolites ensis from the upper Cenomanian of Radovesnice (central Bohemia, the Czech Republic) possesses capillary canals and a triangular flange similar to *Ichthyosarcolites*. However, *I. ensis* was erected for a shell described by Počta with three internal cavities of similar size. The development of the three, large and equal-sized internal cavities (two sockets and the general cavity) is likely a feature of Caprinuloideidae. Initial illustrations and descriptions of *I. ensis* remain insufficient for a taxonomic reappraisal without access to the original material.

1905 *Ichthyosarcolithes* sp. nov. indét. Paquier, pp. 94–95, pl. 9, figs. 7–9.

This form, from the Cenomanian of Lom (Montana, Bulgaria), was based on a quadrangular section of the general cavity, which in itself would differentiate it from *I. triangularis*. However, the outline of the general cavity is insufficient to erect a new species. Moreover, the fossils are fragmentary internal moulds and shell morphology is too incomplete to determine whether they belong to a new species or not.

1994 *Ichthyosarcolites quadratus* Pleničar; Pleničar and Dozet, p. 188.

This form was never formally defined; it is to be considered a *nomen nudum* following ICZN article 13.

2004 *Ichthyosarcolites*? sp.; Masse et al., p. 83, fig. 11.

This form from the lower Aptian of Boztepe (Amasra, Turkey) was described with millimetric aragonitic flanges filled with a unique row of square shaped pallial canals; it is too incomplete to help determine whether or not it belongs to *Ichthyosarcolites*.

Superfamily Caprinoidea d'Orbigny, 1850

Genus *Oryxia* nov.

Type species. *Oryxia sulcata* gen. et sp. nov.

Derivation of name. From the mammal genus *Oryx*, in allusion to the similarity of its long, lightly curved horns to the right valve of the new taxon.

Diagnosis. Rudist bivalve with right valve narrow, gently coiled anteriorly, with a large posteroventral flange and a very slight anteroventral flange with triangular shape in cross section. A ligament groove in dorsal position ends dorsally with a tiny shelly bulb parallel to the anterior tooth socket. A bulge is accreted posteriorly to the ligament groove. Aragonitic shell layer filled with round capillary canals. Presence of an anterior accessory cavity (AAC). Small ovoid anterior and posterior sockets of equal size (5 to 10 mm). Central tooth very small (1 to 2 mm), filled with canals.

Remarks. Oryxia gen. nov. differs from *Ichthyosarcolites* in the possession of a small internal ligament cavity, near the posterior tooth socket and communicating with the outside, where it leads to a longitudinal ligament groove. It does not imply, however, the existence of a ligament (see Steuber, 1999, p. 159), as rudists can lose their ligament while still possessing ligament structures. It differs also by the presence of a small anterior accessory cavity in *Oryxia* gen. nov. (right valve), while it is posterior in *Ichthyosarcolites*. The new genus is a recumbent form, similar to *Ichthyosarcolites*. However, whereas *Ichthyosarcolites* shells lay on their anterior side, *Oryxia* gen. nov.

invariably lay on their ventral side, due to a flat part extended by their posteroventral flange.

Oryxia sulcata sp. nov.

Fig. 9

?1967 *Ichthyosarcolites bicarinatus* Gemmellaro; Polšak, p. 186, fig. 21, pl. 5, fig. 2A.

?1999 *Ichthyosarcolites poljaki* Polšak, 1967; Pleničar and Jurkovšek, p. 75, pl. 7, fig. 2b.

1999 *Ichthyosarcolites bicarinatus* (Gemmellaro); Pleničar and Jurkovšek, p. 75, pl. 8, fig. 2a–b; pl. 11, fig. 2.

1999 *Ichthyosarcolites tricarinatus* (Gemmellaro); Pleničar and Jurkovšek, p. 76, pl. 5, figs 1b, 3; pl. 8, fig. 3; pl. 9, figs 1-6; pl. 10, figs 1a–b, 2; pl. 11, fig. 1a–b.

Derivation of name. From Latin *sulcus*, on account of the presence of a longitudinal ligament groove.

Type material. The holotype consists of three thin slices of a right valve, BJ.1901-HR2; it is from the Cenomanian of Hrušica, Slovenia. Paratypes are BJ.1914-HR2, three thin slices of a right valve (Fig. 9D) and BJ.1942-HR2, two thin slices of a right valve, from the same locality and age.

Diagnosis. Same as genus (monotypy).

Description. Left valve unknown. Right valve tubular, narrow and slightly anteriorly coiled (12 mm of anterior coiling per 100 mm length). Planispiral development. Longest known fragment measuring 220 mm in length (holotype). Diameter of shell varying between 45 and 75 mm. Diameter of general cavity varying between 28 and 35 mm. Shell shape subrectangular because of flanges and shell thickenings. Slight bead of 13 mm width located dorsally to the posterior tooth socket and posterior to the longitudinal ligament groove. Bead lopsided anteriorly, slightly covering the ligament groove. Subtriangular anteroventral thickening, of 13 mm width at its base. Presence of a posteroventral flange. Flange margin broken, but with a minimum of 30 mm in length and a thickness of 0.5 to 5 mm. Ventral plane surface created by simultaneous presence of the posteroventral flange and anteroventral thickening. Very thin ligament groove (8/0.2 mm) connected to the dorsal part of the shell, slightly anteriorly curved in cross section. Groove ending with a little anteroposteriorly elongated cavity (2/0.5 mm) located two millimetres dorsally to the posterior tooth. Aragonitic shell; aragonitic inner shell layer thickness comprised between 10 and 30 mm. Aragonitic shell layer completely filled with round to ovoid capillary canals with a mean diameter of 1 mm. Calcitic outer layer missing, probably thin and smooth. No visible tabulae.

Right valve myocardinal apparatus. Central tooth filled with capillary canals (length/width: 2/1 mm to 3/2 mm). Presence of two flat anterior (4/1 mm to 100/30 mm) and posterior (4/1 mm to 8/2 mm) tooth sockets on the dorsal side of the shell and separated from general cavity by a thin blade devoid of pallial canals. Vertical myophores undifferentiated from inner shell. Ovoid AAC present anteroventrally (under anteroventral thickening), larger than sockets (12/5 mm).

Remarks. AAC possibly homologous to the anterior myophoral cavity in titanosarcolitids. Homology with the PAC in ichthyosarcolitids (Fig. 4A) is impossible in view of its location, presumed by the presence of a posterior ligament groove.

Occurrences. Exclusively Cenomanian, being solely known from the bioherm of Hrušica (Slovenia), on the northern part of the Dinaric carbonate platform. Polšak's (1967) specimens from Istria (Croatia), identified as *I. bicarinatus*, may be conspecific with the new taxon.

5. Conclusions

The Albian–Cenomanian genus *Ichthyosarcolites*, first described by Desmarest in 1812, is known from all around the Tethys, from Mexico to China. Following our study and morpho-anatomical analyses, we accept only four species of *Ichthyosarcolites* out of the 19 published nominal species, with *I. rotundus* lacking flanges, *I. triangularis* possessing a single dorsal flange, *I. monocarinatus* a single ventral flange and *I. bicarinatus* expressing marked polymorphism with the presence of two to seven flanges. Homology of the flanges is redefined from their position on the shell. The number of flanges can no longer serve to differentiate species beyond two flanges. The internal cavity shape is correlated to the external flanges and corroborates the existence of two species bearing a single flange, i.e., *I. triangularis* which possesses a dorsal flange and *I. monocarinatus* with a ventral flange. Specimens previously attributed to

Ichthyosarcolites from Hrušica, Slovenia exhibit a longitudinal ligament groove and a small and flat cavity dorsal to the anterior tooth outwardly opening by the ligament groove. The presence and morphology of a ligament is critical in the evolution of the rudists and supports the erection of a new genus and species, *Oryxia sulcata*, which is assigned to the superfamily Caprinoidea, and may be very close to families losing their ligament groove, such as Trechmannellidae, Antillocaprinidae and Ichthyosarcolitidae. *Oryxia* gen. nov. is important in the phylogeny of rudists and the evolution of the ligament among rudists is certainly a key in the further phylogenetic explorations of Caprinoidea.

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Table 1. Comparison of known morphological features and geographical distribution of all 19 nominal species of *Ichthyosarcolites*, plus the new form described herein, *Oryxia sulcata* nov. gen. et sp. "Unknown" signifies that data were unavailable from the literature or from specimens considered for the present study.

Figures

Fig. 1. A, Earliest illustration of *I. triangularis* as "Cucroïdes" by Guettard (1786), who thought the fossil to be circular ("*pierres circulaires*"). **B**, Original drawings of the internal moulds of *I. triangularis* (Desmarest, 1817). **C**, Specimen of *I. triangularis* (MNHN.F.R08003) from Île d'Oléron, illustrated in d'Orbigny's *Paléontologie Française* (1847); this specimen is here designated neotype of *Ichthyosarcolites triangularis* Desmarest, 1812.

Fig. 2. Illustration of the main morphological attributes of a shell of *Ichthyosarcolites*. **A**, Picture of *Ichthyosarcolites alatus* (Filkorn, 2002) (UNAM.6979). **B**, Interpretative scheme of A with the main morpho-anatomical features and homologues. **C**, Picture of *Ichthyosarcolites rotundus* Polšak, 1967 (LGPZ.778). **D**, Interpretative scheme of C

with the main morpho-anatomical features and homologues. AM: anterior myophore; PM: posterior myophore; ATS: anterior tooth socket; PTS: posterior tooth socket; AT: anterior tooth; PT: posterior tooth; D: general cavity of the right valve; G: general cavity of the left valve; AAC: anterior accessory cavity; PAC: posterior accessory cavity; t: tabulae; d: shell depression, space between aragonitic inner shell and the stem of the myophoral blades.

Fig. 3. Types of species of *Ichthyosarcolites*. All scale bars equal 10 mm. **A**, Holotype of *Ichthyosarcolites rotundus* Polšak, 1967 (LGPZ.778), showing a cylindrical shell; from the Cenomanian of Fontanela Bay (Istria, Croatia). **B**, Holotype of *Ichthyosarcolites monocarinatus* Slišković, 1966 (MB.3470), showing a small flange and round canals; from the Cenomanian of the Dinaric Alps (courtesy of Alceo Tarlao). **C**, Syntype of *Ichthyosarcolites bicarinatus* (Gemmellaro Collection, MGUP.021.2-110), showing two flanges and a twisted body along the umbo-apertural axis; from the Cenomanian of Piemonte (Italy) (courtesy of Tony Costagliola). **D**, Holotype of *Ichthyosarcolites polycarinatus* Slišković, 1966 (MB.3482), showing seven elongated flanges and small capillary canals; from the upper Cenomanian of the Dinaric Alps (courtesy of Alceo Tarlao). **E**, Holotype of *Ichthyosarcolites alatus* (Filkorn, 2002) (UNAM.6979), showing five flanges and a presumed juvenile attached to its ventral side (left valve); the myocardinal apparatus and its associated cavities are visible; from the lower Cenomanian of Guerrero (Mexico) (courtesy of Javier Aguilar-Pérez). **F**, Lectotype of *Ichthyosarcolites doublieri* d'Orbigny, 1847 (MNHN.F.R07971), lacking

tabulae; internal mould showing the highly developed right valve and the short, left valve; from the upper Cenomanian of Martigues (Bouches-du-Rhône, France).

Fig. 4. Shell internal features of *Ichthyosarcolites*. All scale bars equal 10 mm. **A**, *I. rotundus* without any flange (AMU.ICH1) from La Bédoule (Provence, France), with posterior accessory cavity (PAC; arrowed). **B**, Picture of *I. bicarinatus* from Chiki-Aouimeur (2010; Aqaba, Jordan), with flanges and myophores (arrowed). **C**, Thin-sliced right valve of *I. triangularis* with three flanges, two sockets and posterior myophoral cavity (AMU.HBES 85-a). **D**, Specimen of *I. bicarinatus* from Cañón de la Servilleta (Tamaulipas, Mexico), showing four flanges and thin tabulae (courtesy of Javier Aguilar-Pérez). **E**, Mexican right valve with four flanges of *I. bicarinatus* (from Filkorn, 2002); the myocardinal apparatus of the left valve is visible in connection (UNAM.6970) (courtesy of Javier Aguilar-Pérez). **F**, Thin-sliced specimen of *I. coraloidea* (GMUS.Mp1), showing general cavity filled of canals, a thick shell and three cavities invaded by capillary canals (courtesy of Brian Pratt).

Fig. 5. Photographs of shells of *Ichthyosarcolites* illustrating tabulae and coiling patterns. All scale bars equal 10 mm. **A**, Longitudinal thin slice of *I. triangularis* from Île d'Oléron, showing thick tabulae (arrow) in the general cavity and sockets. **B**, Internal moulds of *I. triangularis* from Île d'Oléron (Charentes, France), showing partial or complete dissolution of thin tabulae (arrow) in the general cavity and sockets. **C**, Specimen of *I. triangularis* from Île d'Oléron with intersecting tabulae. **D**, Crushed internal mould of *I. triangularis* from Île Madame, showing tabulae and one socket (d'Orbigny Collection, MNHN.6517–B). **E**, Near-complete coiled right valve (internal

mould) from Provence (France). **F**, Specimen of *I. triangularis* from Île d'Oléron with uncoiled internal mould.

Fig. 6. A, Method for measurement of angular positions of flanges on rudist shells. A circle approximates the general cavity; white circles correspond to the projection of the flange stem on the circle. Angles are measured clockwise with 0° corresponds to the presumed position of the central tooth or central tooth socket. Scale bar equals 10 mm. Specimen UNAM.6978 (courtesy of Javier Aguilar-Pérez). **B**, Flange angle measurement plot in degrees. **C**, Hierarchical classification of flange positions. The two main clusters represent the dichotomy between *I. monocarinatus* ventral flanges and *I. triangularis* dorsal flanges. Each point corresponds to the angular position of a flange, and the colours correspond to the number of flanges of an individual.

Fig. 7. Discriminant analysis plot of 23 general cavities of shell landmarks of *Ichthyosarcolites*. Four clusters are based on the number of flanges: *I. rotundus* (no flange), *I. monocarinatus* (one ventral flange), *I. triangularis* (one dorsal flange) and *I. bicarinatus*. Analysed data are presented as Supplemental Online Material.

Fig. 8. Palaeogeographical map showing the localities of Cenomanian-aged species of *Ichthyosarcolites*. Yellow dots: *I. rotundus*; green dots: *I. triangularis*; brown dots: *I. monocarinatus*; red dots: *I. bicarinatus*; black dots: *Ichthyosarcolites* occurrences for which species-level identification could not be verified; blue star: *Oryxia sulcata* nov. gen. et sp. The palaeogeographical map was generated using the ODSN Plate Tectonic Reconstruction Service (DeConto et al., 1999; http://www.odsn.de/odsn/services/paleomap/paleomap.html).

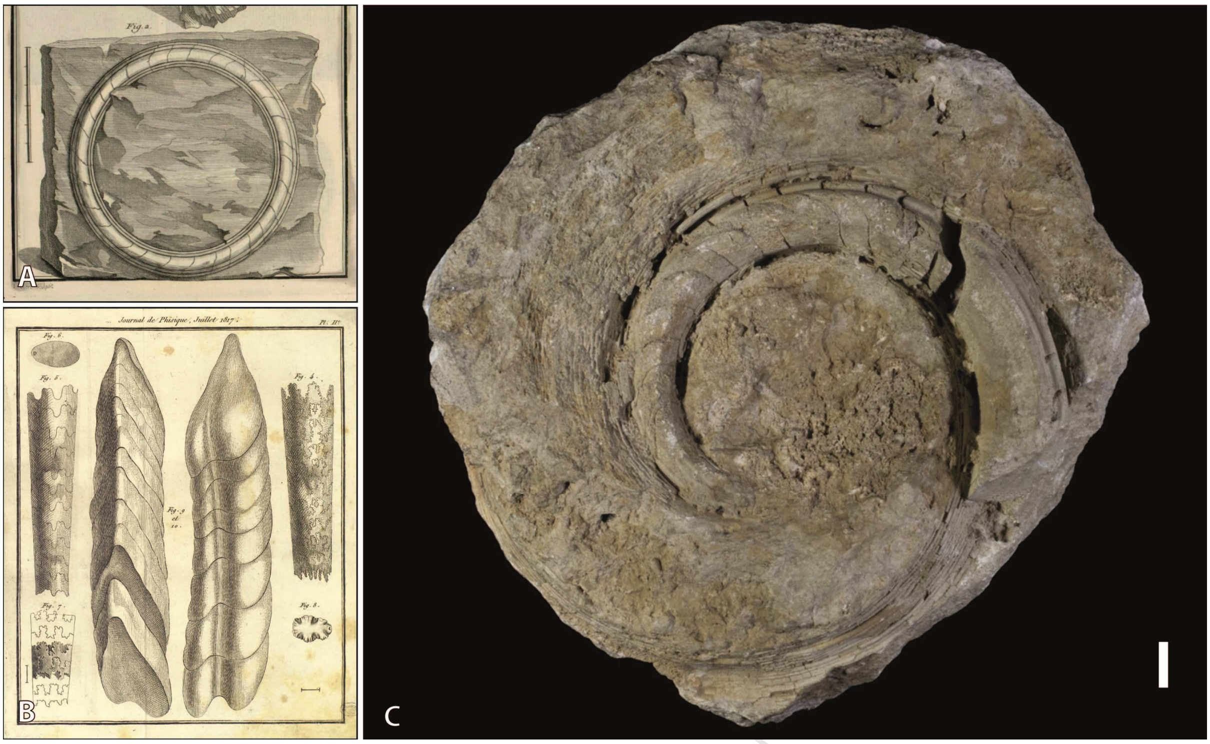
Fig. 9. Holotype of *Oryxia sulcata* nov. gen. et sp. (right valve; BJ.1901-HR2) sliced in three samples. **A**, Transverse view of a thin slice (right sample in C). **B**, Interpretative scheme of A with the main morpho-anatomical features and homologues. AM: anterior myophore; PM: posterior myophore; ATS: anterior tooth socket; PTS: posterior tooth socket; CT: central tooth; D: general cavity of the right valve; AAC: anterior accessory cavity; LG: ligament groove; LB: ligament bulge. **C**, Dorsal view of three samples of the right valve. **D**, Transverse view of paratype BJ.1914-HR2. All pictures courtesy of Bogdan Jurkovšek.

SOM

SOM 1

Shell references and Landmark co-ordinates of the general cavity of 23 shells of *Ichthyosarcolites* using PhyloNimbus.

Nominal species	Flanges	Flange shape in cross section	General cavity shape	Pallial canals	Tabulae	Shell shape	Ligament	Localisation
Ichthyosarcolites triangularis Desmarest, 1812	1 (ventral)	Short and triangular	Triangular to ovoid	Capillary and palissading	Sub-plane to oblique	Coiled to uncoiled	No	Afghanistan, Bosnia and Herzegovina, Egypt, France, Greece, Libya, Spain, Tunisia, Turkey
Ichthyosarcolites obliqua Deshayes, 1825	Unknown	Unknown	Unknown	Unknown	Very oblique (<45° from commissure)	Unknown	Unknown	France
Ichthyosarcolites doublieri Orbigny, 1847a	Unknown	Unknown	Circular	Unknown	No	Coiled	Unknown	France, Portugal
Ichthyosarcolites quadrangularis Tuomey, 1854	Unknown	Unknown	Quadrangular	Capillary and palissading	"regular, abruptly bent downwards"	Loosely coiled	Unknown	USA
Ichthyosarcolites loricatis Tuomey, 1854	Unknown	Unknown	Ovoid	Capillary and palissading	Unknown	Unknown	Unknown	USA
Ichthyosarcolites cornutis Tuomey, 1854	Unknown	Unknown	Unknown	Capillary and palissading	"abruptly bent downwards, and towards the concave side"	Coiled	Unknown	USA
Ichthyosarcolites coraloidea Hall and Meek, 1855	Unknown	Unknown	Ovoid	Capillary and palissading	Sub-plane to oblique	Unknown	Unknown	USA, Canada
Ichthyosarcolites bicarinatus Gemmellaro, 1865	2	Long and narrow	Circular to sub-quadrangular	Capillary and palissadic or large ovoid	Unknown	Uncoiled	No	Algeria, Bosnia and Herzegovina, Croatia, France, Greece, Italy, Libya, Slovenia, Turkey
Ichthyosarcolites marginatus Počta, 1887	Unknown	Unknown	Unknown	Capillary and palissading	Unknown	Loosely coiled	No	Czech republic
Ichthyosarcolites ensis Počta, 1887	1	Short and triangular	Unknown	Capillary and palissading	Unknown	Unknown	No	Czech republic, Italy
Ichthyosarcolites tricarinatus Parona, 1921	3	Long and narrow to short and triangular	Circular to polygonal	Capillary and palissading	Unknown	Loosely coiled	No	Afghanistan, Lybia, Bosnia and Herzegovina, Croatia, Greece, italy, Slovenia, Spain, Turkey
Ichthyosarcolites poljaki Polšak, 1964	3	Long and narrow to short and triangular	Circular to ovoid	Capillary and palissading	Unknown	Unknown	No	Bosnia and Herzegovina, Croatia, Greece, italy, Slovenia, Turkey
Ichthyosarcolites rogi Pleničar, 1965	3	Long and narrow	Triangular	Capillary and palissading	Unknown	Unknown	No	Slovenia
Ichthyosarcolites monocarinatus Slišković, 1966	1 (dorsal)	Short and triangular	Ovoid	Capillary and palissading	Unknown	Unknown	No	Bosnia and Herzegovina, Croatia, Italy, Slovenia, Spain, Turkey
Ichthyosarcolites polycarinatus Slišković, 1966	7	Long, narrow and elongated	Circular	Capillary and palissading	Unknown	Unknown	No	Bosnia and Herzegovina
Ichthyosarcolites rotundus Polšak, 1967	0	Non applicable	Circular	Capillary and palissading	Unknown	Unknown	No	Croatia
Ichthyosarcolites iokungensis Bobkova, 1968	1 (ventral)	Short and triangular	Ovoid	Unknown	Sub-plane	Unknown	No	Russia
Ichthyosarcolites quadratus Pleničar and Dozet, 1994	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	?
Ichthyosarcolites alatus Filkorn, 2002	3 to 5	Long and narrow to short and triangular	Circular to polygonal, irregular	Capillary and palissading	Unknown	Unknown	No	Mexico
Oryxia sulcata n. sp.	3	Short and triangular in section	Circular to ovoid	Capillary and palissading	Unknown	Unknown	Yes	Slovenia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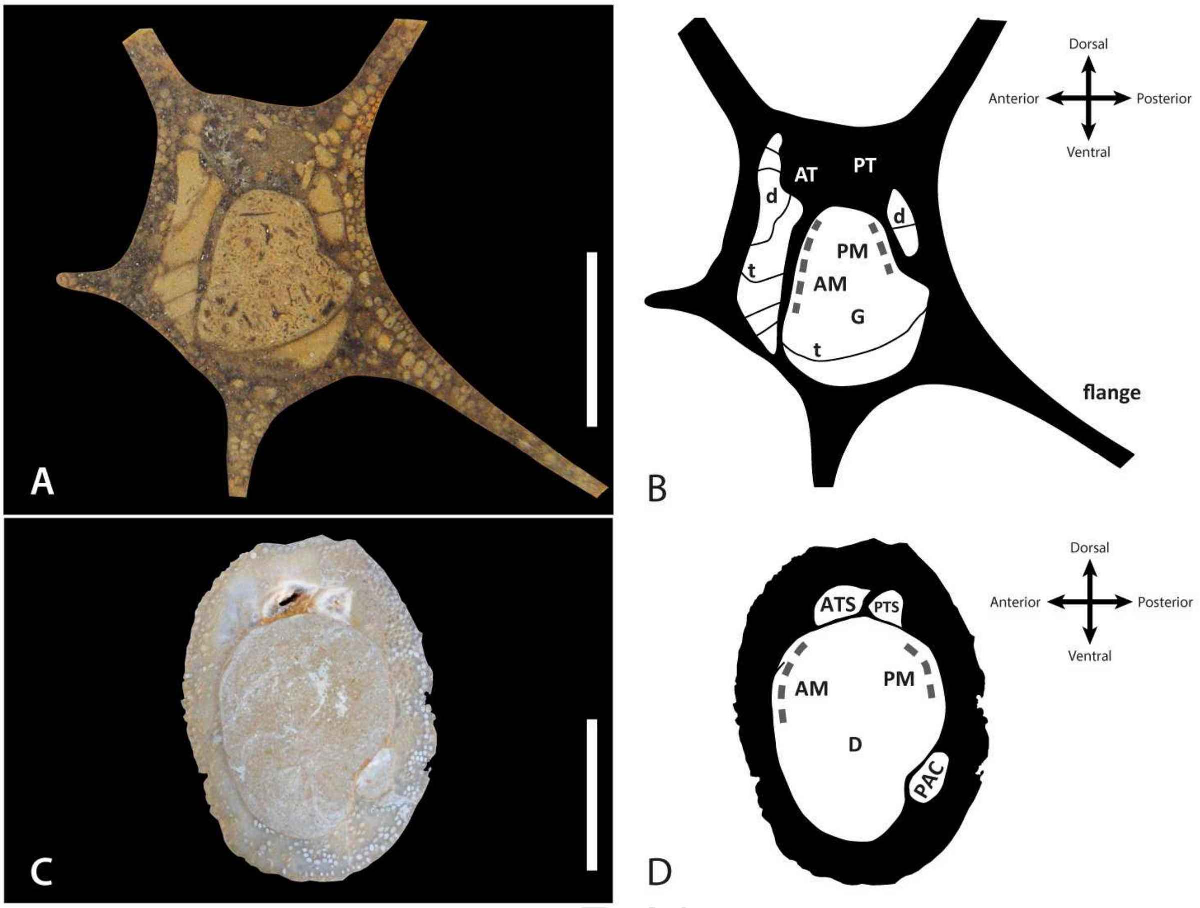
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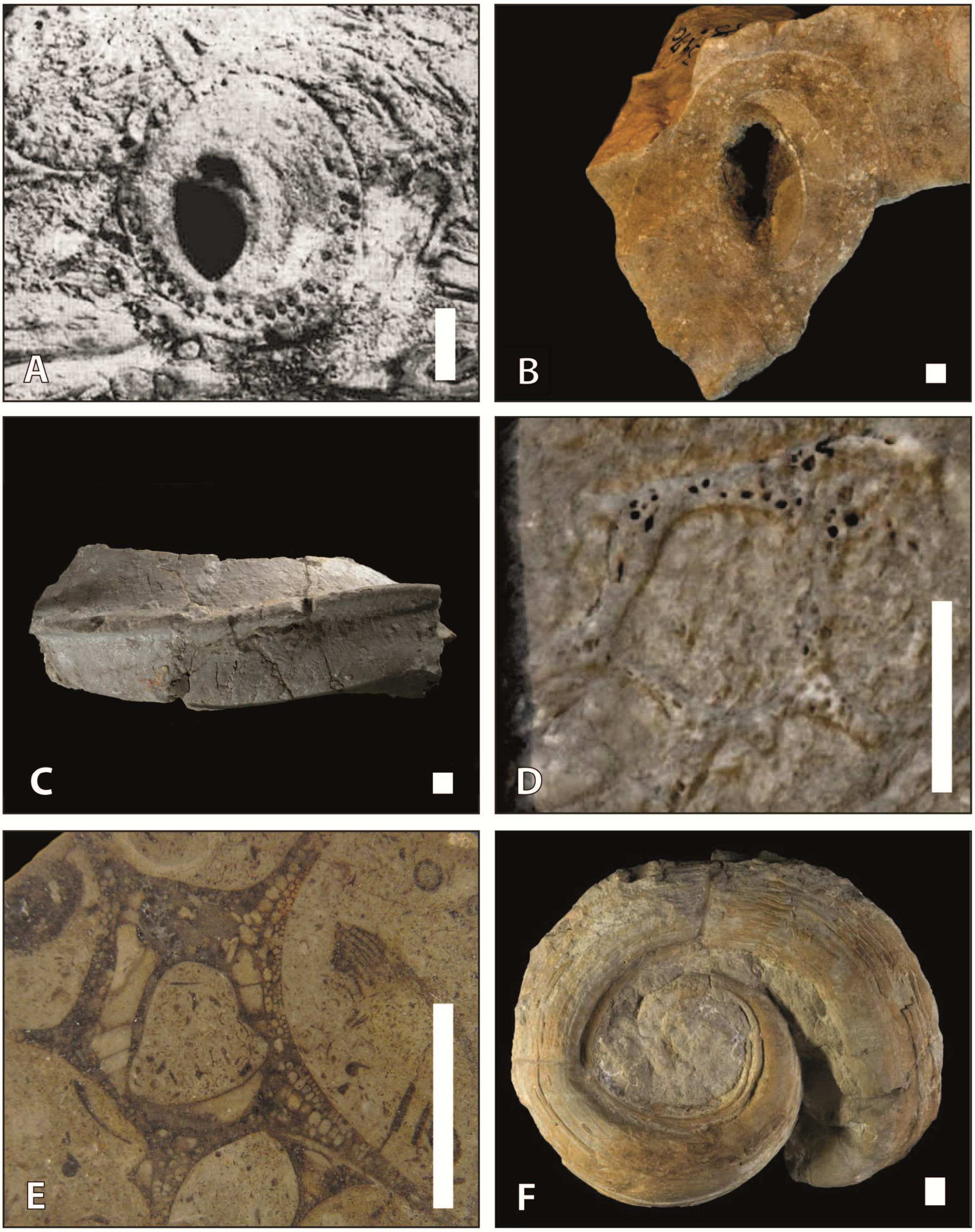
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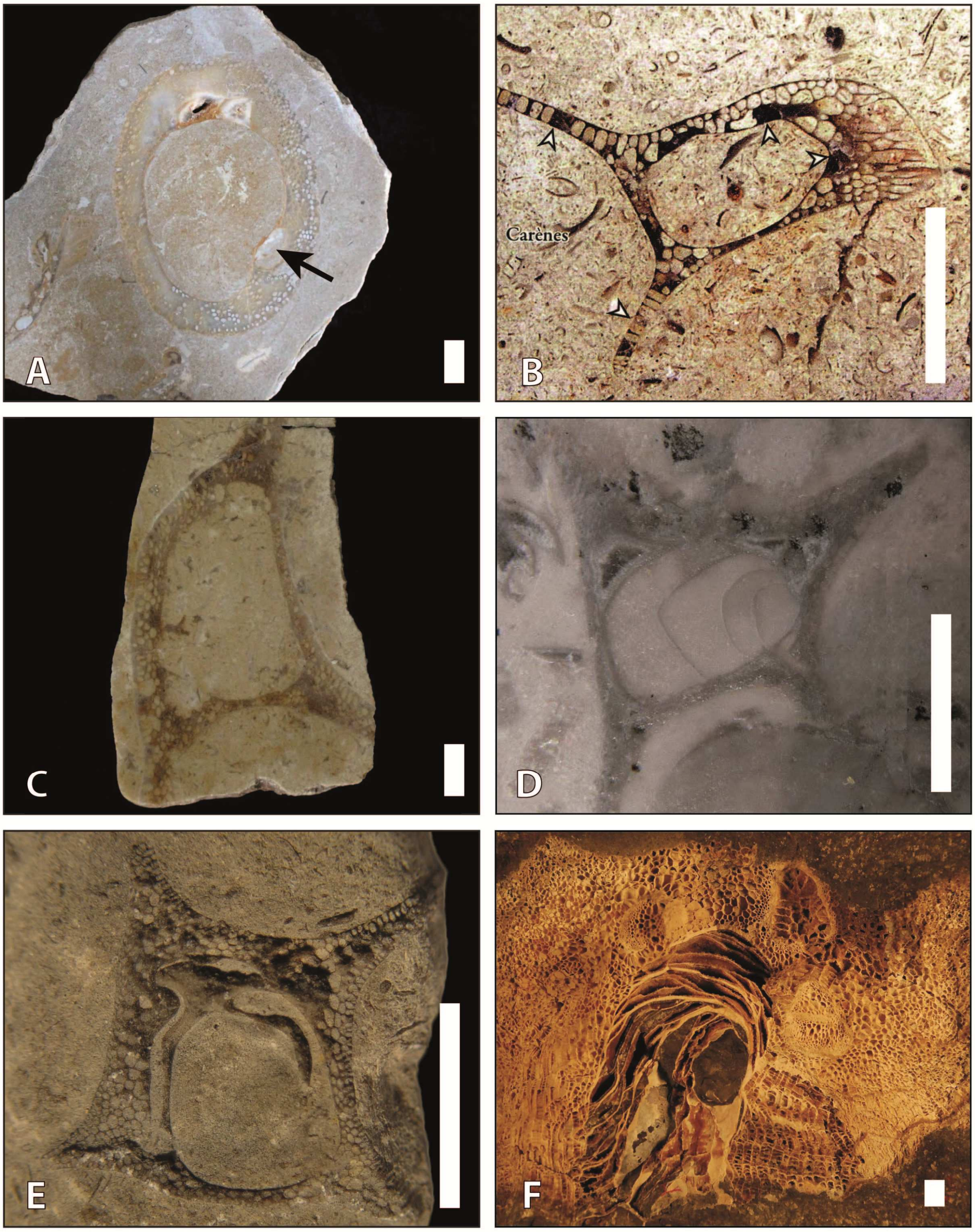
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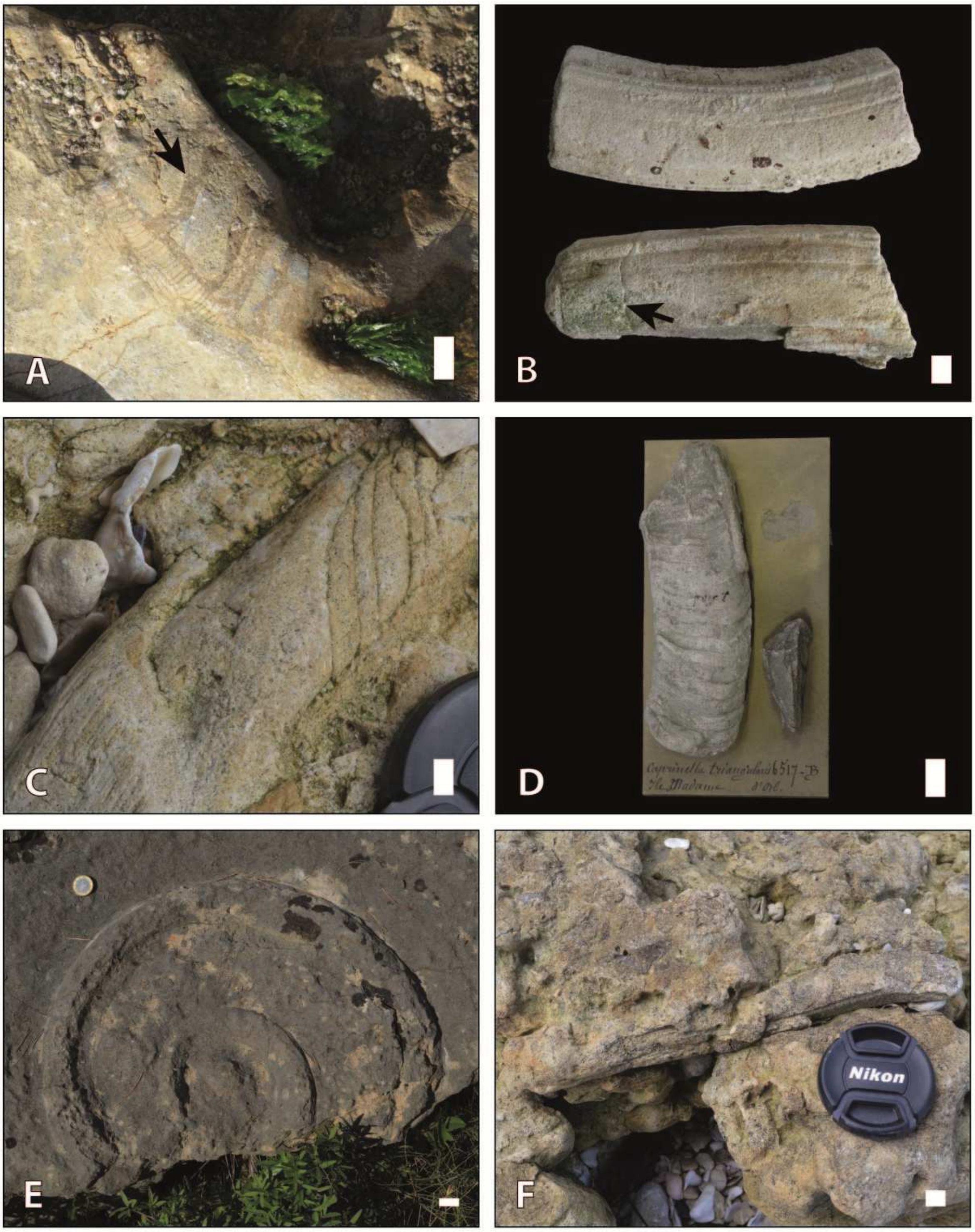
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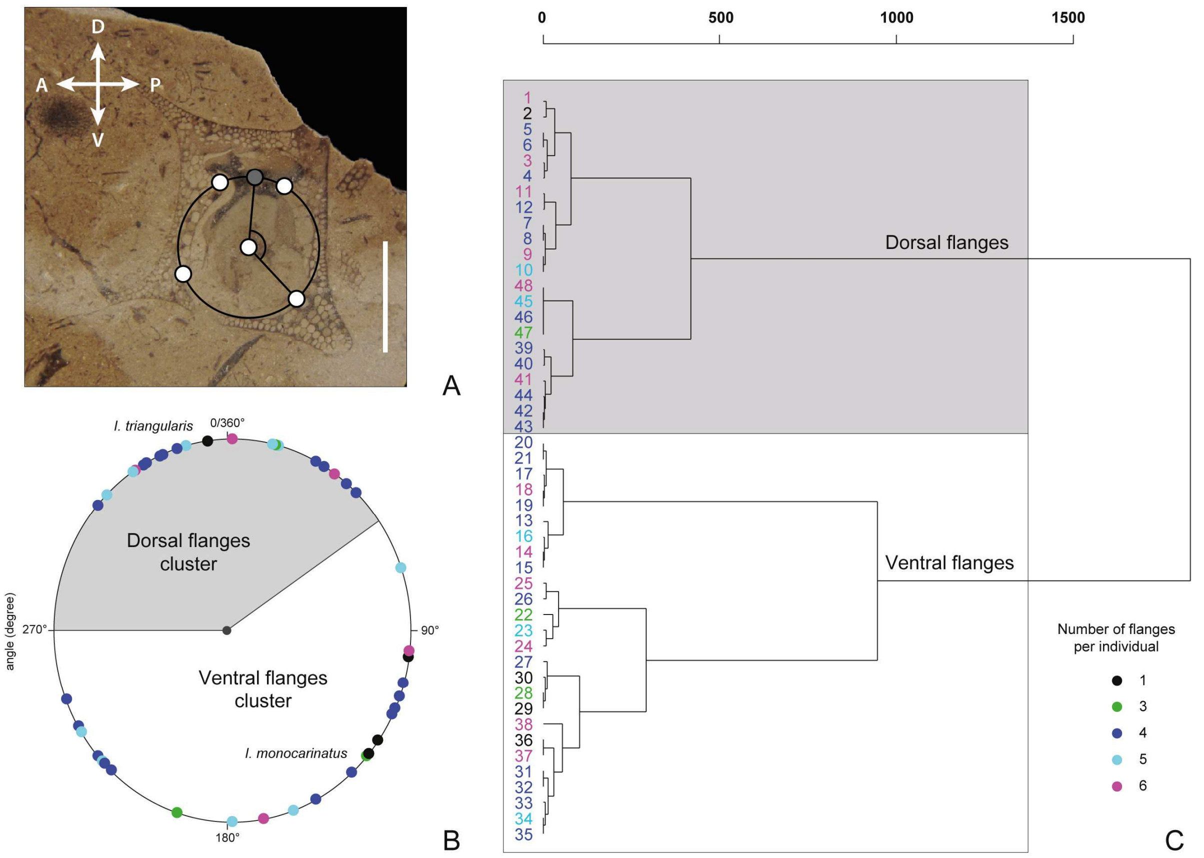
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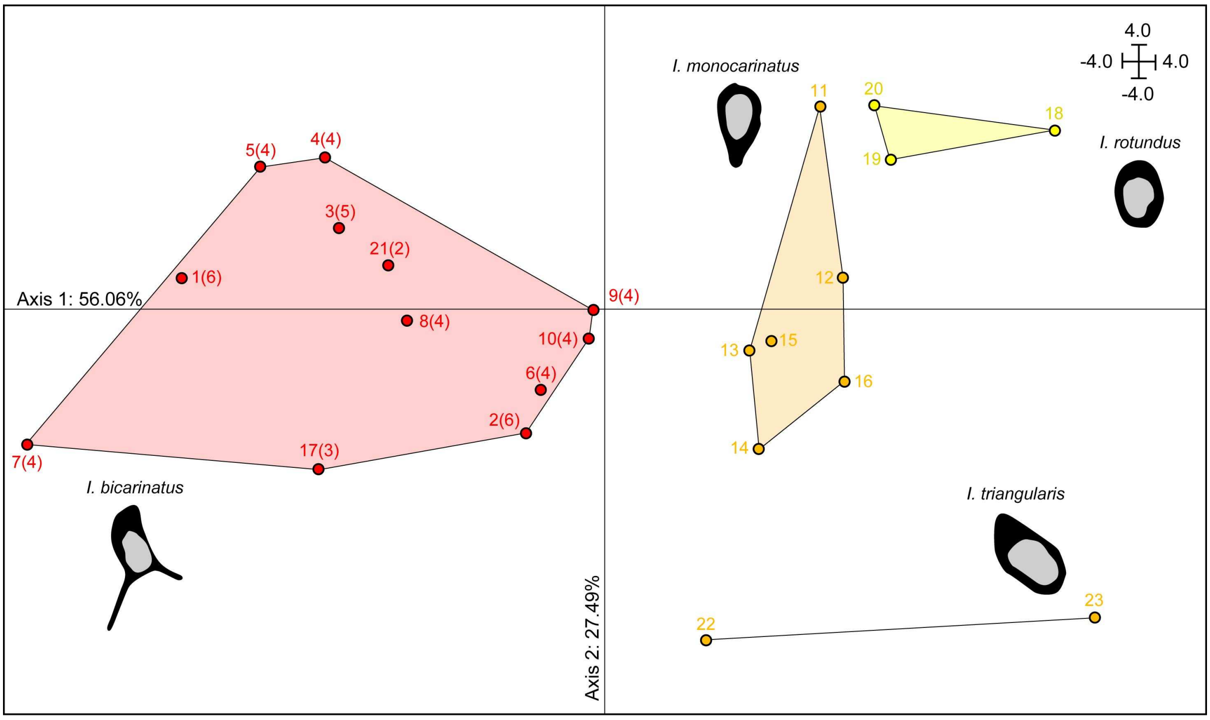
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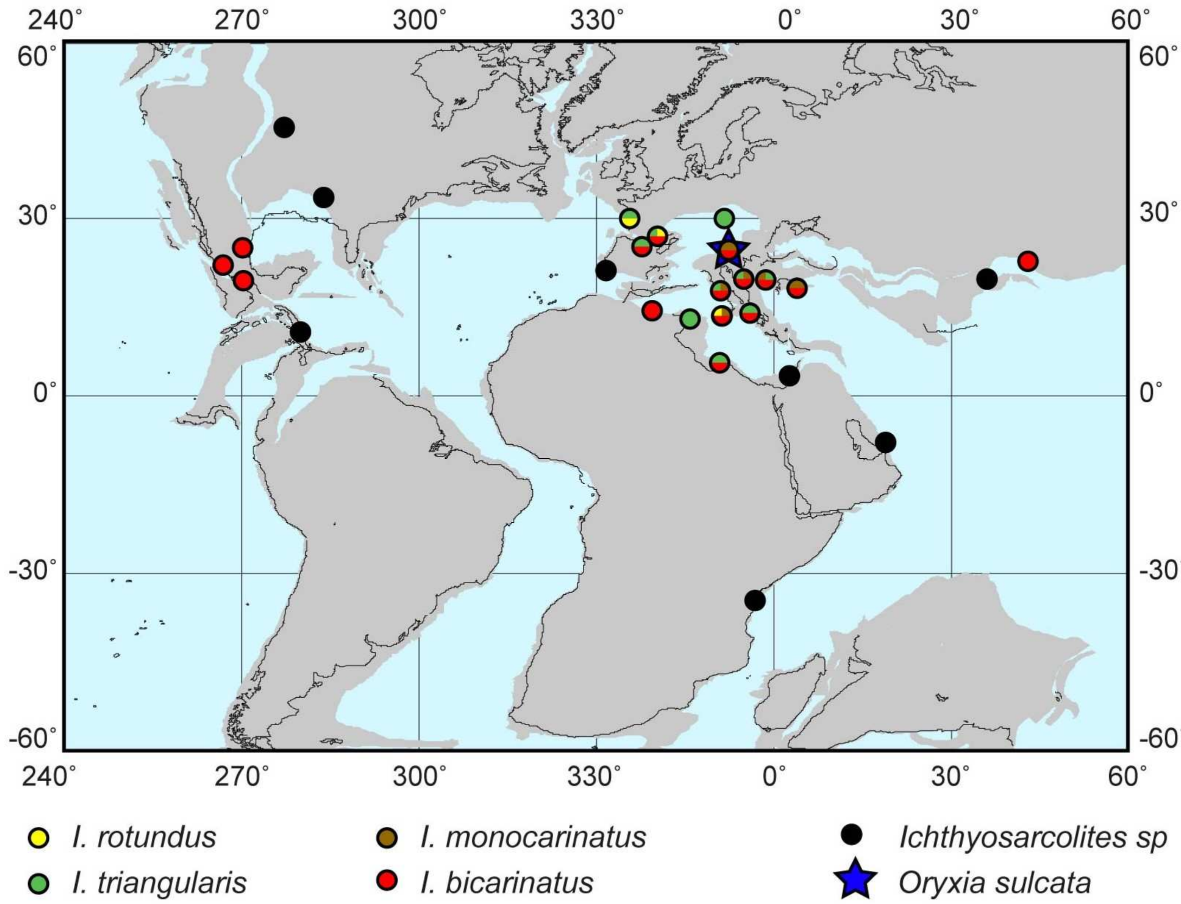

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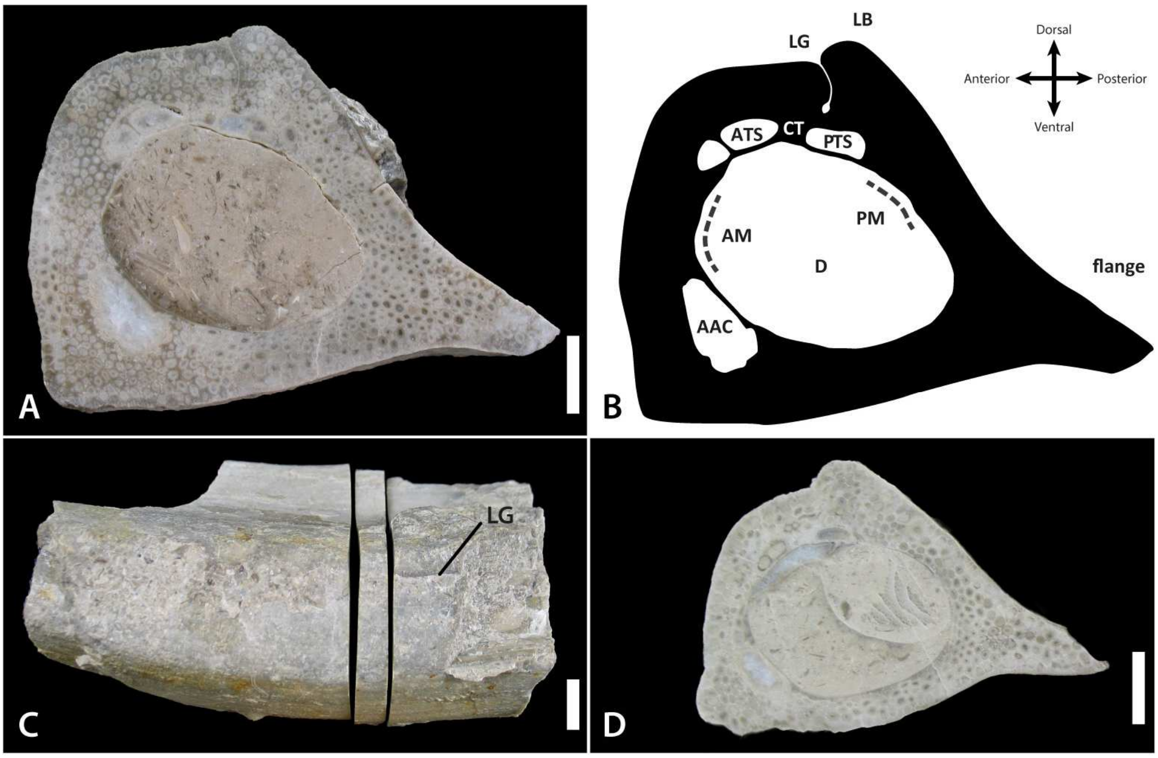
Ichthyosarcolites sp
Oryxia sulcata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A revision of the genus *Ichthyosarcolites* is proposed, based on morphological analyses

Variability in flanges and general cavity shape allow to retain only four species

A new genus and species is described, *Oryxia sulcata*, based on the ligamentary cavity