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**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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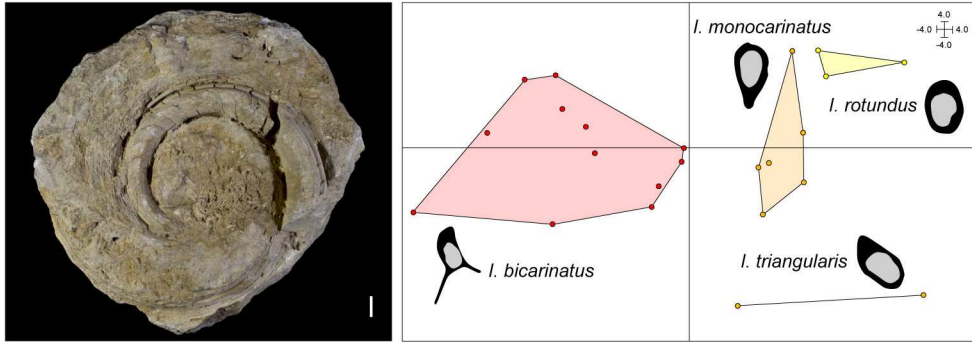
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ACCEPTED MANUSCRIPT

- 1 Taxonomic revision of the genus *Ichthyosarcolites* Demarest, 1812, and description of a
- 2 new canaliculate rudist from the Cenomanian of Slovenia: *Oryxia sulcata* gen. et sp.
- 3 nov. (Bivalvia, Hippuritida).
  
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8 **Taxonomic revision of the genus *Ichthyosarcolites***  
9 **Desmarest, 1812, and description of *Oryxia sulcata* gen.**  
10 **et sp. nov. (Bivalvia, Hippuritida), a new canaliculate**  
11 **rudist from the Cenomanian of Slovenia:**

12 **Abstract**

13 *Ichthyosarcolites* was amongst the first rudist genera to be described. Nineteen species  
14 have been assigned to this genus since its introduction in 1812, all from shallow-marine  
15 tropical carbonates of Albian and Cenomanian age (mid-Cretaceous). Almost all  
16 nominal species suffer from vague original descriptions, and some forms were  
17 inaccurately assigned to the genus. Several species were defined on the basis of the  
18 number of flanges along the shell, such as *Ichthyosarcolites rotundus*, *I. monocarinatus*,  
19 *I. triangularis*, *I. bicarinatus*, *I. tricarinatus*, *I. alatus* and *I. polycarinatus*. An analysis  
20 of the relative position of the flanges on the shell by hierarchical clustering helps with  
21 taxon definition. Two species with a single flange are here recognised, one with a dorsal  
22 flange (*I. monocarinatus*), the other with a ventral one (*I. triangularis*). There is no  
23 consistency in flange distribution on the shells whatever their number is, i.e., two or  
24 more, and homology of individual flanges cannot be demonstrated. Morphometric  
25 analysis finds a link between the shape of the general cavity and flange number and  
26 distribution. Out of the nineteen species named in the literature, only four can be  
27 retained after our thorough morphological analyses, namely *Ichthyosarcolites rotundus*  
28 (defined by a circular shell that lacks flanges), *I. triangularis* (defined by a single dorsal

29 flange), *I. monocarinatus* (defined by a single ventral flange) and *I. bicarinatus* (defined  
30 by two flanges or more). Flanges have very variable morphological features among *I.*  
31 *bicarinatus*. In addition, we here erect *Oryxia sulcata* nov. gen. et sp., a new form based  
32 on specimens previously identified as *I. bicarinatus*, *I. poljaki* and *I. tricarinatus*. This  
33 new taxon is defined by the presence of a ligament groove, this in contrast to  
34 *Ichthyosarcolithes* which never shows any trace of ligament. *Oryxia* nov. gen. may be the  
35 sister group of a clade of canaliculated forms that lost contact between the ligament  
36 support and the shell exterior and includes antillocaprinids, trechmannellids or  
37 ichthyosarcolithids.

38

39 *Keywords:*

40 Rudist bivalves

41 Ichthyosarcolithidae

42 Morphological analysis

43 Species delimitation

44 Mid-Cretaceous

45 Ligament evolution

46

47

48 **1. Introduction**

49 *Ichthyosarcolithes* ranks amongst the oldest named genera of rudist bivalves,  
50 having been erected by Desmarest (1812) on the basis of internal moulds found in  
51 Cenomanian strata of Charentes, western France, although the first mention of these  
52 fossils in the literature can be found in Guettard (1786), who referred to them as  
53 “Cucroïdes” and “corps marins fossiles” with the morphology of “cercles pierreux”  
54 (Fig. 1A). Desmarest (1812, 1817) considered these fossils to be a link between  
55 “hippurites” and “orthoceratites” (interpreted at the time as cephalopods), on account of  
56 a structure that was interpreted as a siphon (Fig. 1B). Later, d’Orbigny (1850) showed  
57 that the structure that had been assumed to be a siphon by Desmarest was in fact a small  
58 cavity filled by tabulations, without communication between the chambers. D’Orbigny  
59 (1850) erected the genus *Caprinella* (= *Ichthyosarcolithes*) within the group of rudists  
60 that were close to *Caprina* because of similar shell coiling and the presence of canals in  
61 the shell. With the discovery of novel forms of rudists during the nineteenth century and  
62 a better understanding of rudist anatomy, the affinities of *Ichthyosarcolithes* became  
63 more difficult to assess. The hinge of *Ichthyosarcolithes* shares similarities with that of  
64 radiolitids (Skelton and Smith, 2000) and shell canals occur also in caprinuloideids and  
65 antilocaprinids (Skelton, 2013a, fig. 2). Douvillé (1887) erected the family  
66 *Ichthyosarcolithidae*, which remained monogeneric until the description of *Curtocaprina*  
67 *clabaughikinsorum* (Mitchell, 2013a). *Ichthyosarcolithes* had been continuously enriched  
68 with new species names, now numbering nineteen, the latest addition being

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

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

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

89

90

91 **2. Material and methods**92 **2.1. Material studied**

93            Investigations are based on a literature survey, access to specimens in the AMU,  
94 MNHN, SB and NMNH collections (abbreviations, see below), complemented with  
95 pictures of collection or field specimens for a number of European countries and  
96 Mexico. Fieldwork in Charentes focused on middle and upper Cenomanian levels in  
97 which *Ichthyosarcolithes* is common as internal moulds. *Ichthyosarcolithes* are found on  
98 the northern part of Île Madame (45°96'N 1°12'W) in two distinct stratigraphical levels,  
99 i.e., units C1 and C2 of the Cenomanian series (Moreau, 1993; Videt, 2003).  
100 *Ichthyosarcolithes triangularis* co-occurs with *Sphaerulites foliaceus* in grey  
101 wackestones and packstones of middle Cenomanian age that represent subtidal, quiet  
102 environments. The aragonitic shell layer is dissolved but frequently encrusted with  
103 oysters and other epibionts that preserved shell outlines. At Pointe de Chaucre on the  
104 west coast of Île d'Oléron (45°98'N 1°39'W), the rocky shore exposes largely units B3  
105 to C3 in which rudists (*Caprina adversa*, *I. triangularis* and *S. foliaceus*) are found in  
106 high density of individuals (Chéreau et al., 1997). The rudists occur in carbonate  
107 deposits together with oysters (*Rhynchostreon suborbiculatum* and *Rastellum*  
108 *carinatum*), nerineid gastropods, chaetetid sponges and diverse benthic foraminifera  
109 depending on initial environmental conditions. At Pointe de Chaucre, a biostrome of  
110 large *C. adversa* and *I. triangularis* develops in beds representing high-energy  
111 environment and shallow-marine, sandy bottoms, whereas quiet environments associate



112 more often *I. triangularis* with *S. foliaceus*. Amongst rudists, *Ichthyosarcolites* is the  
113 most widely distributed form, occurring in a range of sedimentary environments, from  
114 shallow-marine carbonate sands to circa-littoral offshore muds. The genus is interpreted  
115 to have been environmentally tolerant, being the first rudist to settle on shallow-marine  
116 mobile and soft sediments (Chéreau et al., 1997).

117 D'Orbigny (1850) provided good descriptions and illustrations of  
118 *Ichthyosarcolites* among which two figured specimens of *I. triangularis* are from  
119 Charras (Charente-Maritime, France; MNHN.F.R08003; Fig. 1C). An additional  
120 specimen of *I. triangularis* from Charras is available in the Sorbonne University  
121 collections. The d'Orbigny Collection includes additional specimens from Île Madame  
122 (MNHN.F.6517-B). One fragment of *I. triangularis* from an unpublished plate of  
123 material in the Guéranger Collection (MV.2003.1.10900; Le Mans, France) shows its  
124 three-dimensionally preserved shape, along with the syntype of *Ichthyosarcolites*  
125 *bicarinatus* (MGUP.021.2-110; Fig. 3C). The lectotype of *Ichthyosarcolites doublieri*  
126 from Martigues (Bouches-du-Rhône, France) was also accessed (MNHN.F.R07971;  
127 Fig. 3F). One specimen of *Ichthyosarcolites rotundus* from Roquefort-la-Bédoule is  
128 available at Aix-Marseille University (AMU.ICH1; Fig. 4A). M. Floquet provided  
129 field photographs of other *Ichthyosarcolites* specimens from Roquefort-la-Bédoule,  
130 while six thin-sliced specimens of *I. bicarinatus* (AMU-HBES 84a–b) and one thin-  
131 sliced specimen of *I. tricarinatus* (AMU-HBES 85a; Fig. 4C) from Jebel Selloum  
132 (Tunisia) can be found in the Bessaï's Collection (Aix-Marseille University). The  
133 collection of J. Philip houses two thin slices (AMU-PCC 41a) of *Ichthyosarcolites*

134 *poljaki* from Koulovate (Greece). Several additional species are analysed from  
135 photographs taken at Aquismon Ciudad Valles, Canon de la Servilleta (Tamaulipas),  
136 San Joaquin Queretaro and Paso del Rio (Mexico) by Javier Aguilar-Perez (Fig. 4D–E),  
137 inclusive of the holotype of *Ichthyosarcolithes alatus* (Figs. 2A, 3E), from Istria (Croatia)  
138 and Bosnia Herzegovina, including the types of *Ichthyosarcolithes monocarinatus* and  
139 *Ichthyosarcolithes polycarinatus* by Alceo Tarlao (MB.3470, MB.3482, MB.4197 (3);  
140 see Fig. 3B, D) and from Hrušica (Slovenia) by Bogdan Jurkovšek (BJ1901, BJ1914,  
141 BJ1942). Two small pieces of probable myophoral parts of a specimen labelled  
142 “*Ichthyosarcolithes cornutus*” and several unidentifiable specimens from USA, labelled  
143 *Ichthyosarcolithes* sp. (YPM 24697, 24694 and 24696), were also considered and  
144 compared to Old World specimens, completed by photographs of a Canadian specimen  
145 of *Ichthyosarcolithes coraloidea* (GMUS.Mp 1; see Fig. 4F; Caldwell and Evans, 1963).

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

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

## 159 **2.2. Morphological analysis**

160 Only very few three-dimensionally preserved shells of *Ichthyosarcolites* are  
161 available. Fossils usually are internal molds of the general cavity or recrystallised shells  
162 observed in cross sections. The distinction of *Ichthyosarcolites* species in the literature  
163 is based on external features: occurrence of external flanges along the shell (Figs. 2–3),  
164 shape of the internal cavity (Figs. 3–4) and development of internal tabulae (Figs. 4,  
165 5A–D). All of these features were reappraised and analysed using morphometry and  
166 statistical tools to improve species definitions (Table 1) and taken into account as Least  
167 Inclusive Taxonomic Units or LITU (e.g., minimal taxonomic unit; Pleijel and Rouse,  
168 2000).

169 Several species have been defined by the number of flanges (see Polšak, 1967).  
170 However, the relative position of flanges around the shell has received very limited  
171 attention, whereas the location and growth patterns of flanges or other shell ornament  
172 often support homologies in molluscs (Merle, 2005). The anatomical position of a  
173 flange is not recognisable unless the shell can be properly oriented. We quantify the  
174 position of a flange by its angle, measured from the central tooth of the right valve or  
175 the central tooth socket, between the anterior and posterior teeth of the left valve (Fig.  
176 6A). This method requires thin slices that are parallel to the growth lines of the shell  
177 (parallel to the commissural plane for uncoiled shells). Thin slices that deviated too

178 strongly were not used in the present study (specimens such as number 21 – SOM 1 –  
179 are used because shell coiling affects only part of the dorsal outline). The method also  
180 requires to place a landmark at the centre of the general cavity that we approximate as  
181 the centre of the smaller circle including the general cavity. This procedure allows  
182 comparisons of shells of different sizes with flanges of different sizes, morphologies  
183 and directions. The posterior and anterior sides on the left valve can be identified with  
184 the help of the posterior myophore which is always shorter than the anterior one. On the  
185 right valve, a small cavity lies at the anterior side of the shell. The angle is always  
186 measured from the dorsal to the posterior part of the shell. All measurements were done  
187 on pictures of thin-sliced specimens using ImageJ 1.48v (Rasband, 1997).  
188 Measurements proved possible only on 20 shells, yielding a total of 58 measurements of  
189 angles. The angles are plotted in Figure 6B using R (R Development Core Team, 2008)  
190 to summarise the data set. A hierarchical clustering using Ward's method was made on  
191 the basis of angular positions of flanges (Fig. 6C) in order to test for homologous flange  
192 positions.

193 We carried out an analysis using geometric morphometry on the shape of the  
194 internal cavity. Only specimens with clear orientation and no trace of taphonomic  
195 compaction were chosen. Twenty-three shells were considered; those used for analysis  
196 of flange orientation, plus three shells lacking flanges. The general cavities are  
197 described by ten landmarks equally distributed on the outline. Landmark co-ordinates  
198 are digitised from photographs using the website PhyloNimbus (SOM 1). The  
199 procruste-fitted landmark data set were converted to procruste residuals by subtracting

200 the mean shape using Past 3.15 (Hammer et al., 2001). A principal component analysis  
201 (PCA) was implemented from the Procruste residuals (Harper, 2008). The ten principal  
202 components from the PCA were used as uncorrelated variables for a linear discriminant  
203 analysis (LDA; Fig. 7). An LDA is especially suited for maximising inter-group  
204 separation and minimising intra-group separation for predefined groups (McLachlan,  
205 2004). The LDA is used here to check if the clusters constructed with the data of flange  
206 positions are congruent with the analysis of internal anatomy.

### 207 **3. Morphology**

#### 208 **3.1. Pallial canals**

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

222 **3.2. Tabulae**

223 Tabulae are thin skeletal walls produced during shell growth that represent  
224 successive floors of the internal shell cavities. The species of *Ichthyosarcolites* are  
225 described with tabulae grossly parallel to the commissural plane, except for *I. obliquus*  
226 that is defined by obliquely oriented tabulation and for *I. doublieri* which lacks  
227 tabulations. The tabulae are very thin, fragile aragonitic structures that may disappear  
228 easily through taphonomic and diagenetic processes. The tabulations usually are  
229 recrystallised or appear as dissolution voids in internal moulds. Under best-preservation  
230 conditions, tabulae are to be found in the general cavity, the sockets and the posterior  
231 myophoral cavity (Figs. 4D, 5A). In practice, traces of tabulae are often erased (Figs.  
232 3F, 5E–F). In Figure 6B, the tabulae of the lower shell are well visible on the left side,  
233 but disappear nearly completely on the right side. The partial preservation of tabulae  
234 suggests incomplete dissolution prior to lithification. The lack of tabulae in the holotype  
235 of *I. doublieri* (Fig. 3F) is probably due to complete dissolution of the tabulae during  
236 early diagenesis.

237 In fossils, tabulae may appear parallel with or strongly oblique to the  
238 commissural plane (Fig. 5). Oblique tabulae have the shape of a three-quarter cornet  
239 with a downward-pointing dorsal attachment, and an open rounded ventral attachment  
240 to the front wall of the general cavity. The obliqueness of the tabulae can be seen only  
241 in dorsoventral view (Fig. 5C, F). The obliqueness of tabulae appears highly variable  
242 amongst specimens within a local assemblage and may reflect the tilting of individuals  
243 during their life span. In *I. triangularis* from Charentes, the expression of tabulae varies

244 gradually among individual shells from parallel with the commissure to strongly oblique  
245 (Fig. 5A, D). The high variation in tabulae expressed in *I. triangularis* includes the  
246 typical morphology of *I. obliquus*, which challenges the reliability of *I. obliquus* as a  
247 distinct species.

### 248 **3.3. Shell coiling**

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

### 258 **3.4. Ligament**

259 The ligament is totally missing in typical *Ichthyosarcolites* (Fig. 2) along with  
260 associated structures (ligament groove, ligament cavity). Amongst specimens from  
261 Slovenia, described as *I. poljaki*, *I. bicarinatus* and *I. tricarinatus* by Pleničar &  
262 Jurkovšek (1999), few shells exhibit a small dorsal protrusion that was considered a  
263 flange by those authors. This dorsal protrusion is bordered by a ligament groove. This  
264 protrusion should be understood as a bulge of shell stranded posteriorly to the ligament

265 groove, not homologous to a flange. The groove of the shells sinks to the anterior tooth  
266 socket and ends with a tiny shell bulb. Similar dorsal ligamentary bulges are also  
267 recognised in some forms from Istria (Croatia) illustrated by Polšak (1967), even if the  
268 inside of the shell does not permit to see a ligament groove due to poor preservation.  
269 Ligament structures are of critical importance in the phylogeny of rudists (Yonge, 1967;  
270 Skelton and Smith, 2000). Four evolutionary stages are recognised: (1) the ligament  
271 follows the commissure dorsally (e.g., *Diceras*); (2) the verticalised ligament is  
272 perpendicular to the commissure plane (e.g., *Valletia*, monopleurids); (3) the ligament  
273 structures are internalised and only a ligament cavity remains that loses contact with the  
274 exterior (e.g., trechmannellids); (4) the ligament disappears completely, including  
275 ligament cavity and groove (e.g., Titanosarcolitinae, Parasarcolitinae). *Ichthyosarcolites*  
276 represents the fourth stage. However, the ligament groove found in the Slovenian shells  
277 would place them in the second stage, out of the genus *Ichthyosarcolites*.

### 278 3.5. Flanges

279 Flanges, ribs, carinae and ridges are local thickenings of the shell (Fig. 2A–B),  
280 appearing in differential growth patterns. Even if the expression of shell thickenings in  
281 *Ichthyosarcolites* varies from low rounded bulges or ribs to high and thin, blade-like  
282 ridges (Figs. 3–4), all have a similar structure and likely appear following the same  
283 developmental processes. If the number and positions of flanges are consistent amongst  
284 individuals, we can assume homology and use them to define species. Few attempts  
285 were made to homologise flanges, by giving each flange a number or a letter based on  
286 its relative position on the shell (Polšak, 1967; Carbone et al., 1971). However, only the



287 number of flanges have been listed in diagnoses of species of *Ichthyosarcolites*, but not  
288 their positions. *Ichthyosarcolites rotundus* is defined by the absence of flanges. A single  
289 flange occurs both in *I. monocarinatus* and *I. triangularis*, two are seen in *I.*  
290 *bicarinatus*, three in *I. tricarinatus*, three to six in *I. alatus* (Filkorn, 2002; Aguilar-  
291 Pérez, 2008) and seven in *I. polycarinatus*. Flange morphology can vary in multiple  
292 ways: location, orientation and relative development, which can be quantified using the  
293 length to width ratio of the flange in cross section. The recognition of flanges may  
294 become difficult when these are weakly developed. Filkorn (2002) illustrated adults of  
295 *I. alatus* with either four, five or six flanges, but small juveniles with only three flanges  
296 were also assigned to *I. alatus* (see Fig. 3E), suggesting variation of flange number  
297 during ontogeny.

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

305 On shells with more than one flange, groups of the hierarchical clustering may  
306 provide evidence of patterns of flange distribution homologies. In the case of two  
307 flanges, homology is assumed if the two flanges consistently, or never, fall within the  
308 same cluster. The cluster analyses fail to recognise consistent patterns of flange

309 distribution among two-flanged or three-flanged shells. It is not possible to distinguish  
310 consistently homologous flanges among shells. The plasticity of flange distribution  
311 pattern and number of flanges is not reliable from an evolutionary point of view. The  
312 definition of a species on the basis of the number of flanges must be avoided in future.

313 *Ichthyosarcollites* is a recumbent form (Skelton, 1976) that lay on sandy to  
314 muddy substrates. This ecotype constrains the development of flanges around the shell.  
315 Our primary hypothesis was that no flange is likely to have developed on the side of the  
316 shell that lay on the sea floor, and that we can expect the flattest side of any  
317 *Ichthyosarcollites* shell to be in contact with the substrate. The hierarchical classification  
318 of flanges separates ventral flanges from dorsal ones well, with a rare occurrence of  
319 flanges on the anterior side (Fig. 6B). Most species of *Ichthyosarcollites* likely lay on  
320 their anterior side, with usually a stabilising flange in ventral or dorsal position. This is  
321 consistent with the anterior attachment of the juvenile spirogyrate right valve (Skelton,  
322 1974).

### 323 **3.6. General cavity**

324 Some species of *Ichthyosarcollites* were defined solely on the basis of shell cross  
325 sections. The character descriptions focused on external features including bulges,  
326 flanges, relative shell thickness and outline of the general cavity. For example, *I.*  
327 *triangularis* is characterised by a triangular shape in cross section. As observed in many  
328 molluscs, external shell features reflect the shape of internal structures such as the  
329 general cavity. Because flange number and general cavity shape are the two main

330 features used to erect species of *Ichthyosarcollites*, we tested whether the groups defined  
331 by flange distribution could also be recognised in general cavity outline.

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

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

350

#### 351 **4. Systematic palaeontology**

352 Our analyses lead us to retain four species that are characterised by a unique  
353 combination of homologous parts (Wheeler and Platnick, 2000): one with a single  
354 ventral flange, one with a single dorsal flange, one with at least two flanges one without  
355 any flange. The systematic arrangement of the Bivalvia used here follows Carter et al.  
356 (2011) and Skelton (2013a–b).

357

358 Class Bivalvia Linnaeus, 1758

359 Infraclass Heteroconchia Gray, 1854

360 Order Hippuritida Newell, 1965

361 Suborder Hippuritidina Newell, 1965

362 Superfamily Caprinoidea d'Orbigny, 1850

363 Family Ichthyosarcolitidae Douvillé, 1887

364 Genus *Ichthyosarcolites* Desmarest, 1812

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

366 *Diagnosis.* Rudist with small left valve and extremely strongly developed right valve.

367 Both valves loosely coiled with non-contiguous whorls that may uncoil during shell  
368 growth. Presence of none to seven longitudinal flanges along the shell. The relative size

369 and shape of the flanges vary from rounded costae to prominent ridges. Aragonitic shell  
370 layer filled with capillary canals (Fig. 2). Tabulae fill all cavities of the two valves and  
371 the pallial canals. No ligament groove, nor cavity. The two anterior and posterior  
372 sockets of the right valve are of equal size, small and rounded. Small posterior  
373 accessory cavity (PAC; Fig. 2C–D). The two myophores are similar to those of  
374 radiolitids, forming blades attached to the ventral side of the teeth on the left valve. The  
375 myophores of the left valve insert directly in the wall of the general cavity of the right  
376 valve.

377 *Remarks.* The monogeneric family Ichthyosarcolitidae was created by Douvillé (1887)  
378 to reflect the high differentiation of *Ichthyosarcolites* from all other rudists.  
379 *Ichthyosarcolites* possesses such specific features that confusion with other genera can  
380 be ruled out. *Stellacaprina gunteri* shows a similar morphology but the species has two  
381 additional toothlets, i.e., the diagnostic feature of the Antillocaprinidae (Mitchell,  
382 2013b). *Curtocaprina clabaughikinsorum* is the only other member of the  
383 Ichthyosarcolitidae, following Mitchell (2013a). That species utterly differs from  
384 *Ichthyosarcolites* in the structure of its dentition, size and shell shape (right and left  
385 valves of same size, approximately 20 mm, a single ventral flange). If all  
386 *Ichthyosarcolites* identified to species are dated as Cenomanian, a specifically  
387 indeterminate *Ichthyosarcolites* was recorded from the Albian of Sinai, Egypt (Zakhera,  
388 2010). The map (Fig. 8) shows the geographical location of all specimens, making use  
389 of the following references and collection specimens: Mexico (Filkorn, 2002; Aguilar-  
390 Pérez, 2008), USA (YPM 24697, 24694, 24696), Cuba (Rojas, 2004), Portugal

391 (Berthou, 1973), Spain (Troya García, 2015), France (Desmarest, 1812), Italia  
392 (MGUP.021.2-110; Gemmellaro, 1865), Slovenia (Pleničar, 1965; Pleničar and  
393 Jurkovšek, 1999), Croatia (Polšak, 1967), Bosnia and Herzegovina (Slišković, 1968),  
394 Czech Republic (Počta, 1887), Greece (AMU-PCC 41a), Bulgaria (Paquier, 1905),  
395 Turkey (Özer, 1998), Algeria (Van de Fliert, 1952), Tunisia (Toucas, 1908; Razgallah et  
396 al., 1994), Libya (Parona, 1921), Tanzania (Hennig, 1916), Egypt (Bauer et al., 2001;  
397 Zakhera, 2010), Jordan (Chiki-Aouimeur, 2010), Afghanistan (Berizzi Quarto di Palo,  
398 1970) and China (Lan and Wei, 1995).

399 *Ichthyosarcolithes* is a recumbent form that has been recorded from peri-reefal  
400 and fore-reef environments with a high water-energy (Korbar et al., 2001; Filkorn,  
401 2002) to calm mudflats, where it played a pioneer role (Videt, 2003).

402 *Ichthyosarcolithes triangularis* Desmarest, 1812

403 Figs. 1C, 2E.

404 Selected synonymy

405 1786 Cucroides; Guettard, p. 552, pl. 28, fig. 2.

406 1812 *Ichthyosarcolithes triangularis* Desmarest, p. 321.

407 1817 *Ichthyosarcolithes triangularis*; Desmarest, p. 50, pl. 2, figs 9–10.

408 1821 Glossopètes; Defrance, p. 72.

409 1821 Ichthyosarcolite; Defrance, p. 549.

410 1825 *Ichthyosarcolithes triangularis*, Desmarest; Deshayes, p. 501.

411 1825 *Rhabdites triangularis* De Haan, pp. 41–42, 52–53, 57, 160.

- 412 1826 *Ichthyosarcolites*, Desmarest; d'Orbigny, p. 167.
- 413 1827 *Ichthyosarcolite*; Ducrotay de Blainville, pl. 11, fig. 2.
- 414 1846 *Ichthyosarcolithus* A.G. Desmarest 1817; Herrmannsen, p. 554.
- 415 1849 *Caprinella triangularis*, d'Orb., 1847; d'Orbigny, pl. 542.
- 416 1850 *Caprinella triangularis*, d'Orb., 1847; d'Orbigny, p. 192.
- 417 1854 *Ichthiosarcolites quadrangularis* Tuomey, p. 172.
- 418 1855 *Caprinella triangularis* Desm.; Woodward, pp. 52–53, figs 25–27.
- 419 1887 *Ichthyosarcolites marginatus* Počta, p. 207.
- 420 1887 *Ichthyosarcolithus triangularis* Desmarest; Douvillé, p. 791, figs 15–17.
- 421 1887 *Ichthyosarcolites triangularis* Desmarest; Fischer, p. 1057, fig. 804.
- 422 1888 *Ichthyosarcolithes*; Douvillé, pp. 706, 728–729.
- 423 1889 *Ichthyosarcolites marginatus* Poč.; Počta, p. 87, pl. 6, figs 6–7.
- 424 ?1905 *Ichthyosarcolites triangularis* Desmarest 1817; Paquier, p. 94, pl. 9, figs
- 425 7–9.
- 426 ?1916 *Ichthyosarcolites triangularis*; Hennig, p. 461.
- 427 1921 *Ichthyosarcolites triangularis* Desm.; Parona, p. 10, pl. 1, figs 1a–b, 9.
- 428 1930 *Caprinella triangularis*; Repelin, p. 61, pl. 7, fig. 5.
- 429 1937 *Ichthyosarcolites triangularis* Desmarest; MacGillavry, p. 47.
- 430 1968 *Ichthyosarcolites triangularis*; Damestoy, pp. 2–6, figs 1–3.
- 431 1969 *Ichthyosarcolites triangularis*; Dechaseaux, p. N795, fig. 4a–b.
- 432 1970 *Ichthyosarcolites triangularis* Desmarest; Berizzi Quarto di Palo, p. 107,
- 433 pl. 15, fig. 1.

434 2000 *Ichthyosarcolithes triangularis* Desmarest; Skelton and Smith, pp. 110–111,  
435 117, 123, fig. 4c–d.

436 2010 *Ichthyosarcolithes triangularis* Desmarest; Chikhi-Aouimeur, p, 96, fig.  
437 87.1.

438 2015 *Ichthyosarcolithes triangularis* Desmarest; Troya García, pp. 248–254, 267,  
439 271, figs 139–141.

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

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

447 *Description.* Shell markedly inequivalve; left valve very small (approximately one tenth  
448 of length of right valve) and slightly coiled. Right valve narrowly tubular, extremely  
449 strongly developed and ventrally coiled (dorsal external side) with non-contiguous  
450 whorls (Fig. 1C). Planispiral growth of the shell (Figs. 1C, 5E). Left valve loosely  
451 ventrally coiled and very small compared to the right valve. Shape of right valve highly  
452 variable, ranging from 0.5 to 2 coils, the space between two coils ranging from a  
453 distance of 30 to 500 mm for completely coiled specimens (Figs. 1C, 5E). Both valves  
454 of equal diameter. General cavity of both valves of equal diameter, between 10 and 80  
455 mm for adults (e.g., Figs. 1C, 4E, respectively), flange not included. A unique flange is



456 present, always in dorsal position (Fig. 1C), of triangular shape, of equal width and  
457 height. Flange straight with a rounded external margin. External aspect of shell  
458 completely smooth or with presence of small tightened costae of approximately 0,1 mm  
459 in height and 1 mm in width. Shell composed of an outer calcitic layer of approximately  
460 0,5 mm and an inner aragonitic shell layer with a thickness of approximately 15 per cent  
461 of the diameter of the body cavity in transverse section, flange not included. The  
462 aragonitic shell layer is densely canaliculated with close-set, small capillary canals  
463 (approximately 1 mm in diameter), round to slightly ovoid (occasionally honey  
464 combed) except for the myophores and the anterior and posterior teeth. The external  
465 side of the aragonitic shell layer is bordered with a single row of  
466 subrectangular/pallisading canals of same width as capillary canals. Tabulae present on  
467 both valves with highly variable thickness and surface orientation in the general cavity,  
468 pallial canals, sockets and the PAC. Tabulae flat to highly curved dorsally. When highly  
469 oblique, presence of a horizontal part in the middle of the tabulae in dorsoventral axis  
470 (Fig. 1C). Tabulae within the pallial canals; tabulae of a canal are regularly spaced and  
471 independent of other canals. Single other ovoid PAC present posteroventrally on the  
472 right valve, slightly larger than sockets and filled with tabulae (Fig. 5A). No ligament  
473 groove, nor cavity.

474 *Left valve myocardial apparatus.* Inverse dentition, composed on the left valve of an  
475 anterior and a posterior conical tooth of similar shape and size, separated by a central  
476 tooth socket that is never observable as a distinct cavity. Thin vertical, wall-like  
477 myophore ventrally adjoined to each tooth. The two myophores constitute a U-shaped

478 myophoral arcade, attached to the teeth, protruding directly into the general cavity of  
479 the right valve. Development of vertical myophores generates a space between them and  
480 the inner shell, looking like a cavity that may be filled with a few thin, oblique tabulae  
481 arranged along an anteroposterior axis. Whole myocardinal apparatus is U-shaped and  
482 extends itself to make a connection with the ventral edge of the shell.

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

489 *Remarks.* The type species of the genus, primarily based on internal moulds of the  
490 general cavity and sockets segmented by tabulae, was first described by Desmarest  
491 (1812) as « Coquille droite et épaisse, presque triangulaire, munie intérieurement de  
492 cloisons obliques en forme de mi-cônes ou cornets, et d'un sinus ou siphon longitudinal  
493 et latéral ». *Ichthyosarcolithes triangularis* was illustrated for the first time by Desmarest  
494 (1817) (see Fig. 1B). The main distinctive feature was the triangular shell shape. The  
495 type locality of Desmarest's species remained unknown to himself, but it is certain that  
496 it originated from Charentes in western France. The dorsal thickening of the aragonitic  
497 shell layer was correctly represented in d'Orbigny's illustration (see Fig. 1C).

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

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

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

509

510 ***Ichthyosarcolites rotundus* Polšák, 1967**

511 Figs. 3A, 4A

512 Selected synonyms

513 \*1967 *Ichthyosarcolites rotundus* Polšák, pp. 80–81, 187, pl. 6, fig. 2; pl. 9, figs.

514 2–3.

515 1971 *Ichthyosarcolites rotundus* Polšák; Carbone et al., p. 147, fig. 16.

516 1998 *Ichthyosarcolites monocarinatus* Sliškovic; Cestari et al., p. 70, figs 1–2.

517 1998 *Ichthyosarcolites rotundus* Polšák; Özer, p. 240, figs 6–7.

518 1999 *Ichthyosarcolites rotundus* Polšák; Özer, p. 69, pl. 1, fig. 4.

519 2001 *Ichthyosarcolites rotundus* Polšák; Özer et al., p. 860, figs 10–11.

520 2015 *Ichthyosarcollites monocarinatus* Desmarest; Troya García, p. 260, figs  
521 145–147.

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

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

531 *Description.* Left valve unknown. Right valve narrowly tubular and nearly straight;  
532 length unknown. Section circular (35 to 150 mm in diameter) to elliptical along  
533 dorsoventral axis (length/width: 60/45 mm). Shell thickness constant on all shell for  
534 approximately one third to one quarter of diameter. Aragonitic shell layer of the right  
535 valve densely canaliculated with close-set, very small, round to slightly ovoid capillary  
536 canals, sometimes honey combed (diameter 0.5 to 3 mm). The external side of the  
537 aragonitic shell layer is bordered with a single row of radial palisading canals of same  
538 width as capillary canals, but subrectangular in cross section. Outer calcitic shell layer  
539 unknown. Ovoid cavity (length/width: 7/10 mm) present posteroventrally, of equal size  
540 as sockets (PAC; Fig. 4A) on the right valve. Very thin tabulae occurring in general  
541 cavity, canals, sockets and PAC. The blade between this cavity and general cavity is so

542 thin that it contains no canal, as the blades separating sockets from the general cavity.

543 No ligament groove, nor cavity.

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

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

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

565

566 ***Ichthyosarcolites monocarinatus*** Slišković, 1966

567 Fig. 3B

568 Selected synonyms

569 \*1966 *Ichthyosarcolites monocarinatus* Slišković, p. 177, fig. 1.

570 1967 *Ichthyosarcolites monocarinatus* Slišković; Polšak, pp. 80, 186, pl. 6, fig.  
571 1; pl. 8, figs 1–5, pl. 9, fig. 1.

572 1968 *Ichthyosarcolites iokungensis* Bobkova, pp. 289–290, pl. 68.

573 1976 *Ichthyosarcolites monocarinatus* Slišković; Praturlon and Sirna, pp. 90–  
574 100, pl. 1, fig. 18.

575 1983 *Ichthyosarcolites monocarinatus major* Slišković; Slišković, pp. 19–21,  
576 fig. 1.

577 1992 *Ichthyosarcolites monocarinatus* Slišković; Turnšek et al., p. 220, pl. 14,  
578 fig. 2.

579 1998 *Ichthyosarcolites monocarinatus* Slišković; Cestari et al., pp. 70–72, figs 1,  
580 2/1–6.

581 ?1999 *Ichthyosarcolites monocarinatus* Slišković; Pleničar and Jurkovšek, p. 77,  
582 pl. 11, fig. 3a–b.

583 2005 *Ichthyosarcolites* cf. *monocarinatus* Slišković; Pleničar, p. 34, pl. 5, fig. 1.

584 2015 *Ichthyosarcolites monocarinatus* Desmarest; Troya García, pp. 260–264,

585 269, figs 145–147.

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

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

592 *Description.* Left valve unknown. Right valve planispiral, known only from a 400-mm-  
593 long, butt-shaped fragment, rotating 90 degrees over 200 mm, followed by 200 mm of  
594 substraight shell. Elliptical section in dorsoventral axis: 30/40(+ 3) mm, 110/130(+ 20)  
595 mm, 40/44(+ 10) mm, these three values representing individual specimen length/width  
596 and flange length. Shell thickness approximately constant on all shell for one half to one  
597 fifth of diameter. Presence of a unique flange, in anteroventral position. Flange shaped  
598 as a little bulge rounded and protruding only 5 mm to a more developed one forming an  
599 isosceles triangle of 20 mm in length with a largely rounded end (Fig. 3B). Because of  
600 this flange, the cylindrical shell presents a flat ventral side. The aragonitic shell layer of  
601 the right valve is densely canaliculated with close-set, very small capillary canals, round  
602 to slightly ovoid (diameter approximately of 1 mm). Outer calcitic shell layer unknown.  
603 A single other ovoid cavity 4/10 mm is present posteroventrally in the right valve, of  
604 equal size to slightly more important than sockets and PAC. Very thin tabulae present

605 on the general cavity, canals, sockets and the PAC. Blade between PAC and the general  
606 cavity so thin that it contains no canal, with blades separating sockets from the general  
607 cavity. No ligament groove, nor cavity.

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

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

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

624



- 625 *Ichthyosarcolithes bicarinatus* Gemmellaro, 1865
- 626 Figs. 3C–D, 4B–E, 6A
- 627 Selected synonyms
- 628 \*1865 *Caprinella bicarinata* Gemmellaro, pp. 236–237, pl. 4, figs 5–6.
- 629 1898 *Caprinella bicarinata*; Douvillé, p. 150.
- 630 1914 *Ichthyosarcolithes bicarinatus* Gemmellaro; Parona, p. 21.
- 631 1921 *Ichthyosarcolithes bicarinatus* (Gemm); Parona, p. 12, pl. 2, figs 1, 7, 10.
- 632 1921 *Ichthyosarcolithes tricarinatus* Parona, p. 13, pl. 2, figs. 2, 8, 11.
- 633 1937 *Ichthyosarcolithes bicarinatus* (Gemmellaro); MacGillavry, pp. 49, 51, 54–
- 634 56.
- 635 1937 *Ichthyosarcolithes tricarinatus* Parona; MacGillavry, pp. 49, 54–56.
- 636 1964 *Ichthyosarcolithes poljaki* Polšak, p. 66.
- 637 1965 *Ichthyosarcolithes rogi* Pleničar, pp. 97–98, 100–101, figs 8–10.
- 638 1966 *Ichthyosarcolithes polycarinatus* Slišković, p. 178, fig. 2.
- 639 1967 *Ichthyosarcolithes bicarinatus* Gemmellaro; Polšak, p. 186, pl. 5, fig. 1B–C.
- 640 ?1967 *Ichthyosarcolithes bicarinatus* Gemmellaro; Polšak, p. 186, fig. 21, pl. 5,
- 641 fig. 2A.
- 642 1967 *Ichthyosarcolithes tricarinatus* Parona; Polšak, pp. 76, 185, fig. 19, pl. 4,
- 643 figs 5, 7; pl. 5, fig. 2.
- 644 1967 *Ichthyosarcolithes poljaki* Polšak; Polšak, pp. 77, 185, pl. 4, fig. 6; pl. 5, fig.
- 645 1.
- 646 1971 *Ichthyosarcolithes bicarinatus* (Gemm.); Carbone et al., p. 146, fig. 14.

- 647 1971 *Ichthyosarcolites poljaki* (Gemm.); Carbone et al., p. 147, fig. 15.
- 648 1971 *Ichthyosarcolites tricarinatus* Parona; Carbone et al., p. 147, fig. 17.
- 649 1982 *Ichthyosarcolites bicarinatus* (Gemmellaro); Sirna, p. 84, fig. 7, pl. 1, fig.
- 650 f.
- 651 1988 *Ichthyosarcolites bicarinatus* Gemmellaro; Accordi et al., p. 139, fig. 5, pl.
- 652 1, fig. 7.
- 653 1988 *Ichthyosarcolites bicarinatus* Gemmellaro; Accordi et al., p. 165, pl. 2, fig.
- 654 7.
- 655 1993 *Ichthyosarcolites bicarinatus* (Gemmellaro); Cherchi et al., p. 93, fig. 2, pl.
- 656 4, fig. 5.
- 657 1998 *Ichthyosarcolites bicarinatus* Gemmellaro; Özer, p. 240, fig. 6-5.
- 658 1998 *Ichthyosarcolites tricarinatus* Polšak; Özer, p. 240, fig. 6-6.
- 659 1998 *Ichthyosarcolites poljaki* Polšak; Özer, p. 240, fig. 6-4.
- 660 ?1999 *Ichthyosarcolites poljaki* Polšak, 1967; Pleničar and Jurkovšek, p. 75, pl.
- 661 7, fig. 2b.
- 662 non1999 *Ichthyosarcolites bicarinatus* (Gemmellaro); Pleničar and Jurkovšek, p.
- 663 75, pl. 8, fig. 2a–b; pl. 11, fig. 2.
- 664 non1999 *Ichthyosarcolites tricarinatus* (Gemmellaro); Pleničar and Jurkovšek,
- 665 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
- 666 1a–b.
- 667 2001 *Ichthyosarcolites tricarinatus* Parona; Özer et al., p. 860, figs. 10, 11-4.
- 668 2002 *Mexicaprina alata* Filkorn, pp. 681–686, figs 4–7.

- 669 2008 *Ichthyosarcolithes alatus* (Filkorn 2002); Aguilar-Pérez, pp. 113–116, fig.  
670 64/1–4.
- 671 2009 *Ichthyosarcolithes bicarinatus* (Gemmellaro); Sarı and Özer, p. 367, fig. 9a.
- 672 2010 *Ichthyosarcolithes bicarinatus* (Gemmellaro, 1865); Chikhi-Aouimeur, p.  
673 96, fig. 87/2–4.
- 674 2010 *Ichthyosarcolithes tricarinatus* (Gemmellaro, 1865); Chikhi-Aouimeur, p.  
675 97, fig. 88/2–3.
- 676 2013b *Ichthyosarcolithes alatus* (Filkorn); Mitchell, pp. 85–87, fig. 1/f–g.
- 677 2015 *Ichthyosarcolithes tricarinatus* Parona; Troya García, pp. 254–260, 269–  
678 271, figs 142–143, 148, 150

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

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

691 *Description.* Left and right valves of similar diameters (6/5 to 25/45 mm, flange not  
692 included). Relative length between valves unknown. Coiling pattern unknown. Always  
693 a minimum of two flanges and a maximum of up to seven. Shell cross section varying in  
694 shape from grossly rounded to polygonal (triangular or quadrate) according to the  
695 number of flanges. When two flanges occur they usually appear at two contiguous  
696 vertices of a square (Fig. 4B). Shape section appearing grossly triangular in case of  
697 three flanges (Fig. 4C), more quadrate with four flanges (Fig. 4D–E). When flange  
698 number increases, shell sides change from convex to flat or even concave (Fig. 3E);  
699 distribution of flanges globally equidistant when four or more flanges are present (Fig.  
700 3E). Flange development highly variable among individuals and among flanges of  
701 single individuals. Flanges regularly extend to a size larger than the diameter of the  
702 shell. Flanges usually narrow, parallel sided and reaching a large size, occasionally  
703 short, triangular with rounded extremity. End of a flange always rounded, keel like,  
704 occasionally with enlarged margin. Number of flanges increases during shell growth.  
705 Flanges generally oriented perpendicularly to shell at their base, but can make an angle  
706 of 70–120° with shell surface. Outer calcitic layer unknown. Inner aragonitic shell layer  
707 thickness varying between 6 and 25 per cent of diameter of the body cavity. Aragonitic  
708 shell layer densely canaliculated with tiny, round to honeycomb capillary canals  
709 (diameter of approximately 1 mm), except in myophores, posterior and anterior teeth.  
710 External side of aragonitic shell layer bordered by a single row of radial canals of same  
711 diameter as capillary canals, but subrectangular to pyriform in cross section. Single row  
712 of enlarged rounded canals in the middle of large flanges. Ovoid PAC on the  
713 posteroventral side on the right valve, slightly larger than sockets and filled with

714 tabulae. Tabulae present on both valves in the general cavity, the pallial canals, the  
715 sockets and the PAC.

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

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

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

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

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

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

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

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

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

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

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

767

#### 768 ***Incertae sedis species***

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

775 1825 *Ichthyosarcollites obliqua* Deshayes, p. 501.

776 1937 *Ichthyosarcollites obliquus* Deshayes 1825; MacGillavry, p. 52.

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

785           1850 *Caprinella doublieri*, d'Orb., 1847; d'Orbigny, p. 191, pl. 541.

786           1967 *Ichthyosarcolithes doublieri* (d'Orb); Philip, p. 498.

787           1973 *Caprinula doublieri* d'Orbigny; Berthou, p. 97, pls 57–58.

788           2007 *Caprinula doublieri* d'Orbigny; Macé-Bordy, p. 173.

789 *Ichthyosarcolithes doublieri* d'Orbigny, 1847 from the upper Cenomanian of Martigues  
790 (Bouches-du-Rhône, France) was first described as a species of *Ichthyosarcolithes*  
791 without any tabulae. There are records from Charentes (Fig. 3F), Provence (Philip,  
792 1967) and Portugal (Berthou, 1973), invariably occurring as internal moulds. The  
793 number of flanges is unknown in *I. doublieri*. The tabulae are fragile and very thin  
794 structures (Fig. 3D). On the internal mould in Figure 5B, at the bottom of the mould the  
795 presence of tabulae can be seen; these progressively disappear in the same individual.  
796 The thickness and development of tabulae varies among specimens (Figs 4D, 5A), some  
797 specimens showing tabulae at variable preservational states, some disappearing partially  
798 or completely, while they are entirely lost in other shells. It is likely that *I. doublieri*



799 corresponds to a preservational state of another congener in which tabulae dissolved.  
800 Due to the unilobate form of the internal moulds, *I. doublieri* cannot be assigned to the  
801 genus *Caprinula* (bilobate because of the strong development of CTS in relation to the  
802 general cavity), contrary to what Berthou (1973) and Macé-Bordy (2007) noted.

803 1854 *Ichthiosarcolites loricatis* Tuomey, p. 172.

804 1854 *Ichthiosarcolites cornutis* Tuomey, p. 172.

805 1854 *Ichthiosarcolites quadrangularis* Tuomey, p. 172.

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

818 1855 *Caprinella coraloidea* Hall and Meek, p. 380, pl. 2, fig. 3a–f.

819 *Ichthyosarcollites coralloidea* from the upper Campanian of Sage Creek (South Dakota,  
820 USA) was differentiated from *I. triangularis* by “being curved not exactly in the same  
821 plane, in increasing much more rapidly in size from the apex, and in having the fibrous  
822 portion of the shell so thick upon the inner side of the volution as to bring the sides in  
823 contact if continued a single turn” (Hall and Meek, 1855). Shell coiling is variable  
824 enough not to be considered as a valuable criterion for species definition. Desmarest  
825 originally described *I. triangularis* on the basis of straight internal molds, but 30 years  
826 later, d’Orbigny (1850) illustrated a highly coiled right valve as *I. triangularis* (see Fig.  
827 1C). The large shells from Charentes show that coiling pattern can change during  
828 ontogeny (Fig. 5F). In southeastern France, other specimens can be seen to be  
829 completely coiled up to large sizes (Fig. 5E). In *I. coralloidea*, “The septa are also much  
830 more irregular than in the European species, those which are distinct upon the back of  
831 the shell often converging so that two unite in a single one on the inner side of the  
832 volution” (Hall and Meek, 1855). The diversity of forms, expressed only in populations  
833 of Charentes, shows the diversity of tabulae obliqueness, some of them occasionally  
834 converging (Fig. 5C). The number of flanges is unknown in *I. coralloidea* and pending  
835 description of new, complementary material, the species name should be considered  
836 *incertae sedis*. The unique specimen described as *I. coralloidea* by Caldwell and Evans  
837 (1963) is related to antillocaprinids and not to *Ichthyosarcollites*. This specimen has its  
838 sockets and myophoral cavities filled with pallial canals, a characteristic feature of  
839 Titanosarcollitinae and Parasarcollitinae.

840 1887 *Ichthyosarcollites ensis* Pořta, p. 207.

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

848           1905 *Ichthyosarcolithes* sp. nov. indét. Paquier, pp. 94–95, pl. 9, figs. 7–9.

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

854           1994 *Ichthyosarcolithes quadratus* Pleničar; Pleničar and Dozet, p. 188.

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

857           2004 *Ichthyosarcolithes?* sp.; Masse et al., p. 83, fig. 11.

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

861 Superfamily Caprinoidea d'Orbigny, 1850

862 Genus *Oryxia* nov.

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

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

866 *Diagnosis.* Rudist bivalve with right valve narrow, gently coiled anteriorly, with a large  
867 posteroventral flange and a very slight anteroventral flange with triangular shape in  
868 cross section. A ligament groove in dorsal position ends dorsally with a tiny shelly bulb  
869 parallel to the anterior tooth socket. A bulge is accreted posteriorly to the ligament  
870 groove. Aragonitic shell layer filled with round capillary canals. Presence of an anterior  
871 accessory cavity (AAC). Small ovoid anterior and posterior sockets of equal size (5 to  
872 10 mm). Central tooth very small (1 to 2 mm), filled with canals.

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

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

883 *Oryxia sulcata* sp. nov.

884 Fig. 9

885

886 ?1967 *Ichthyosarcolites bicarinatus* Gemmellaro; Polšak, p. 186, fig. 21, pl. 5,  
887 fig. 2A.

888 ?1999 *Ichthyosarcolites poljaki* Polšak, 1967; Pleničar and Jurkovšek, p. 75, pl.  
889 7, fig. 2b.

890 1999 *Ichthyosarcolites bicarinatus* (Gemmellaro); Pleničar and Jurkovšek, p. 75,  
891 pl. 8, fig. 2a–b; pl. 11, fig. 2.

892 1999 *Ichthyosarcolites tricarinatus* (Gemmellaro); Pleničar and Jurkovšek, p.  
893 76, pl. 5, figs 1b, 3; pl. 8, fig. 3; pl. 9, figs 1–6; pl. 10, figs 1a–b, 2; pl. 11, fig.  
894 1a–b.

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

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

901 *Diagnosis.* Same as genus (monotypy).

902 *Description.* Left valve unknown. Right valve tubular, narrow and slightly anteriorly  
903 coiled (12 mm of anterior coiling per 100 mm length). Planispiral development. Longest  
904 known fragment measuring 220 mm in length (holotype). Diameter of shell varying  
905 between 45 and 75 mm. Diameter of general cavity varying between 28 and 35 mm.  
906 Shell shape subrectangular because of flanges and shell thickenings. Slight bead of 13  
907 mm width located dorsally to the posterior tooth socket and posterior to the longitudinal  
908 ligament groove. Bead lopsided anteriorly, slightly covering the ligament groove.  
909 Subtriangular anteroventral thickening, of 13 mm width at its base. Presence of a  
910 posteroventral flange. Flange margin broken, but with a minimum of 30 mm in length  
911 and a thickness of 0.5 to 5 mm. Ventral plane surface created by simultaneous presence  
912 of the posteroventral flange and anteroventral thickening. Very thin ligament groove  
913 (8/0.2 mm) connected to the dorsal part of the shell, slightly anteriorly curved in cross  
914 section. Groove ending with a little anteroposteriorly elongated cavity (2/0.5 mm)  
915 located two millimetres dorsally to the posterior tooth. Aragonitic shell; aragonitic inner  
916 shell layer thickness comprised between 10 and 30 mm. Aragonitic shell layer  
917 completely filled with round to ovoid capillary canals with a mean diameter of 1 mm.  
918 Calcitic outer layer missing, probably thin and smooth. No visible tabulae.

919 *Right valve myocardinal apparatus.* Central tooth filled with capillary canals  
920 (length/width: 2/1 mm to 3/2 mm). Presence of two flat anterior (4/1 mm to 100/30 mm)  
921 and posterior (4/1 mm to 8/2 mm) tooth sockets on the dorsal side of the shell and  
922 separated from general cavity by a thin blade devoid of pallial canals. Vertical

923 myophores undifferentiated from inner shell. Ovoid AAC present anteroventrally (under  
924 anteroventral thickening), larger than sockets (12/5 mm).

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

928 *Occurrences.* Exclusively Cenomanian, being solely known from the bioherm of  
929 Hrušica (Slovenia), on the northern part of the Dinaric carbonate platform. Polšak's  
930 (1967) specimens from Istria (Croatia), identified as *I. bicarinatus*, may be conspecific  
931 with the new taxon.

## 932 **5. Conclusions**

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

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

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1181

1182 **Table 1.** Comparison of known morphological features and geographical distribution of  
1183 all 19 nominal species of *Ichthyosarcollites*, plus the new form described herein, *Oryxia*  
1184 *sulcata* nov. gen. et sp. “Unknown” signifies that data were unavailable from the  
1185 literature or from specimens considered for the present study.

1186

## 1187 **Figures**

1188 **Fig. 1. A,** Earliest illustration of *I. triangularis* as “Cucroïdes” by Guettard (1786), who  
1189 thought the fossil to be circular (“*pierres circulaires*”). **B,** Original drawings of the  
1190 internal moulds of *I. triangularis* (Desmarest, 1817). **C,** Specimen of *I. triangularis*  
1191 (MNHN.F.R08003) from Île d’Oléron, illustrated in d’Orbigny’s *Paléontologie*  
1192 *Française* (1847); this specimen is here designated neotype of *Ichthyosarcollites*  
1193 *triangularis* Desmarest, 1812.

1194 **Fig. 2.** Illustration of the main morphological attributes of a shell of *Ichthyosarcollites*.  
1195 **A,** Picture of *Ichthyosarcollites alatus* (Filkorn, 2002) (UNAM.6979). **B,** Interpretative  
1196 scheme of A with the main morpho-anatomical features and homologues. **C,** Picture of  
1197 *Ichthyosarcollites rotundus* Polšak, 1967 (LGPZ.778). **D,** Interpretative scheme of C

1198 with the main morpho-anatomical features and homologues. AM: anterior myophore;  
1199 PM: posterior myophore; ATS: anterior tooth socket; PTS: posterior tooth socket; AT:  
1200 anterior tooth; PT: posterior tooth; D: general cavity of the right valve; G: general  
1201 cavity of the left valve; AAC: anterior accessory cavity; PAC: posterior accessory  
1202 cavity; t: tabulae; d: shell depression, space between aragonitic inner shell and the stem  
1203 of the myophoral blades.

1204 **Fig. 3.** Types of species of *Ichthyosarcolites*. All scale bars equal 10 mm. **A**, Holotype  
1205 of *Ichthyosarcolites rotundus* Polšak, 1967 (LGPZ.778), showing a cylindrical shell;  
1206 from the Cenomanian of Fontanela Bay (Istria, Croatia). **B**, Holotype of  
1207 *Ichthyosarcolites monocarinatus* Slišković, 1966 (MB.3470), showing a small flange  
1208 and round canals; from the Cenomanian of the Dinaric Alps (courtesy of Alceo Tarlao).  
1209 **C**, Syntype of *Ichthyosarcolites bicarinatus* (Gemmellaro Collection, MGUP.021.2-  
1210 110), showing two flanges and a twisted body along the umbo-apertural axis; from the  
1211 Cenomanian of Piemonte (Italy) (courtesy of Tony Costagliola). **D**, Holotype of  
1212 *Ichthyosarcolites polycarinatus* Slišković, 1966 (MB.3482), showing seven elongated  
1213 flanges and small capillary canals; from the upper Cenomanian of the Dinaric Alps  
1214 (courtesy of Alceo Tarlao). **E**, Holotype of *Ichthyosarcolites alatus* (Filkorn, 2002)  
1215 (UNAM.6979), showing five flanges and a presumed juvenile attached to its ventral  
1216 side (left valve); the myocardinal apparatus and its associated cavities are visible; from  
1217 the lower Cenomanian of Guerrero (Mexico) (courtesy of Javier Aguilar-Pérez). **F**,  
1218 Lectotype of *Ichthyosarcolites doublieri* d'Orbigny, 1847 (MNHN.F.R07971), lacking

1219 tabulae; internal mould showing the highly developed right valve and the short, left  
1220 valve; from the upper Cenomanian of Martigues (Bouches-du-Rhône, France).

1221 **Fig. 4.** Shell internal features of *Ichthyosarcolithes*. All scale bars equal 10 mm. **A**, *I.*  
1222 *rotundus* without any flange (AMU.ICH1) from La Bédoule (Provence, France), with  
1223 posterior accessory cavity (PAC; arrowed). **B**, Picture of *I. bicarinatus* from Chiki-  
1224 Aouimeur (2010; Aqaba, Jordan), with flanges and myophores (arrowed). **C**, Thin-  
1225 sliced right valve of *I. triangularis* with three flanges, two sockets and posterior  
1226 myophoral cavity (AMU.HBES 85-a). **D**, Specimen of *I. bicarinatus* from Cañón de la  
1227 Servilleta (Tamaulipas, Mexico), showing four flanges and thin tabulae (courtesy of  
1228 Javier Aguilar-Pérez). **E**, Mexican right valve with four flanges of *I. bicarinatus* (from  
1229 Filkorn, 2002); the myocardinal apparatus of the left valve is visible in connection  
1230 (UNAM.6970) (courtesy of Javier Aguilar-Pérez). **F**, Thin-sliced specimen of *I.*  
1231 *coraloidea* (GMUS.Mp1), showing general cavity filled of canals, a thick shell and  
1232 three cavities invaded by capillary canals (courtesy of Brian Pratt).

1233 **Fig. 5.** Photographs of shells of *Ichthyosarcolithes* illustrating tabulae and coiling  
1234 patterns. All scale bars equal 10 mm. **A**, Longitudinal thin slice of *I. triangularis* from  
1235 Île d'Oléron, showing thick tabulae (arrow) in the general cavity and sockets. **B**,  
1236 Internal moulds of *I. triangularis* from Île d'Oléron (Charentes, France), showing  
1237 partial or complete dissolution of thin tabulae (arrow) in the general cavity and sockets.  
1238 **C**, Specimen of *I. triangularis* from Île d'Oléron with intersecting tabulae. **D**, Crushed  
1239 internal mould of *I. triangularis* from Île Madame, showing tabulae and one socket  
1240 (d'Orbigny Collection, MNHN.6517-B). **E**, Near-complete coiled right valve (internal



1241 mould) from Provence (France). **F**, Specimen of *I. triangularis* from Île d'Oléron with  
1242 uncoiled internal mould.

1243 **Fig. 6. A**, Method for measurement of angular positions of flanges on rudist shells. A  
1244 circle approximates the general cavity; white circles correspond to the projection of the  
1245 flange stem on the circle. Angles are measured clockwise with 0° corresponds to the  
1246 presumed position of the central tooth or central tooth socket. Scale bar equals 10 mm.  
1247 Specimen UNAM.6978 (courtesy of Javier Aguilar-Pérez). **B**, Flange angle  
1248 measurement plot in degrees. **C**, Hierarchical classification of flange positions. The two  
1249 main clusters represent the dichotomy between *I. monocarinatus* ventral flanges and *I.*  
1250 *triangularis* dorsal flanges. Each point corresponds to the angular position of a flange,  
1251 and the colours correspond to the number of flanges of an individual.

1252 **Fig. 7.** Discriminant analysis plot of 23 general cavities of shell landmarks of  
1253 *Ichthyosarcolites*. Four clusters are based on the number of flanges: *I. rotundus* (no  
1254 flange), *I. monocarinatus* (one ventral flange), *I. triangularis* (one dorsal flange) and *I.*  
1255 *bicarinatus*. Analysed data are presented as Supplemental Online Material.

1256 **Fig. 8.** Palaeogeographical map showing the localities of Cenomanian-aged species of  
1257 *Ichthyosarcolites*. Yellow dots: *I. rotundus*; green dots: *I. triangularis*; brown dots: *I.*  
1258 *monocarinatus*; red dots: *I. bicarinatus*; black dots: *Ichthyosarcolites* occurrences for  
1259 which species-level identification could not be verified; blue star: *Oryxia sulcata* nov.  
1260 gen. et sp. The palaeogeographical map was generated using the ODSN Plate Tectonic  
1261 Reconstruction Service (DeConto et al., 1999;  
1262 <http://www.odsn.de/odsn/services/paleomap/paleomap.html>).

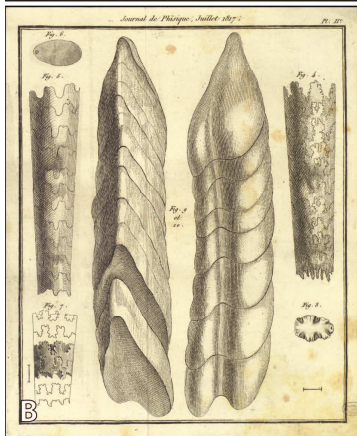
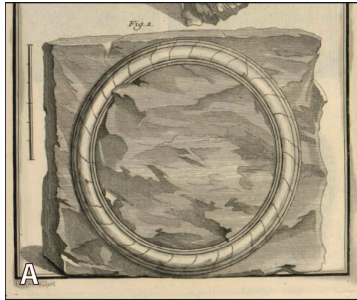
1263 **Fig. 9.** Holotype of *Oryxia sulcata* nov. gen. et sp. (right valve; BJ.1901-HR2) sliced in  
1264 three samples. **A**, Transverse view of a thin slice (right sample in C). **B**, Interpretative  
1265 scheme of A with the main morpho-anatomical features and homologues. AM: anterior  
1266 myophore; PM: posterior myophore; ATS: anterior tooth socket; PTS: posterior tooth  
1267 socket; CT: central tooth; D: general cavity of the right valve; AAC: anterior accessory  
1268 cavity; LG: ligament groove; LB: ligament bulge. **C**, Dorsal view of three samples of  
1269 the right valve. **D**, Transverse view of paratype BJ.1914-HR2. All pictures courtesy of  
1270 Bogdan Jurkovšek.

1271 **SOM**

1272 *SOM 1*

1273 Shell references and Landmark co-ordinates of the general cavity of 23 shells of  
1274 *Ichthyosarcolites* using PhyloNimbus.

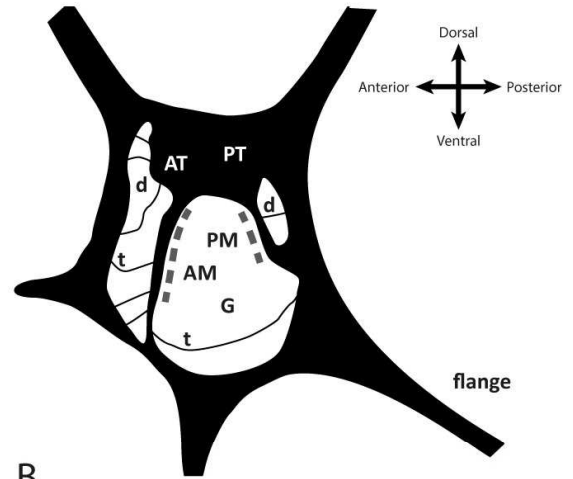
Nominal species	Flanges	Flange shape in cross section	General cavity shape	Pillal cavity	T-tubule	Shell shape	Ligament	Localisation
<i>Ichthyosarcoptes elongatorius</i> Desmarest, 1812	1 (ventral)	Short and triangular	Triangular to ovoid	Capillary and palisading	Sub-plane to oblique	Cosid to uncoiled	No	Afghanistan, Bosnia and Herzegovina, Egypt, France, Greece, Libya, Spain, Tunisia, Turkey
<i>Ichthyosarcoptes obliquus</i> Dechayres, 1825	Unknown	Unknown	Unknown	Unknown	Very oblique (<45° from commissure)	Unknown	Unknown	France
<i>Ichthyosarcoptes doublieri</i> Origny, 1847a	Unknown	Unknown	Circular	Unknown	No	Coiled	Unknown	France, Portugal
<i>Ichthyosarcoptes quadrangulus</i> Tonnay, 1854	Unknown	Unknown	Quadrangular	Capillary and palisading	"regular, abruptly bent downwards"	Locally coiled	Unknown	USA
<i>Ichthyosarcoptes borcisti</i> Tonnay, 1854	Unknown	Unknown	Ovoid	Capillary and palisading	Unknown	Unknown	Unknown	USA
<i>Ichthyosarcoptes carinatus</i> Tonnay, 1854	Unknown	Unknown	Unknown	Capillary and palisading	"abruptly bent downwards, and towards the concave side"	Coiled	Unknown	USA
<i>Ichthyosarcoptes corvobolus</i> Hill and Meek, 1855	Unknown	Unknown	Ovoid	Capillary and palisading	Sub-plane to oblique	Unknown	Unknown	USA, Canada
<i>Ichthyosarcoptes bicarinatus</i> Gemmelaro, 1855	2	Long and narrow	Circular to sub-quadrangular	Capillary and palisadic or large ovoid	Unknown	Uncoiled	No	Algeria, Bosnia and Herzegovina, Croatia, France, Greece, Italy, Libya, Slovenia, Turkey
<i>Ichthyosarcoptes marginatus</i> Poča, 1887	Unknown	Unknown	Unknown	Capillary and palisading	Unknown	Locally coiled	No	Czech republic
<i>Ichthyosarcoptes ensis</i> Poča, 1887	1	Short and triangular	Unknown	Capillary and palisading	Unknown	Unknown	Unknown	Czech republic, Italy
<i>Ichthyosarcoptes rotundus</i> Parona, 1921	3	Long and narrow to short and triangular	Circular to polygonal	Capillary and palisading	Unknown	Locally coiled	No	Afghanistan, Libya, Bosnia and Herzegovina, Croatia, Greece, Italy, Slovenia, Spain, Turkey
<i>Ichthyosarcoptes poljakii</i> Poljak, 1964	3	Long and narrow to short and triangular	Circular to ovoid	Capillary and palisading	Unknown	Unknown	No	Bosnia and Herzegovina, Croatia, Greece, Italy, Slovenia, Turkey
<i>Ichthyosarcoptes rogi</i> Plešičar, 1965	3	Long and narrow	Triangular	Capillary and palisading	Unknown	Unknown	No	Slovenia
<i>Ichthyosarcoptes manicomistis</i> Šiškočič, 1966	1 (dorsal)	Short and triangular	Ovoid	Capillary and palisading	Unknown	Unknown	No	Bosnia and Herzegovina, Croatia, Italy, Slovenia, Spain, Turkey
<i>Ichthyosarcoptes polycarinatus</i> Šiškočič, 1966	7	Long, narrow and elongated	Circular	Capillary and palisading	Unknown	Unknown	No	Bosnia and Herzegovina
<i>Ichthyosarcoptes rotundus</i> Poljak, 1967	0	Non applicable	Circular	Capillary and palisading	Unknown	Unknown	No	Croatia
<i>Ichthyosarcoptes salungensis</i> Bobkov, 1968	1 (ventral)	Short and triangular	Ovoid	Unknown	Sub-plane	Unknown	No	Russia
<i>Ichthyosarcoptes quadratus</i> Plešičar and Dozet, 1994	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	?
<i>Ichthyosarcoptes albus</i> Filimon, 2002	3 to 5	Long and narrow to short and triangular	Circular to polygonal, irregular	Capillary and palisading	Unknown	Unknown	No	Mexico
<i>Oryzia subcava</i> n. sp.	3	Short and triangular in section	Circular to ovoid	Capillary and palisading	Unknown	Unknown	Yes	Slovenia



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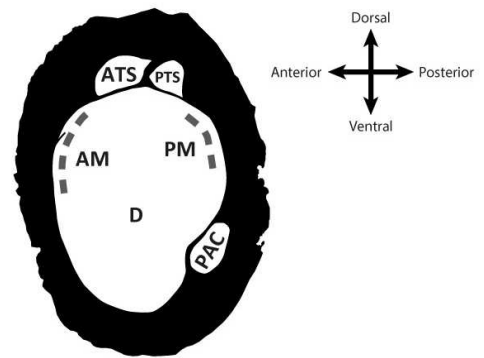
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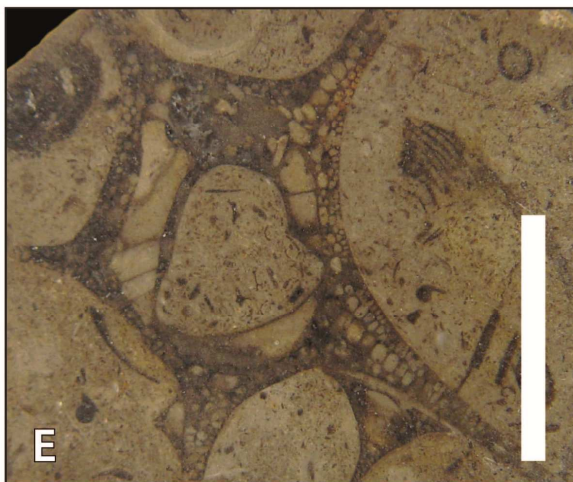
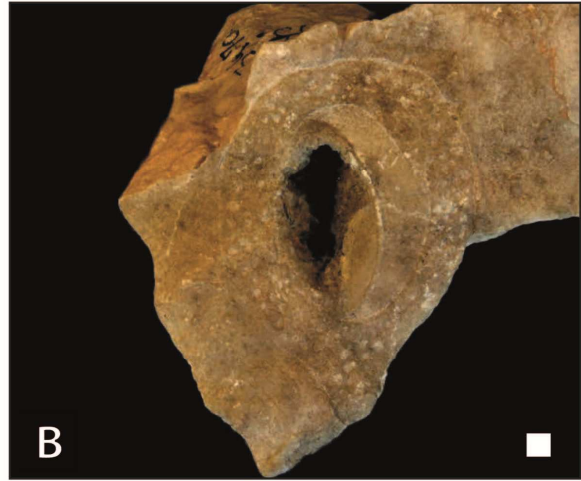
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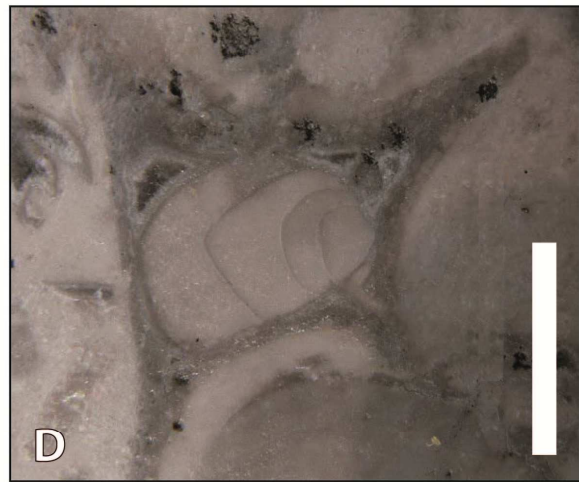


C



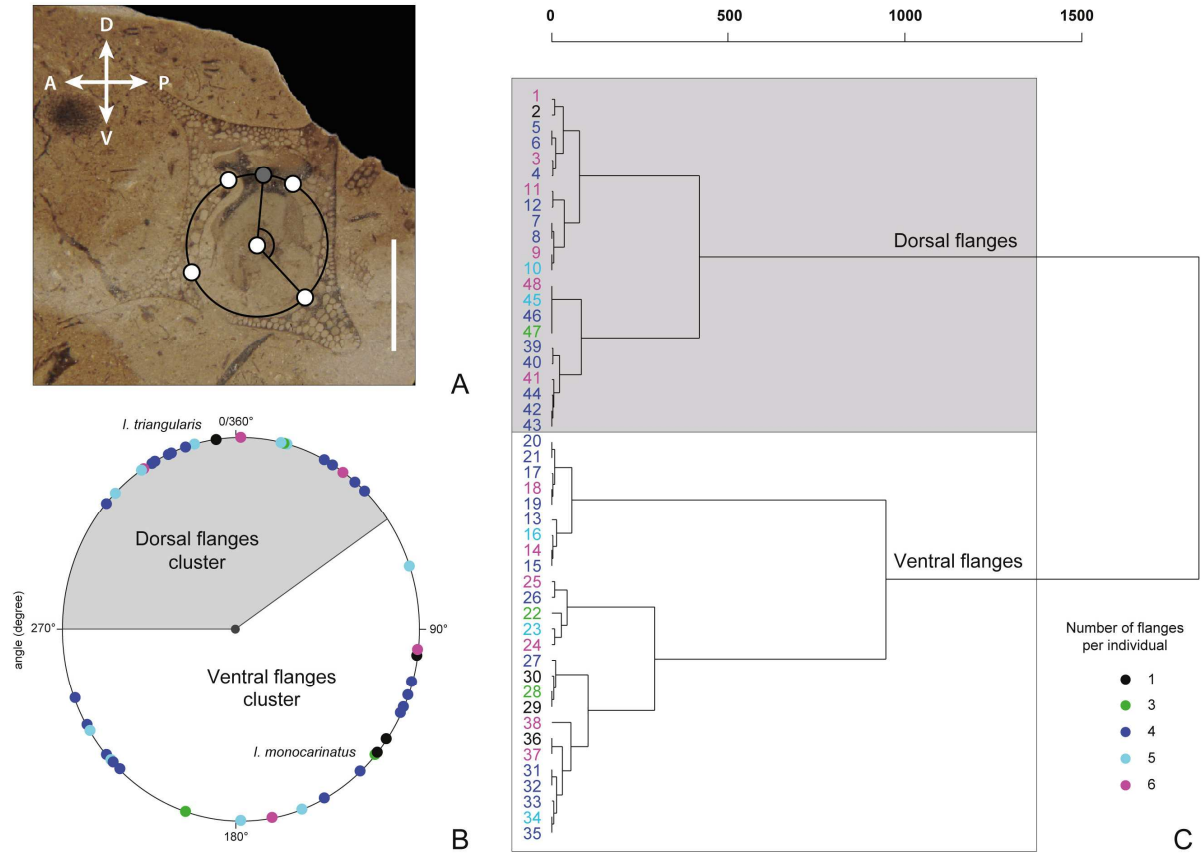
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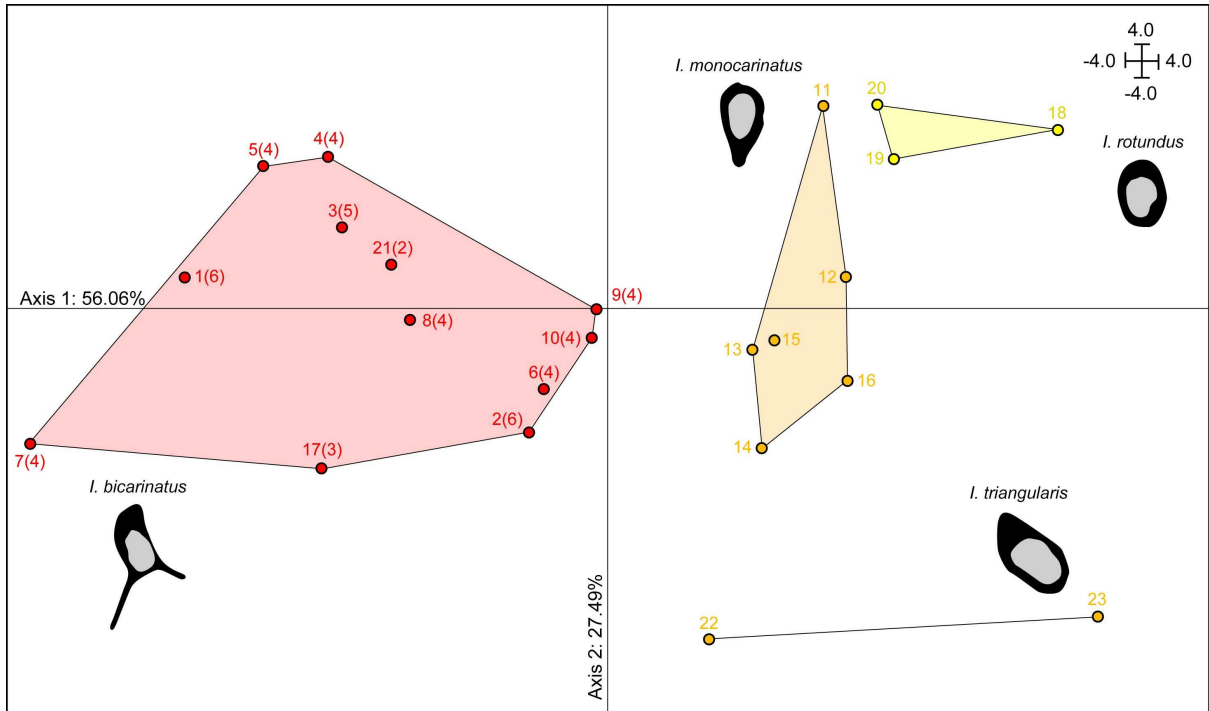


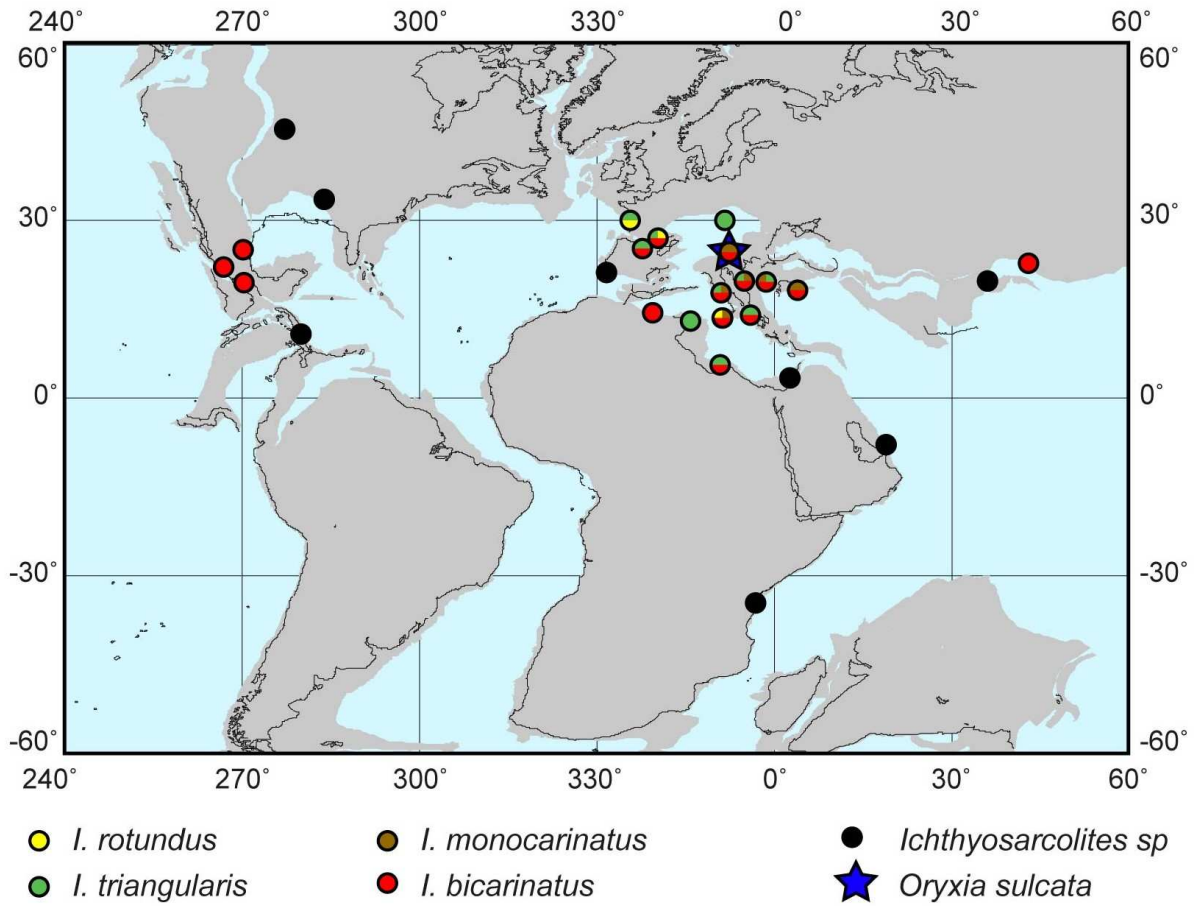


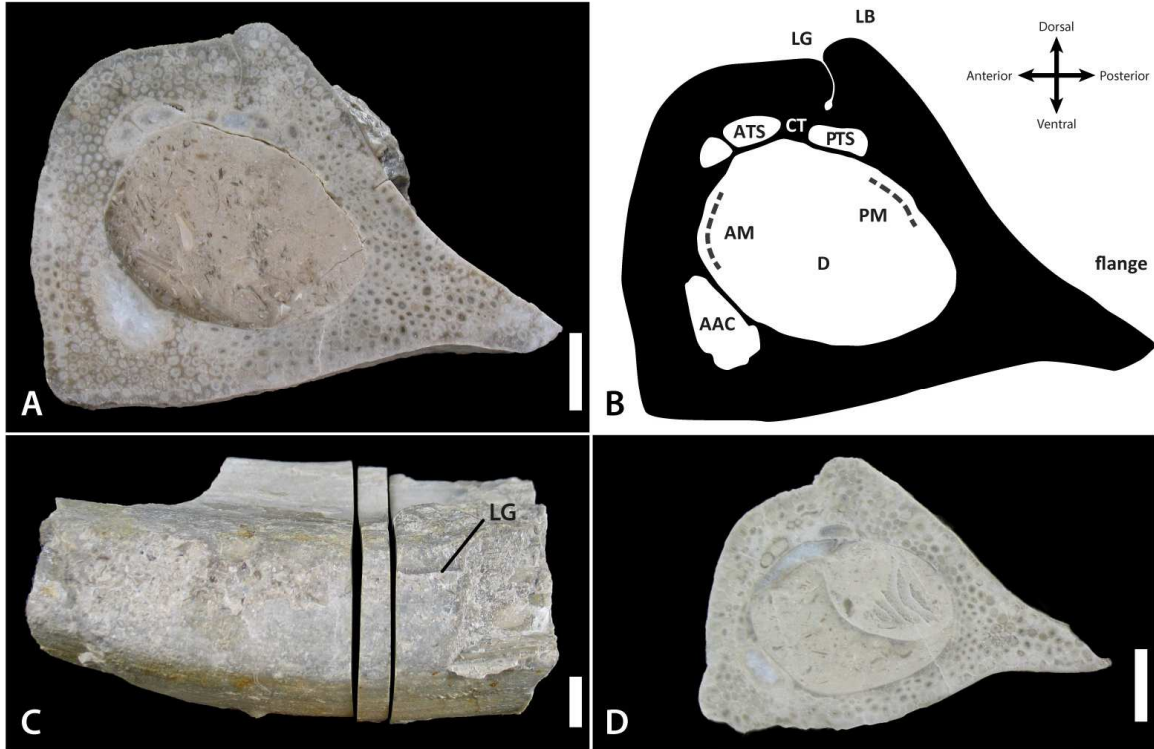












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A revision of the genus *Ichthyosarcolites* is proposed, based on morphological analyses

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

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