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Eocene crinoids (Echinodermata) from Cava Boschetto near Chiampo (Veneto, north-eastern Italy)

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ABSTRACT - A Lutetian (middle Eocene) crinoid assemblage from the Cava Boschetto outcrop, near the town of Chiampo (Veneto, north-eastern Italy) comprises cups of *Conocrinus veronensis, Lessinicrinus suessi, Pseudoconocrinus elongatus*, as well as columnals of *Isocrinus archiaci.* In addition, cups of three new genera (*Chiampocrinus* n. gen., *Fabianicrinus* n. gen. and *Lessinicrinus* n. gen.) are described, and an update of the systematics of conocrinids is proposed, resulting in the introduction of one new superfamily (Conocrinoidea) and three new families (Conocrinidae n. fam., Chiampocrinidae n. fam. and Paraconocrinidae n. fam.) and a redefinition of the genus *Conocrinus.* The present assemblage differs from other Eocene faunas in Italy, especially in the presence of a greater number of species. Moreover, a comparison with important Eocene assemblages from the Pyrenees (France, Spain) shows significant differences in composition, because in the Pyrenees area the assemblages consist of a larger number of isocrinids and a smaller number of conocrinids.

Keywords: Lutetian; Bourgueticrinina; Conocrinoidea; Isocrinida; Lessini Mountains; Italy; new taxa.

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1. INTRODUCTION

An Eocene crinoid assemblage from the collections of the Museum of Geology and Palaeontology of the University of Padua (MGP-PD) has been studied. This material, comprising several cups, numerous columnals, a few brachials and rare attachment discs, was collected at a limestone quarry (Cava Boschetto) in the eastern Lessini Mountains, not far from the town of Chiampo (municipality of Vicenza) along the valley of the river Chiampo (Veneto, north-eastern Italy; Fig. 1). Part of this material (holopodids) has recently been published by Manni and Pacioni (2021).

In general, dissociated crinoid ossicles are relatively common in Cenozoic strata across northern Italy. In particular, deposits in the Turin hills (Piedmont, north-western Italy) and the Berici Mountains (Veneto, north-eastern Italy) have yielded skeletal material of conocrinids (columnals and cups), bourgueticrinids (columnals), isocrinids (columnals), as well as cups and centrodorsals of comatulids. These crinoids were first discovered and studied in the 19th and first half of the 20th century by several researchers, among whom were Michelotti (1847, 1861), Meneghini (1876), Schlüter (1878), Di Rovasenda (1892), Noelli (1900), Oppenheim (1902), Sacco (1905), Fabiani (1908, 1915), Pasotti (1929) and Albus (1930). During the last two decades, new studies of Paleogene crinoids from the Veneto region have been carried out by Manni (2005), Merle and Roux (2018), Roux and Giusberti (in Frisone et al., 2020) and Manni and Pacioni (2021).

2. GEOLOGICAL SETTING

Cava Boschetto is a quarry near Chiampo, on the right side of the valley of the river Chiampo (Fig. 1) in the eastern Lessini Mountains. This locality has already been referred to in the palaeontological literature, with records of several genera and species of crabs (Beschin et al.,1994) and holopodid crinoids (Manni and Pacioni, 2021).

The Lessini Mountains belong to the Southern Alps. During the Paleocene, this area was divided into two basins: an eastern and a western basin. The area of the present-day Lessini Mountains, located in the western basin, was largely characterized by wide-spread deposition of shallow-water carbonates and intense volcanic activity (Bassi et al., 2008; Nebelsick et al., 2005). A carbonate platform, the Lessini Shelf developed; this

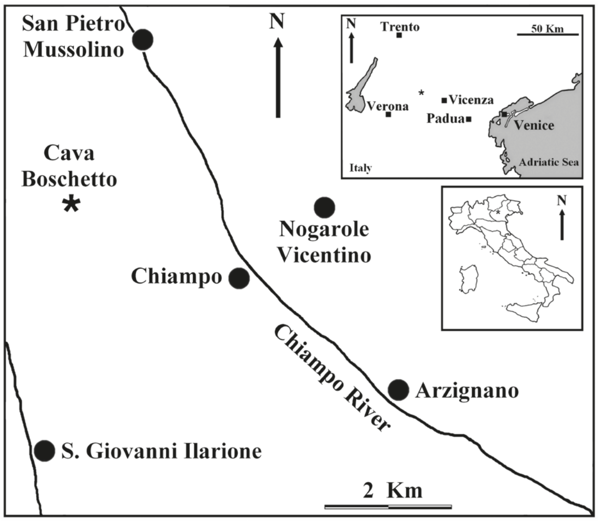

Fig. 1 - Simplified map of the study area, showing the location of the Cava Boschetto quarry (asterisk) and the valley of the river Chiampo (from Manni and Pacioni, 2021). The inset maps show Italy and the Veneto area (dot) in the north-east of the country.

was delimited in the north by land and was in existence from the Paleocene to Oligocene (Papazzoni et al., 2014a, b). The crinoid specimens described herein were recovered from a layer of ruditic tuffites of the "Calcari Nummulitici" Formation. The age of this crinoid fauna is Lutetian (Eocene) based on the presence of key index taxa of the *Nannotetrina fulgens-Sphenolithus radians* nannoplankton Zone (Beccaro et al., 2001). The layer that yields crinoid remains appears to have formed in the distal part of a high-energy carbonate ramp. For a detailed discussion of the stratigraphical sequence at the Cava Boschetto quarry, see Beccaro et al. (2001) and Manni and Pacioni (2021).

3. EOCENE CRINOID FAUNAS FROM VENETO

Paleogene crinoids from Veneto were studied mostly during the 19th and early 20th centuries. Among the most important works are those by Meneghini (1876), Schlüter (1878), Oppenheim (1902) and Fabiani (1908, 1915).

Meneghini (1876) described, but failed to illustrate, several ossicles of isocrinids and bourgueticrinids from some localities in Veneto, such as Mossano, Monte Spilecco, Monte Berici, and Possagno, and he introduced the following new species (in original nomenclature): *Pentacrinus guiscardii, P. pellegrinii*, *Conocrinus seguenzai* and *Rhizocrinus*? *santagatai*. In addition, he recorded *Pentacrinus didactylus* d'Orbigny, 1850, *Conocrinus pyriformis* (von Münster, in Goldfuss 1826-1833), *C. thorenti* (d'Archiac, 1846), *Bourgueticrinus*? *cornutus* (Schafhäutl, 1854) and *B.*? *didymus* von Schauroth, 1855. Two years later, Schlüter (1878) studied a crinoid fauna from Eocene rocks at Monte Spilecco, describing two new species, *Antedon italicus* and *Cyathidium spileccense*, as well as ossicles of *Conocrinus thorenti*, *C.* cf. *pyriformis, Pentacrinus* sp.? and *Rhizocrinus biforatus* (von Schlotheim, 1822).

When reviewing echinoderms from Veneto, Oppenheim (1902) described and illustrated *Conocrinus suessi* Munier-Chalmas, in Hébert and Munier-Chalmas, 1877, and mentioned and/or described, without illustrating these, the following crinoid species: *Conocrinus didymus*, *C. pyriformis*, *Tormocrinus veronensis*, *Holopus spileccensis* [*sic*], *Antedon italicus, Pentacrinus diaboli* Bayan, 1870, *P. guiscardii* and *P. pellegrinii*.

Fabiani (1908, 1915) studied the stratigraphy of Cenozoic strata in Veneto and recorded several species of crinoid from Eocene levels, in particular, *Conocrinus suessi*, *Holopus spileccense*, *Antedon italicus* and *Pentacrinus diaboli* from Spileccian (= Ypresian) strata; *Conocrinus didymus*, *Pentacrinus diaboli*, *P. guiscardii* and *P. pellegrinii* from Lutetian levels; *Pentacrinus diaboli* and *P. subbasaltiformis* Miller, 1821 from Auversian (=Bartonian) rocks and *Conocrinus pyriformis*, *C. didymus* and *Pentacrinus didactylus* from Priabonian levels. Fabiani (1915) pointed out that crinoid fragments were more frequent in lower and upper Eocene levels, but only two genera predominated: *Conocrinus* and *Pentacrinus*. In addition, *Holopus* and *Antedon* were also found, but both comprised only a single species. The latter author also believed crinoid-bearing strata had been deposited in the deepest neritic zone.

Having studied crinoids in an old collection (Michelotti Collection), Manni (2005) described specimens of *Conocrinus* and *Holopus* from the Veneto region, while Merle and Roux (2018) added a new genus, *Eocenocrinus*, and data on columnals of *Eocenocrinus bayani* Merle and Roux, 2018 and *Eocenocrinus didymus*, from Lutetian and Priabonian levels, respectively, at different localities in the Lessini Mountains.

Roux and Giusberti (in Frisone et al., 2020) mentioned some ossicles of Eocene cyrtocrinids, rhizocrinids, and isocrinids from the Cengio dell'Orbo quarry, near the town of Chiampo. Finally, Manni and Pacioni (2021) described cups and brachials of Eocene holopodid genera (*Holopus* and *Cyathidium*) from Cava Boschetto in the Lessini Mountains.

In summary, Eocene crinoids from the Veneto region belong to four different types: isocrinids, bourgueticrinids, comatulids, and holopodids, the first being the commonest. The rarest taxon is *Holopus spileccense*, which appears to represent an endemic species, with records exclusively from Eocene levels (Manni and Pacioni, 2021).

4. SYSTEMATIC PALEONTOLOGY

The adjustments in the systematics of conocrinids recently proposed by Roux et al. (2019) have been widely adopted in the present paper, although some adaptations are suggested here to differentiate better between the various types of conocrinids. These adaptations basically involve the main characters of the cup, such as the type of radial facets, the depth, and width of the ventral cavity, the size of the basals compared to radials, as well as the presence or absence of interradial processes. Columnal types are not considered here, because it is difficult to assign these to any cup-based genus or species and are therefore considered not to be a reliable character in the distinction of taxa. One new superfamily and three new families are erected, namely Conocrinoidea n. superfam., Chiampocrinidae n. fam., Conocrinidae n. fam. and Paraconocrinidae n. fam.

The material described in the present paper is housed in the collections of the Museum of Geology and Palaeontology of the University of Padua (MGP-PD) (A. Lovato Collection).

Class Crinoidea Miller, 1821
Subclass Articulata von Zittel, 1879
Order Comatulida A.H. Clark, 1908
Suborder Bourgueticrinina Sieverts-Doreck, in Ubaghs, 1953
Superfamily Conocrinoidea nov.

Etymology: From the genus *Conocrinus* d'Orbigny, 1850.
Diagnosis: Small bourgueticrinids with cups characterized by five radial and five basal plates. Radial facets are small to moderately wide, separated from each other by interradial projections. Sutures between plates are not very evident.
Families included: Chiampocrinidae n. fam., Conocrinidae n. fam. and Paraconocrinidae n. fam.
Remarks: In this new superfamily are placed all conocrinid crinoids with interradial projections, the presence of which easily differentiates conocrinids from rhizocrinids. In addition, their presence means that conocrinids have smaller, proximally non-contacting arms. In contrast, rhizocrinids, which have interradial ridges, and larger radial facets, but lack processes, on average have wider arms that are in contact proximally.

Family Chiampocrinidae nov.

Etymology: From the genus *Chiampocrinus* nov. (see below).
Diagnosis: Small conocrinids with low basals and taller radials. Radial facets are very narrow and oblong, separated by low and narrow interradial projections. The ventral cavity is very wide and relatively deep. The dorsal side of the cup is entirely occupied by the articular surface of the stem. Brachial and columnals are unknown.
Remarks: The main distinguishing characters of this family are the oblong and very narrow radial facets, the small and low interradial projections, the poorly visible sutures between basals and radials, the latter being taller than the former, and the very wide and deep ventral cavity.
Discussion: See below.
Genera included: Only *Chiampocrinus* n. gen.

Chiampocrinus gen. nov.

Etymology: From Chiampo Valley, the most important geographical structure near the Cava Boschetto quarry (Fig. 1).
Type species: Chiampocrinus lobatus n. gen., n. sp.
Diagnosis: Small, semi-conical cups with basal and radial circlets. Basals are sturdy and low; radials are tall, thin on top, and sturdy below; sutures between basals and radials are not always well evident. Ventral cavity is quite large and deep. Radial facets are quite narrow and oblong, occupying the entire upper surface of each radial. Interradial projections are low and narrow. The lower side of the cup is small, circular, and entirely occupied by an articular surface for the stem.
Remarks: The main distinguishing features of this new genus are the robust basals, thin radials (in the upper part), the narrow and oblong radial facets, a quite large ventral cavity, and the bottom of the ventral cavity deep within the radial circlet.
Discussion: At first sight, cups of *Chiampocrinus* n. gen. are closely similar to those of *Dadocrinus* von Meyer, 1847, *Neodadocrinus* Manni and Nicosia, 1990, *Sacariacrinus* Nicosia, 1991, *Plicatocrinus* von Münster, 1839 and *Bathycrinus* Thomson, 1872. In fact, cups of all these genera are small and have thin radial plates. However, those of *Chiampocrinus* n. gen. differ from cups of *Dadocrinus* and *Neodadocrinus* mainly because of their robust basals. Furthermore, cups of *Chiampocrinus* n. gen. can be distinguished from those of *Dadocrinus* because they lack infrabasals; from those of *Neodadocrinus* and *Sacariacrinus* mainly because of their narrower radial facets; from those of *Plicatocrinus* on account of smaller interradial projections and of the ventral morphology of the radials. Finally, *Chiampocrinus* n. gen. differs from *Bathycrinus* in having narrower radial facets and a larger and deeper ventral cavity. Moreover, this new genus can be differentiated from the others in having the bottom of the ventral cavity within the lower part of the radial circle.

It has been quite difficult to determine the systematic position of *Chiampocrinus* n. gen. As far as the order is concerned, the type of radial facets (similar to those of cotyledermatids) and the size and depth of the ventral cavity, might have been allied with the Cyrtocrinida. However, there are no columnals of cyrtocrinid type in the present fauna. In view of its large ventral cavity, *Chiampocrinus* n. gen. might also have been placed in the Millericrinida, but the radial facets are utterly different. The new genus cannot be assigned to the family Bourgueticrinidae de Loriol, 1882 either, because the radial facets are very much narrower, and the ventral cavity is too wide and deep. In addition, *Chiampocrinus* n. gen. differs from genera belonging to the families Hyocrinidae Carpenter, 1884 and Bathycrinidae Bather, 1899 in having a very deep ventral cavity and much narrower and oblong radial facets.

Cups of the present new genus (and family) differ from those of the Conocrinidae n. fam., Paraconocrinidae

n. fam. and Rhizocrinidae in having narrower radial facets and a deeper, wide ventral cavity. Taken together, these characters are not shared with any other Cenozoic crinoid, so that the erection of a new genus and family are warranted.

Stratigraphical and geographical distribution: Lutetian (Eocene) of north-eastern Italy.

Species included: Chiampocrinus lobatus n. gen., n. sp. and *C. conicus* n. gen., n. sp.

Chiampocrinus lobatus n. gen., n. sp. Figs. 2, 9A

Etymology: From Latin *lobatus*, meaning lobed, in reference to the swollen basals.

Type material: Holotype is MPG-PD 32439; 47 additional cups (MPG-PD 32440-32446), plus MPG-PD 32447 (collected by S. Manfrin) are paratypes.

Type locality: Cava Boschetto, near Chiampo (municipality of Vicenza, Veneto, north-eastern Italy).

Type level: Lutetian (Eocene).

Diagnosis: Small, semi-conical cups with basal and radial circlets. Basals are sturdy and low; radials are tall, thin the top, and sturdy below; sutures between basals and radials are not always well evident. The ventral cavity is quite large and deep, its floor being in the lower part of the radial circlet. Radial facets are quite narrow and oblong, occupying the entire upper surface of each radial. Interradial projections are low and narrow. The lower side of the cup is circular and small and entirely occupied by an articular surface for the stem.

Description: Cups, with a subcircular to the pentagonal cross-section, are characterized by an inverted subconical shape and relatively small size, consisting of a circlet of swollen basals that is distinct from that of the radials which are flared at the top. The five basals are quite lobed and swollen, while the five radials are only slightly convex and significantly taller than the basals. The outer surface is smooth, with rather poorly expressed sutures, whole interradial projections are tiny and low.

Each basal is subpentagonal, very sturdy, yet low, the boundary between two adjacent basals being slightly depressed. The outer contour of the basal circlet is markedly pentalobate. Each radial is tall and thin, yet sturdy at the base and characterized by an inverted pentagonal shape. The outer contour of the radial circlet is subcircular, but occasionally five-lobed.

The radial facets occupy the entire upper edge of the radials and are long, but quite narrow. The aboral surface is tilted outwards, while the adoral surface slants inwards. The ligament area, with a subtriangular shape, is small and oblong, with a deep ligament pit. The axial canal lies just behind the fulcral ridge, close to the ventral cavity. Two muscle fossae, separated by a radial groove, are in the upper part of the ventral cavity; they are subvertical, narrow, and moderately deep. The interarticular ligament fossae are not identifiable.

The ventral cavity is conical, very wide, and deep. The walls are smooth; sutures between the radials cannot be seen. Five very narrow radial grooves and five narrow interradial ridges can be made out. Each radial groove is the continuation, within the ventral cavity, of the groove that separates the two muscle fossae of each radial facet. In contrast, each ridge is the continuation of each projection within the cavity. Both structures almost reach the center of the ventral cavity. At that center, a tiny dome-shaped bulge is occasionally visible.

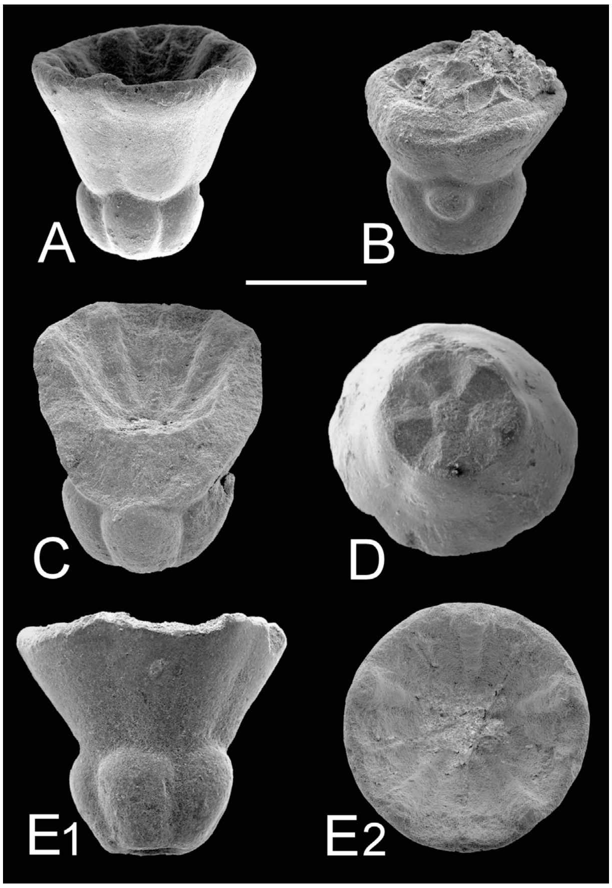

Fig. 2 - Isolated cups and radial circlets of *Chiampocrinus lobatus* n. gen., n. sp. A) MPG-PD 32442 (paratype), oblique view. B) MPG-PD 32443 (paratype), oblique view, with a small basal (pathological?). C) MPG-PD 32440 (paratype), oblique view, with the bottom of the ventral cavity clearly seen. D) MPG-PD 32441 (paratype), basal view of the dissociated radial circlet, with ventral 'bulge'. E1–E2) MPG-PD 32439 (holotype), in lateral and ventral views, respectively. The scale bar equals 1 mm.

The lower part of the cups, which are small and circular, is entirely occupied by a shallow cylindrical cavity. In this cavity, no articular elements supporting the stem are visible. In the center sits a relatively wide axial canal.

Remarks: Chiampocrinus lobatus n. gen., n. sp. is the commonest species at Cava Boschetto, being about six times more frequently than other species and accounting for about 50 percent of all crinoid cups recovered there. Only bourgueticrinid columnals are more common. Usually, specimens of this new species are quite well preserved, but some are highly abraded. Only the smallest elements of the radial facets are not clearly visible. For instance, the interarticular ligament fossae cannot be identified; they probably are very small and oblong and placed ventrally, behind the fulcral ridge. The basals are usually very swollen and well distinguished from the radials. One specimen (Fig. 2B) has a single, very small basal (probably pathological). Radial and basal circlets are probably not fused together, because the material includes also isolated radial circlets (Fig. 2D). Of interest is a central "bulge", a small structure placed between the basal and radial circlets whose function is unknown. This bulge, characterized by five tiny canals (Fig. 2D), is a complex structure; it might correspond to a small circlet of vestigial infrabasal plates.

Discussion: Chiampocrinus lobatus n. gen., n. sp. differs from *C. conicus* n. gen., n. sp. (see below) in having quite swollen basals and a basal circlet that is distinct from the radial one. Roux and Giusberti (in Frisone et al., 2020, p. 306) quoted but without showing "aboral cups with globulous basals and flared radials belong to yet undescribed" taxa, from the Cengio dell'Orbo quarry (Veneto, Italy), which appear to be like those of *Chiampocrinus lobatus* n. gen., n. sp.

Chiampocrinus conicus n. gen., n. sp. Figs. 3, 9B

Etymology: In reference to the conical cup shape.

Type material: Holotype is MPG-PD 32448; 15 additional cups (MPG-PD 32449–32451) are paratypes.

Type locality: Cava Boschetto, near Chiampo (municipality of Vicenza, Veneto, north-eastern Italy).

Type level: Lutetian (Eocene).

Diagnosis: Small, inverted conical cups with basal and radial plates. Basals are low and not lobed; radials are tall, thin at the top, and sturdy at the bottom. Sutures are not distinct, or only slightly so. The ventral cavity is large and deep. Radial facets are narrow and oblong, occupying the entire upper surface of each radial. Low and narrow interradial projections. The lower cup surface is circular and small, entirely occupied by a cavity for the articular surface of the stem.

Description: These cups, with a subcircular to the pentagonal cross-section, are characterized by an inverted and truncated conical shape, consisting of five basals and five radials and with a smooth outer surface. The sutures between the plates are only visible under favorable light. The basal circlet usually is not distinct from the radial one, having the same inclination. The interradial projections are small and low.

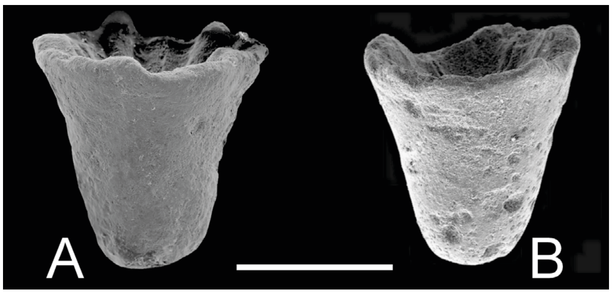

Fig. 3 - Cups of *Chiampocrinus conicus* n. gen., n. sp., in lateral view. A) MPG-PD 32448 (holotype). B) MPG-PD 32449 (paratype). The scale bar equals 1 mm.

Each basal plate is subpentagonal and very sturdy, yet low, the outer contour of the basal circlet being slightly pentalobate to circular. Each radial plate is pentagonal in shape, slightly taller than basal, and thin, yet sturdy, at the bottom. The outer contour of the radial circle is subcircular.

The radial facets occupy the entire upper edge of the radials and are long, but very narrow. The aboral surface is tilted outwards, while the adoral surface is slightly tilted inwards. The ligament area, which is subcrescentic, is also very small with a deep ligament pit. The axial canal is just behind the fulcral ridge. Two muscle fossae, separated by a radial groove, are placed centrally in the upper part of the ventral cavity; these are relatively small, sub-vertical, and not deep. The interarticular ligament pits are not visible.

The ventral cavity is conical, very large, and deep. The walls are smooth and sutures between the radial plates are not visible. Five narrow radial grooves and five narrow interradial ridges can be observed. Each of the other radial grooves is the continuation, within the ventral cavity, of the groove that separates the two muscle fossae of each radial facet. Each ridge is, on the other hand, the continuation of each projection within the cavity. Both structures almost reach the center of the ventral cavity, the bottom of which is the lower part of the radial circlet. The lower surface of the cups is very small and circular and entirely occupied by a shallow circular cavity. In this cavity, no articular elements supporting the stem are visible. In the center, a relatively wide axial canal is seen.

Remarks: Most specimens of this new species are quite well preserved, but some are slightly abraded. The main distinguishing feature of this new species is the basal circlet which is not distinct from the radial one because basals are not swollen.

Discussion: The external morphology of cups of the present species is similar to that of some individuals of *Monachocrinus* A.H. Clark, 1917, but the radial facets are much thinner and the ventral cavity is quite large and deeper in the former.

Specimens of *C. conicus* n. gen., n. sp. are close to *Cherbonniericrinus requiensis* Roux, Martinez, and Vizcaïno, 2021, especially in reference to their conical shape. However, unlike these, they have oblong, much narrower radial facets and low interradial projections.

Family Conocrinidae nov.

Etymology: From the genus *Conocrinus* d'Orbigny, 1850.

Diagnosis: Cups are small and characterized by five tall basals and five lower radials with interradial projections; sutures are not always visible. Proximal usually missing.

Radial facets are small, separated by well-developed interradial projections. The ventral cavity is large to small and shallow to deep. Columnals with different morphologies along the same stem; distal ones with synarthries, proximal ones with synostoses. Stem with radicular cirri for anchorage.

Remarks: The main characters of cups of this genus are the small radial facets between interradial projections, the sutures between plates that are only poorly visible, the tall basals and lower radials, and the presence of moderately tall interradial projections.

Discussion: Species belonging to this new family differ from those of all other families of Cenozoic crinoids in having much smaller radial facets and taller interradial projections. The presence of very small radial facets and well-developed interradial projections denotes that these crinoids had relatively thin arms that were clearly separated from each other proximally.

Genera included: Conocrinus and *Fabianicrinus* n. gen.

Genus ***Conocrinus*** d'Orbigny, 1850 herein emended

Type species: Bourgueticrinus thorenti d'Archiac, 1846.

Emended diagnosis: Crinoids with small to moderately large cups, characterized by tall basals and lower radials; the boundary between two adjacent plates is never depressed; sutures not always visible. Small radial facets between moderately tall interradial projections of subcircular cross-section. Interradial ribs are often visible. Moderately large to small ventral cavity. The lower side of the cup is narrow and entirely occupied by an articular surface supporting the stem.

Remarks: The main characters of the cups of this genus are the small radial facets that are placed between interradial projections, the sutures between the plates that are not clearly visible, the tall basals, and the presence of tall interradial projections with a subcircular cross-section.

Stratigraphical and geographical distribution: Eocene of Crimea, France, and Italy.

Species included: Conocrinus archiaci Roux, 1978a, *C. cahuzaci* Roux, Eléaume and Améziane, 2019, *C. thorenti* and *C. veronensis.*

Conocrinus veronensis (Jaekel, 1891), Figs. 4, 9C

1891 *Tormocrinus veronensis* Jaekel, p. 657, pl. 42, fig. 6.

1978 *Conocrinus thorenti* (d'Archiac) - Wienberg Rasmussen, p. T844, text-fig. 567/3A-3B.

1982 *Conocrinus* cf. *veronensis* Jaekel - Klikushin, p. 823, text-fig. 8B.

Material: Seven cups (MPG-PD 32468–32471).

Description: Large cups, characterized by long, thorn-shaped interradial projections. Cup shape varies from inverted conical to fusiform; contour varies from pentagonal to circular. Basals tall; radials much lower. Deformations in the contour of basals are also visible. Sutures are just visible in a favorable light; no ornamentation. Interradial projections are long and tilted outwards; subcircular in cross-section. The ventral cavity is conical, relatively large, and shallow. Radial facets, placed between interradial projections, are small and subcircular. Clearly visible articular elements are wide, crescentic ligament fossa with a deep ligament pit, axial canal, and two relatively large subcircular muscle fossae, separated by a radial groove. Interarticular ligament fossae are not clearly visible. The lower side of the cup is small and characterized by a very small circular cavity for the stem: no articular elements are visible, except for the axial canal.

Remarks: Conocrinus veronensis is the largest conocrinid species on record. All specimens studied here have long and stout interradial projections and almost all are abraded, explaining why some features, such as articular elements of radial facets, are not clearly identifiable. Interradial projections usually are abraded or broken (Fig. 4A, 4B); interradial ribs are not seen.

Discussion: In the crinoid literature, doubts have been expressed over the systematic assignment of crinoid cups of this type. Jaekel (1891) described cups that were characterized by "Zapfen" (= cone) as *Tormocrinus veronensis*; this was considered a valid species by Biese and Sieverts-Doreck (1939). However, Wienberg Rasmussen (1978) interpreted Jaekel's specimen as an "old specimen"

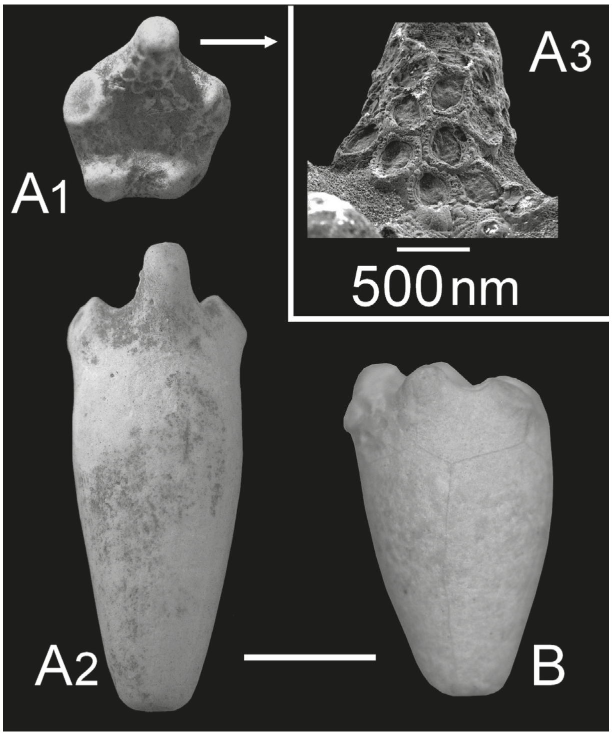

Fig. 4 - Cups of *Conocrinus veronensis* (Jaekel) with the broken interradial process. A1–A2) MPG-PD 32468, in ventral and lateral views, respectively. A3) colony of cribrimorph (cheilostome) bryozoans encrusting one interradial projection (MPG-PD 32468). B) MPG-PD 32469, in lateral view. The scale bar equals 1 mm.

of *C. thorenti*. Lately, Manni (2005) and Roux et al. (2019) considered *T. veronensis* to be a valid species but of the genus *Conocrinus*.

Conocrinus archiaci and *C. cahuzaci* both resemble *C. veronensis*; Roux (1978a, p. 266) pointed out that *C. archiaci* "présente de fortes affinités avec *C. veronensis*". Klikushin (1982), while describing a cup of *C.* cf. *veronensis* from Eocene strata in Crimea, remarked that *C. archiaci* and *C. veronensis* were almost similar. *Conocrinus archiaci* would seem to differ from *C. veronensis* especially in the presence of interradial ribs and from *Conocrinus cahuzaci* in the "abrupt enlargement of cup diameter at the level of basal/radial transition" (Roux et al., 2019, p. 77). The specimen that Klikushin (1982) recorded as *Conocrinus* cf. *C. veronensis* is here considered to belong to *C. veronensis.*

Stratigraphical and geographical distribution: Eocene of Crimea and Italy.

Genus ***Fabianicrinus*** nov.

Type species: Fabianicrinus fusus n. gen., n. sp.

Etymology: In honour of Ramiro Fabiani (1879-1954), who studied the geology and palaeontology of the territory of Vicenza.

Diagnosis: Small crinoids with cups consisting of five tall basals and five lower radials; basals much taller than radials, but sutures not visible or not clearly so. Radial facets occupy a small space between two interradial projections; projections are low, subtrapezoidal in cross-section, with a wide base and flat ventral side. The ventral cavity is moderately deep and relatively small. The lower side of the cup is small and entirely occupied by an articular surface supporting the stem.

Remarks: The main characters of cups of this new genus are the small radial facets placed between interradial projections, the poorly visible sutures between plates, the much taller basals, in comparison with radials and the low and wide interradial projections with subtriangular dorsal contour.

Discussion: This new genus is erected to aid in better differentiation of conocrinids. Thus, crinoids with squat and moderately tall interradial projections with a subcircular cross contour are assigned to *Conocrinus*, while those with lower and wide interradial projections with a subtrapezoidal cross contour are here placed in *Fabianicrinus* n. gen. The use of interradial projections for crinoid distinction is not new. Phyllocrinids (Cyrtocrinida of Mesozoic age), are divided into two genera on the basis of the size and shape of their interradial projections. *Phyllocrinus* d'Orbigny, 1850 and *Apsidocrinus* Jaekel, 1907 are, in fact, closely similar having the same type of radial facet, but interradial projections that differ in shape, height, and width. *Phyllocrinus* has low projections, *Apsidocrinus* taller and stout ones. *Fabianicrinus* n. gen. differs from *Paraconocrinus* Roux, Eléaume and Améziane, 2019 and *Pseudoconocrinus* Roux, Eléaume and Améziane, 2019, especially in the significantly smaller radial facets.

Stratigraphical and geographical distribution: Eocene of Crimea, France, and Italy.

Species included: Fabianicrinus cazioti (Valette, 1924), *F. duperrieri* (Roux, 1978a) and *F. vogdti* (Weber, 1949).

Fabianicrinus fusus n. gen., n. sp., Figs. 5, 9D1–D2

1929 *Conocrinus pyriformis* (von Münster) - Pasotti, p. 72, pl. 1, fig. 2.

Etymology: From Latin fusus, meaning spindle, in reference to cup shape.

Type material: Holotype is MPG-PD 32452; fourteen additional cups (MPG-PD 32453–32455) are paratypes.

Type locality: Cava Boschetto, near Chiampo (municipality of Vicenza, Veneto, north-eastern Italy).

Type level: Lutetian (Eocene).

Description: Cups, consisting of five tall basals and five lower radials of this species are small, fusiform, and with low interradial projections; the outer surface is smooth, and sutures between plates are visible only under favorable light. The upper edge of each radial plate is characterized by an articular radial facet and two interradial projections; facets are subcircular, very small, and placed between two interradial projections. In each facet, the aboral surface tilted outwards; the adoral surface slightly tilted inwards. The ligament fossa is crescentic and wide, with a deep ligament pit. Axial canal clearly visible behind fulcral ridge. Muscle fossae are small and suboval but clearly visible. The radial groove separates two muscle fossae of the same facet and descends into the ventral cavity.

Interradial projections are wide, low, moderately narrow, and slightly ventrally developed, trapezoidal in transverse section, with the dorsal side convex and ventral side slightly concave. The lower side is relatively wide. The ventral cavity is moderately wide, subconical to subcylindrical, and not very deep.

The lower part of the cups is circular and very small, entirely occupied by a shallow subcylindrical cavity where the articular surface supports the stem and central axial canal; no articular elements are seen.

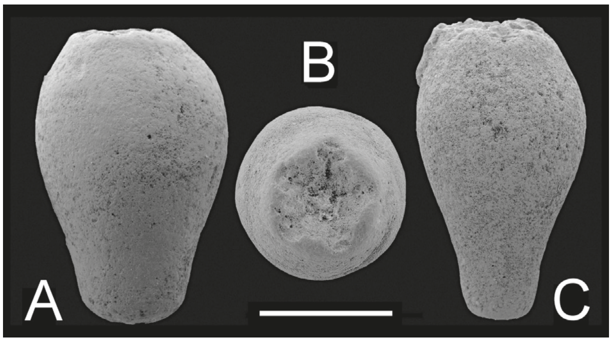

Fig. 5 - *Fabianicrinus fusus* n. gen., n. sp., cups. A) MPG-PD 32452 (holotype), in lateral view. B) MPG-PD 32454 (paratype), in ventral view. C) MPG-PD 32453 (paratype), in lateral view. Scale bar equals 1 mm.

Remarks: These specimens are quite well preserved, but elements of the radial facets are not clearly visible. The sutures between the plates are rarely perceptible; no interradial ribs. The ventral cavity is moderately wide and not very deep; but, as already pointed out by Pasotti (1929) for some *Conocrinus* of Eocene age, the smallest cups have a wider ventral cavity. The bottom of the ventral cavity is rarely visible because the cavity is either matrix filled or has adnate bryozoans or is partially eroded. In some specimens, the adoral side is not visible because of overgrowth by bryozoans.

MPG-PD 32453 probably possesses a proximale. In this particular cup, the basals are not very tall, and the proximale is slightly taller than the basals (Figs. 5C, 9D1); it is difficult to be certain whether or not this is a rare case or is typical of mature individuals. More material is needed to determine this.

Discussion: This new species is not rare; it differs from the other three species of the genus, especially in the presence of very small radial facets that are separated by large, yet low interradial projections. It can be distinguished from *Conocrinus veronensis* and *C. thorenti* in the wider and lower interradial projections; from *Lessinicrinus suessi* (see below) in the shape and size of the basals and in the smaller radial facets; from *Pseudoconocrinus elongatus* (see below) in the smaller radial facets and a different general morphology (mainly pyriform). Moreover, this new species also resembles *Fabianicrinus cazioti*, *F. duperrieri*, *F. vogdti*, *Paraconocrinus handiaensis* (Roux, 1978a), and *P. pyriformis* (von Münster, *in* Goldfuss 1826-1833). However, *Paraconocrinus handiaensis* and *P. pyriformis* have oblong radial facets and interradial projections with different morphology. Of the other species, *F. cazioti* has significantly taller interradial projections, while in *F. duperrieri* radial facets are placed more ventrally and there are interradial ribs, and *F. vogdti* has wider radial facets.

Specimens identified by Pasotti (1929) as *Conocrinus pyriformis* are here considered to belong to this new species, on the basis of their small radial facets that are separated by wide interradial projections.

Stratigraphical and geographical distribution: Eocene of Piedmont and Veneto (north-western and north-eastern Italy).

Family Paraconocrinidae nov.

Etymology: From the genus *Paraconocrinus* Roux, Eléaume and Améziane, 2019.

Diagnosis: Cups are characterized by tall basals and low radials; sutures between plates are not always visible. Radial facets are moderately wide and large, separated by low interradial projections. The ventral cavity is usually wide and moderately deep. The lower side of the cup is small and entirely occupied by a circular cavity for the stem.

Remarks: Crinoids belonging to this new family differ from chiampocrinids and conocrinids overall in the radial facets which are wider, and from those of rhizocrinids (Jaekel, 1894), especially in the presence of interradial projections.

Genera included: *Paraconocrinus* only.

Family Rhizocrinidae Jaekel, 1894 (emend. Roux et al., 2019)

Diagnosis: Crinoids with small cups characterized by high basals and low radials; sutures between these are not always visible. Wide, subhorizontal radial facets, separated by interradial ridges; no real interradial projections. The ventral cavity is usually small and not very deep; the cup base is small and entirely occupied by an articular surface for the stem.

Remarks: This family includes crinoids with wide and subhorizontal radial facets, and interradial ridges are present. The arms had to be robust because of the wide radial facets.

Composition: To date, this family includes seven genera [*Carstenicrinus* Roux, Eléaume and Améziane, 2019; *Cherbonniericrinus* Roux, Eléaume and Améziane, 2019; *Democrinus* Perrier, 1883; *Gastecrinus* Roux and Philippe, 2021 (sole specimen of this genus poorly preserved; not assignable here firmly); *Globulocrinus* Roux, Martinez, and Vizcaïno, 2021; *Pseudoconocrinus* and *Rhizocrinus* Sars, 1868], to which the new genus, *Lessinicrinus* n. gen., described below, is added.

Genus ***Lessinicrinus*** nov.

Etymology: From the Lessini Mountains of the Venetian Prealps (north-eastern Italy).

Type species: Conocrinus suessi de Loriol, 1879.

Diagnosis: Small crinoids with low cups, consisting of five basals and five radials, often of similar size. Sutures poorly visible, or not at all. Radial facets occupying the almost entire upper side of each radial, wide and mainly ventrally developed. Low interradial ridges separating radial facets. The ventral cavity is small and not deep. The lower part of cups, not too wide, is entirely occupied by an articular surface for the stem.

Remarks: The main characters of this new genus are low cups, basals almost of the same height as radials, sutures between them being poorly visible; wide radial facets, interradial ridges between radial facets, as well as a small ventral cavity.

These characters allow to differentiate this new genus easily from all other conocrinids. In fact, *Lessinicrinus* n. gen. differs from *Democrinus*, *Paraconocrinus,* and *Pseudoconocrinus* in that its basals and radials are almost of the same size. Some specimens described by Wienberg Rasmussen (1961) as *Monachocrinus*? *regnelli*, albeit with well-visible sutures, may belong to this new genus.

Crinoids assigned to this new genus, with wide radial facets separated by thin interradial ridges, must have had squat arms, with the proximal-most brachials probably in contact with each other.

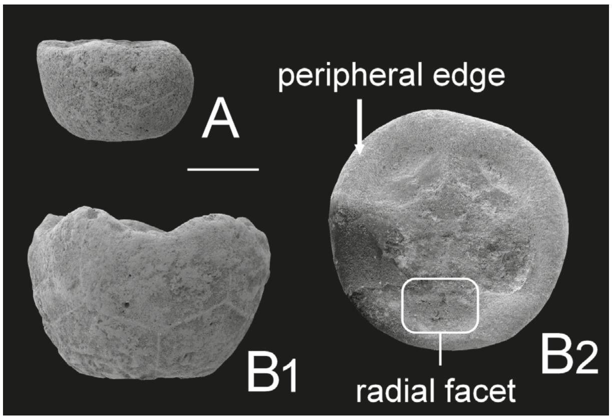

Fig. 6 - *Lessinicrinus suessi* (de Loriol), cups. A) MPG-PD 32457, in lateral view. B1-B2) MPG-PD 32456, in lateral and ventral views, respectively. The scale bar equals 1 mm.

Stratigraphical and geographical distribution: Eocene of France and northern Italy.

Species included: Conocrinus suessi and *Pseudoconocrinus lavadensis* Roux, Martinez and Vizcaïno, 2021.

Lessinicrinus suessi (de Loriol, 1879), Figs. 6, 9E

1879 *Conocrinus suessi* (Munier-Chalmas, 1877); de Loriol, p. 191, pl. 19, figs 33-34.

Material: Five cups (MPG-PD 32456-32459).

Description: The cups are small, sturdy, low and bowl-shaped. In some specimens, the axis of the cup is slightly oblique. The outer surface is smooth, while sutures between the plates are usually visible. Basals and radials have a pentagonal contour and are robust. In some specimens, the basals are slightly lower than the radials, while in others these are almost of the same height. The upper edge of the cup is wavy due to the presence of 'false' interradial projections.

The upper edge of each radial plate is almost entirely occupied by a wide articular facet. The radial facets are located inwards, behind a peripheral edge (Fig. 6B2). These facets are well developed at the ventral level and are separated from each other by low interradial ridges. In each facet, the aboral surface is tilted outwards, while the adoral surface is slightly tilted inwards. The ligament fossa is crescent shaped and wide, with a deep ligament pit. The axial canal is well evident near the fulcral ridge. The muscle fossae, subrectangular, are wide and not too deep. A radial groove separates the two muscle fossae of the same facet. Between the muscle fossae and fulcral ridge, there are two small, subtriangular interarticular ligament fossae, not always clearly visible. In front of each radial facet, there is a distinct peripheral edge.

The ventral cavity is small and shallow, its floor being five lobed, with five narrow and evident radial grooves, each of which ends in a radial hole. In the centre of the cavity, there is a small central hole, not always visible. The lower part of the cups, not too wide, is entirely occupied by a moderately deep subcylindrical cavity where there is a central axial canal and no articular elements are visible, but the sutures between the basal plates are evident.

Remarks: The main distinctive characters of this species include the presence of a distinct peripheral edge, in front of each radial facet, basal and radial plates of almost the same size, and radial facets separated from each other by low interradial ridges. Usually, the cup axis is not oblique; however, our material includes two cups that have such a slightly oblique axis. All specimens here described have weak and slightly raised sutures, and some are markedly abraded.

Discussion: This species differs from *L. lavadensis* in the flatter general morphology. On account of shape and size, *L. suessi* might be considered to represent a juvenile specimen of *Paraconocrinus pyriformis*. However, this is not the case, because the smallest specimens (here considered to reflect the juvenile stage) of *P. pyriformis* have oblong cups and basals that are much taller than radials. Moreover, the radial facets of *L. suessi* are much wider.

Monachocrinus? *regnelli* is similar to *L. suessi* especially as far as cup size, wide radial facets, and near-equally high basals and radials are concerned. However, the former has a clearly depressed boundary between the plates, while *L. suessi* has a well-marked peripheral edge and non-depressed boundary.

The validity of the present species has been debated on numerous occasions. Munier-Chalmas (*in* Hébert and Munier-Chalmas 1877) erected *Bourgueticrinus suessi* without describing and illustrating cups, and thus it is a *nomen nudum*. De Loriol (1879, Pl. 19, Figs. 33-34) described and figured this form, but did not compare his material to those provided by Munier-Chalmas, which is clear from what he wrote, "comme je ne puis pas comparer des calices, il peut rester encore quelque doute sur ma determination" (= as I cannot compare the cups,

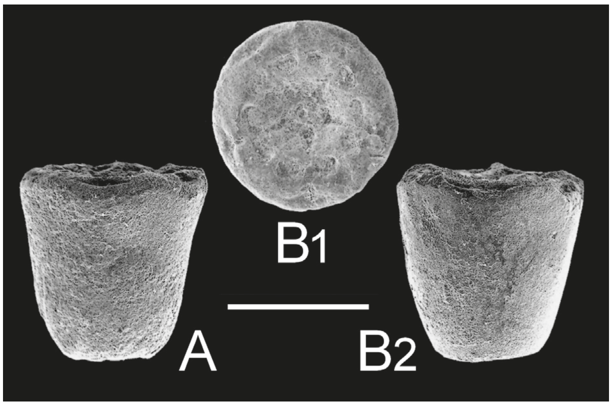

Fig. 7 - *Lessinicrinus minutus* n. gen., n. sp., cups. A) MPG-PD 32461 (paratype), in lateral view. B1-B2) MPG-PD 32460 (holotype), in ventral and lateral views, respectively. The scale bar equals 1 mm.

there may still be some doubt about my determination) (de Loriol, 1879, p. 192).

Oppenheim (1902, Pl. 9, Fig. 7) attributed to *Conocrinus suessi* an elongated cup from the Ypresian of Monte Spilecco, near Bolca (north-eastern Italy), pointing out a remarkable similarity with *Phyllocrinus* (as noted above, *Phyllocrinus* is a Middle Jurassic to Early Cretaceous cyrtocrinid characterized by prominent interradial projections and small radial facets).

Biese and Sieverts-Doreck (1939) did not consider specimens studied by Munier-Chalmas to be valid. Fabiani (1908, 1915) quoted the presence of *Conocrinus suessi* in Eocene sedimentary rocks but did not provide any descriptions or illustrations, while Roux et al. (2019, p. 63) considered Oppenheim's specimen to belong to *Conocrinus*.

Cups referred by de Loriol (1879, Pl. 19, Figs. 33-34) to *Conocrinus suessi* are very similar to the material studied here, although the specimen of his figure 33 differs in the greater height of the cup. In view of its height and shape, the specimen identified by Oppenheim as *C. suessi* is probably a cup of *C. thorenti*.

According to Article 50.1.2 of the ICZN (1999) ("In the case of original fixation of a type species by the deliberate employment of a species-group name in the sense of a previous misidentification, the person who deliberately uses the misidentification is deemed to be the author of a new specific name"), this species should be attributed to de Loriol.

Stratigraphical and geographical distribution: Eocene of Switzerland (Weesen-Saint Gall) and Italy (Monte Spilecco, Veneto).

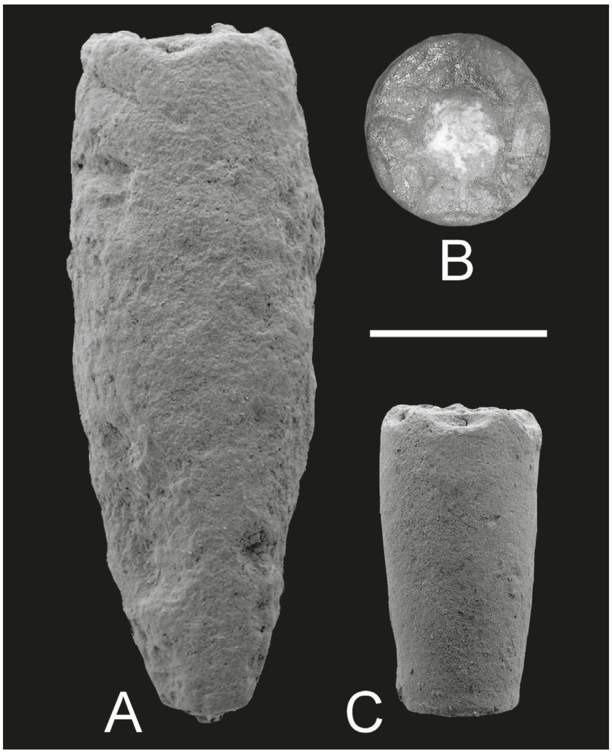

Fig. 8 - *Pseudoconocrinus elongatus* (Roux), cups. A) MPG-PD 32464, mature specimen in lateral view. B) MPG-PD 32467, in ventral view. C) MPG-PD32465, probable juvenile specimen in lateral view. The scale bar equals 1 mm.

Lessinicrinus minutus n. gen., n. sp., Figs. 7, 9F1-F2

Etymology: From Latin *minutus*, in reference to the diminutive cup size.

Type material: MPG-PD 32460 is the holotype; the other specimens (MPG-PD 32461-32463) are paratypes.

Type locality: Cava Boschetto, near Chiampo (municipality of Vicenza, Veneto, north-eastern Italy).

Type level: Lutetian (Eocene).

Description: These cups are very small and conical to funnel-shaped. The outer surface is smooth. The sutures between the plates are usually not visible, or occasionally under low-angle light. Generally, basals are slightly taller than radials.

The upper edge of the cup is slightly wavy due to the presence of interradial ridges; these are very low and tiny and poorly developed at the ventral level. Two-thirds of the upper edge of the cup are occupied by the articular facets. In each facet, the aboral surface is subvertical or tilted outwards, while the adoral surface is subhorizontal or slightly tilted inwards. The ligament fossa is crescent-shaped, moderately wide, and with a deep ligament pit. The axial canal is almost behind the fulcral ridge. Laterally to the axial canal, there are two flat and subrectangular interarticular ligament fossae. The two muscle fossae are subhorizontal to slightly inclined inwards; they are wide, well developed at the ventral level, and separated by a radial groove. The ventral cavity is moderately wide, shallow, and star-shaped.

The lower part of the cups, which is small and circular, is entirely occupied by a flat and shallow cavity, where there is the articular surface of the stem with a clearly visible central axial canal.

Remarks: These cups are quite well preserved. The morphology of the basals and radials can be seen only under favorable light conditions since the sutures are usually not apparent. Rarely, the basals are taller than the radials (Fig. 9F2). The ventral cavity is mainly shallow and rarely deep. The interarticular ligament fossae are usually not visible.

Discussion: The specimen identified by Wienberg Rasmussen (1961, Pl. 31, Fig. 9) as *Democrinus gisleni* Wienberg Rasmussen, 1961 is similar to the material of *L. minutus* n. gen., n. sp., but has a wider and deeper ventral cavity. A cup of *Democrinus simmsi* Ciampaglio, Donovan, and Weaver, 2007 (see Ciampaglio et al., 2007, Fig. 3F) is also similar, but has higher muscular fossae. Material assigned to *Monachocrinus*? *gallicus* Wienberg Rasmussen, 1961 (see Wienberg Rasmussen, 1961, Pl. 31, Fig. 11) and Jagt (1999, Pl. 30, Figs. 4-13) is similar, but cups of *L. minutus* n. gen., n. sp. has a more angular edge between the basals and radials. Living specimens of *M. recuperatus* (Perrier, 1885) are also close, but have a more

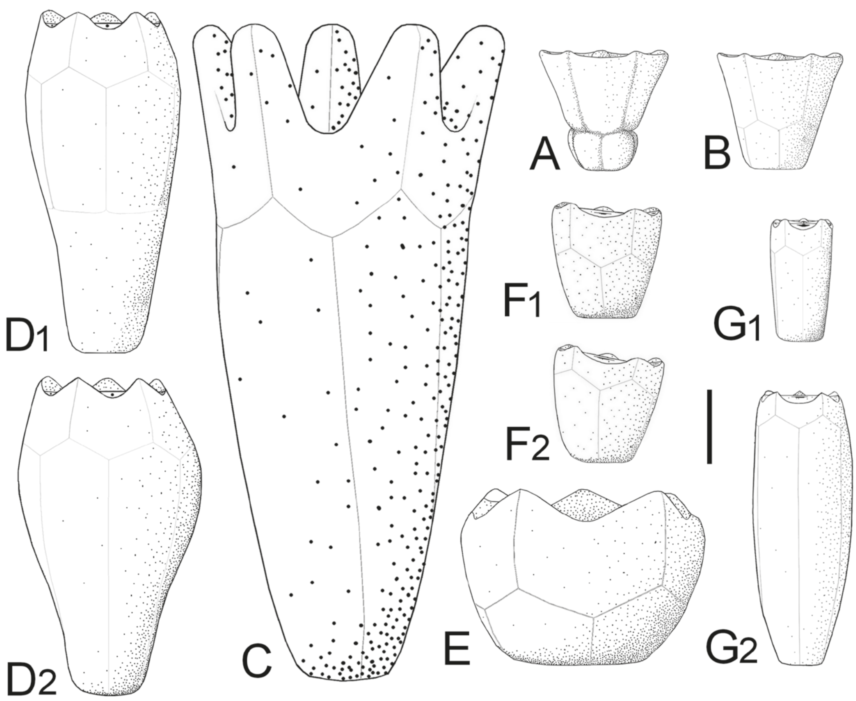

Fig 9 - Reconstruction of cups of species studied herein, in lateral views. A) *Chiampocrinus lobatus* n. gen., n. sp. B) *Chiampocrinus conicus* n. gen., n. sp. C) *Conocrinus veronensis* (Jaekel). D) *Fabianicrinus fusus* n. gen., n. sp.: D1) cup with proximale, basals and radials, D2) cup with only basals and radials. E) *Lessinicrinus suessi* (de Loriol). F) *Lessinicrinus minutus* n. gen., n. sp.: F1) cup with basals and radials of similar size, F2) cup with basals taller than radials. G) *Pseudoconocrinus elongatus* (Roux): G1, cup of juvenile specimen, G2) cup of a mature specimen. The scale bar equals 1 mm.

oblong cup with clearly visible sutures.

As far as general morphology is concerned, the present specimens of *L. minutus* n. gen., n. sp. recall cups of *Democrinus* Perrier, 1883, *Dunnicrinus* Moore, 1967, *Monachocrinus* A.H. Clark, 1917 and *Pseudoconocrinus*. However, they differ from *Democrinus* in having basals that are slightly taller than radials, from *Dunnicrinus* in the muscular fossae that are ventrally tilted and not high, from *Monachocrinus* in the angular border between basals and radials and in unfused basals. Finally, conocrinids do not appear to be related to these cups mainly on account of their wider radial facets. Unfortunately, the ontogenetic development of most Cenozoic crinoids is poorly known, or not at all and, therefore, it is not possible to determine beyond doubt whether these cups belong to juvenile or adult specimens of other crinoids (Wienberg Rasmussen, 1961; Kjaer and Thomsen, 1999).

Genus ***Pseudoconocrinus*** Roux, Eléaume and Améziane, 2019

Type species: Conocrinus doncieuxi Roux, 1978b, by original designation.

Diagnosis: Small cups with high basals and lower radials; conical to elongated. Sutures are usually not clearly visible. Radial facets are wide and well-developed at the ventral level, often tilted outwards or subhorizontal. Facets separated by raised interradial ridges. Muscle fossae, are suboval and moderately deep, with a raised ventral edge. No interradial projections. Ventral cavity is shallow and small to moderately small. The lower cup side is entirely occupied by the articular surface for a stem.

Remarks: The main characters that allow distinguish this genus from the others here described include the wide radial facets, the muscle fossae with a raised ventral edge, the presence of interradial ridges, and the basals that are much taller than the radials.

Stratigraphical and geographical distribution: Paleocene of Denmark and Crimea; Eocene of France and northern Italy.

Species included: Conocrinus doncieuxi Roux, 1978b, *Democrinus maximus* Brünnich Nielsen, 1915 and *Conocrinus tauricus* Klikushin, 1982.

Pseudoconocrinus elongatus (Roux, 1978a), Figs. 8, 9G1-G2

1978a *Conocrinus elongatus* Roux, p. 265, fig. 1C.

1982 *Conocrinus* cf. *elongatus* Roux - Klikushin, p. 823, text-fig. 8A.

2018 *Bourgueticrinus* sp. - Zamora et al., p. 788, fig. 10G.

2019 ?*Democrinus elongatus* (Roux) - Roux et al., p. 66, text-figs. 8G-J.

2021 ?*Democrinus elongatus* (Roux) - Roux et al., p. 226, text-fig. 8G-I.

Material: Six cups (MPG-PD 32464-32467).

Description: The cups are oblong, subcylindrical to slightly conical. The outer cup surface is smooth; the sutures between the plates are not clearly visible. When they are, these show an irregular pattern. The basals and radials have a subpentagonal contour and are robust. The basals are much taller than the radials. The radials are low, their upper edge being entirely occupied by radial facets that are separated by a low and narrow interradial ridge, curved upwards by the inner edge of two adjacent radials.

Radial facets are large but narrow. In each facet, the aboral surface is tilted outwards, while the adoral surface is subhorizontal and slightly tilted inwards. The ligament fossa, in the shape of a half moon, is wide and has a relatively deep, central ligament pit. The axial canal is slightly further back than the fulcral ridge and is relatively wide. The interarticular ligament fossae are not clearly visible. The muscle fossae are wide and deep, with a low ventral border, a radial groove separating two muscle fossae of the same facet. The ventral cavity is moderately wide, not very deep, and with a steep wall. Its bottom is moderately flat. The lower part of the cups is entirely occupied by a small and shallow cavity. In the center, there is an axial canal and no articular elements are visible.

Remarks: The main character of this species is the oblong cup. All specimens at hand are oblong, the largest measuring 10 mm in length and 3.3 mm in width. Sutures between the plates are visible only in a single specimen. The available specimens are moderately abraded and/or damaged, or partially encrusted with bryozoans. Small cups have no dorsal cavity. The smallest individual (MPG-PD 32465) (see Figs. 8C, 9G1) is considered to be a juvenile on account of its very small size.

Discussion: Pseudoconocrinus elongatus differs from other crinoid species from Cava Boschetto in being markedly oblong. It can be differentiated from *Lessinicrinus minutus* n. gen., n. sp. in the taller basals.

Stratigraphical and geographical distribution: Ilerdian (lower Eocene) of Fontcouverte (France) and La Puebla de Roda (Spain); Bartonian (Eocene) of Biarritz (France); upper Eocene of Crimea.

Bourgueticrinid columnals and holdfasts, Fig. 10

Material: Two hundred and ninety-three columnals (MPG-PD 32475-32482).

Description: Rare columnals (Fig. 10A) with two articular surfaces without evident articular elements (synostosis) (MPG-PD 32475-32476) probably represent proximal columnals. Others (Fig. 10B-C), also rare, have two smooth articular surfaces, slightly concave and with an insignificant fulcral ridge (cryptosynarthry?) (MPG-PD 32477-32479).

The commonest columnals are barrel-shaped, cylindrical, or flared. Occasionally, columnals have lateral ramifications. In these branches, the articular surfaces have no fulcral ridge. The two articular surfaces of columnals are elliptical and concave and have a variable orientation of their fulcral ridges. Each fulcral ridge is moderately raised and narrow, with a rarely visible crenularium. The ligament fossa is shallow to deep and divided into two parts, often shaped as the figure 8. The profile of each depression is subcircular to subelliptical. Often, concentric lines can be observed within each depression, which are growth lines.

Remarks: On account of ligamentary synarthries, these columnals belong to the Bourgueticrinina. Determining their family and/or generic assignment is difficult because these columnals are rarely attached to their cups. In addition, Cenozoic crinoids have a xenomorphic column, which means that the same column could have dissimilar columnals. The proximal column is called "proxistele", the middle part "mesistele" and the distal part "distele". Each of these parts is characterized by columnals with their own morphology. Wienberg Rasmussen (1978, p. T844) pointed out that, "indeterminable columnals of Tertiary Bathycrinidae have been registered under different generic names (*Rhizocrinus*, *Conocrinus,* and *Bourgueticrinus*)". When analyzing the synarthries of bourgueticrinid columnals, Roux (1977) identified four types: the *Bourgueticrinus*-type, *Conocrinus*-type, *Democrinus*-type and *Porphyrocrinus*-type. Following studies conducted by Donovan (1996) and Roux et al. (2019), the *Democrinus*-type is considered to be a peramorphic variation of the *Conocrinus*-type and, therefore, only

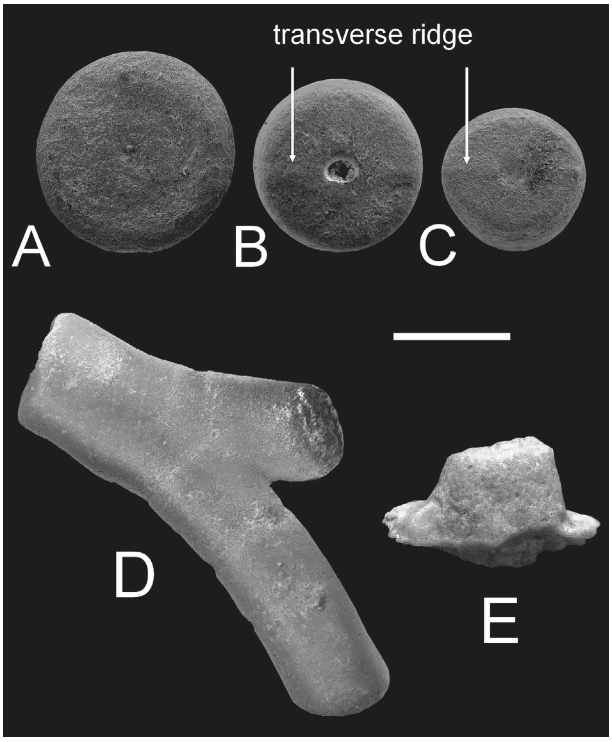

Fig. 10 - Columnals of indeterminate bourgueticrinids. A) MPG-PD 32475, with synostosis. B-C) with cryptosynarthries: B) MPG-PD 32477, with a low profile. C) MPG-PD 32478, with tall profile. D) MPG-PD 32474, branching cirri. E) MPG-PD 32472, encrusting disc. The scale bar equals 1 mm.

three types of columnal synarthry can be distinguished. In the *Bourgueticrinus*-type, the areola is concave, and the ligament pit is not clearly visible; in the *Conocrinus*-type, the areola is partially occupied by a deep 8-shaped ligament pit, while in the *Porphyrocrinus*-type, the whole areola is occupied by a deep ligament pit, with a suspended fulcral ridge. Here, only columnal types are briefly discussed and these are not assigned to genus and/or species.

Holdfasts

In general, stalked crinoids (other than isocrinids) cement to hard substrates by means of an encrusting disc which may have a subcircular contour or small, root-like digitations. Some crinoids, such as bourgueticrinids, attach to the substrate by means of branching cirri or also branching roots.

Branching cirri, Fig. 10D

Material: One specimen (MPG-PD 32474).
Description: A fragment of branched radicular cirrus consists of six small elements of varying length attached to each other. Each element is subcylindrical, oblong and dorsally smooth. The branched element seems to be the shorter element. The articular surfaces are almost flat with a central circular axial canal. No articular elements are visible (synostosis?).
Remarks: This fragment of branching cirrus may belong either to bourgueticrinids or bathycrinids (Wienberg Rasmussen, 1978; Hess, 2011b). Unfortunately, since it is rare to find such elements, no further details can be provided at this point.

Encrusting discs, Fig. 10E

Material: Three terminal discs (MPG-PD 32472-32473).
Description: These are small basal expansions in the shape of a disc, with an irregular contour due to short digitations. The lower side is concave and has an irregular surface. The upper part is slightly convex and supports a cylindrical, stem-like structure, with the articular surface for the distalmost columnal. The articular elements of these surfaces are not evident. The axial canal is faintly visible.
Remarks: These discs are not common. Unfortunately, they are encrusted with bryozoans, which explains why the articular surfaces for the distalmost columnals are never visible.
Discussion: The presence of these discs poses a problem, because, in general, Cenozoic crinoids lack such discs. Cyrtocrinids have similar holdfasts; bourgueticrinids, in contrast, usually have a root system. Unfortunately, the articular surface of these holdfasts is not preserved, and therefore it is quite difficult to determine the systematic assignment of these holdfasts. One might assume an unknown cyrtocrinid to have been present, but this is only speculation at this point. In addition, the diameter of the stem-like part is too large, and no cup studied here has such a large articular surface for columnals.

Order Isocrinida Sieverts-Doreck, *in* Moore, Lalicker and Fischer, 1952 (*emend*. Hess, 2011a)

Diagnosis: Crinoids with small cup (basals and radials), long arms and long stem. Stem characterized by cirri, at regular intervals along column. No holdfasts or encrusting discs (except for *Proisocrinus* A.H. Clark, 1910). Arms are slender and characterized by different types of brachials; brachial articulations both muscular and non-muscular.
Remarks: The systematics of isocrinids has been widely debated. In fact, there is no agreement among researchers which characters should be used to classify them. Klikushin (1979) used ligament pores, while Roux (1970, 1974) had earlier referred to microstructures found in the articular surfaces of columnals. Other workers such as Carpenter (1882), Wienberg Rasmussen (1978) and Oji (1985) considered the type of articulation between primibrachials 1 and 2 to be the most important. Recently, Améziane et al. (2021) and Roux and Philippe (2021, p. 314) have considered the classification of the Isocrinida proposed by Hess (2011 a) to be unsatisfactory in being based on plesiomorphic characters without phylogenetic significance.
Stratigraphical and geographical distribution: Middle Triassic to Holocene, worldwide.

Family Isocrinidae Gislén, 1924
Subfamily Isocrininae Gislén, 1924
Genus ***Isocrinus*** von Meyer, 1836

Type species: Isocrinites pendulus von Meyer, 1836.
Diagnosis: Stem with pentangular, five lobed or circular section. Internodals short; nodals larger than internodals, with five cirrus sockets facing outwards. Columnal articulation characterised by elliptical petals.
Stratigraphical and geographical distribution: Triassic to Holocene; worldwide.

Isocrinus archiaci Pasotti, 1929, Fig. 11

1929 *Isocrinus archiaci* Pasotti, p. 80, pl. 2, figs. 12-15.

Material: Forty-three columnals; two of Type A (MPG-PD 32483-32484), five of type B (MPG-PD 32485-32487) and thirty-six of type C (MPG-PD 32487-32490).
Description: Small and rather low columnals with circular, pentalobate, or star-shaped contours, with a smooth external surface. One type of nodal (here referred to as type A columnal) and two types of internodal (here referred to as type B and type C) have been identified.

Type A (nodal) is relatively tall and characterized by a symplexy and a cryptosymplexy; type B (internodal) also has a symplexy and a cryptosymplexy; type C (internodal) is relatively tall and characterized by two symplexies.

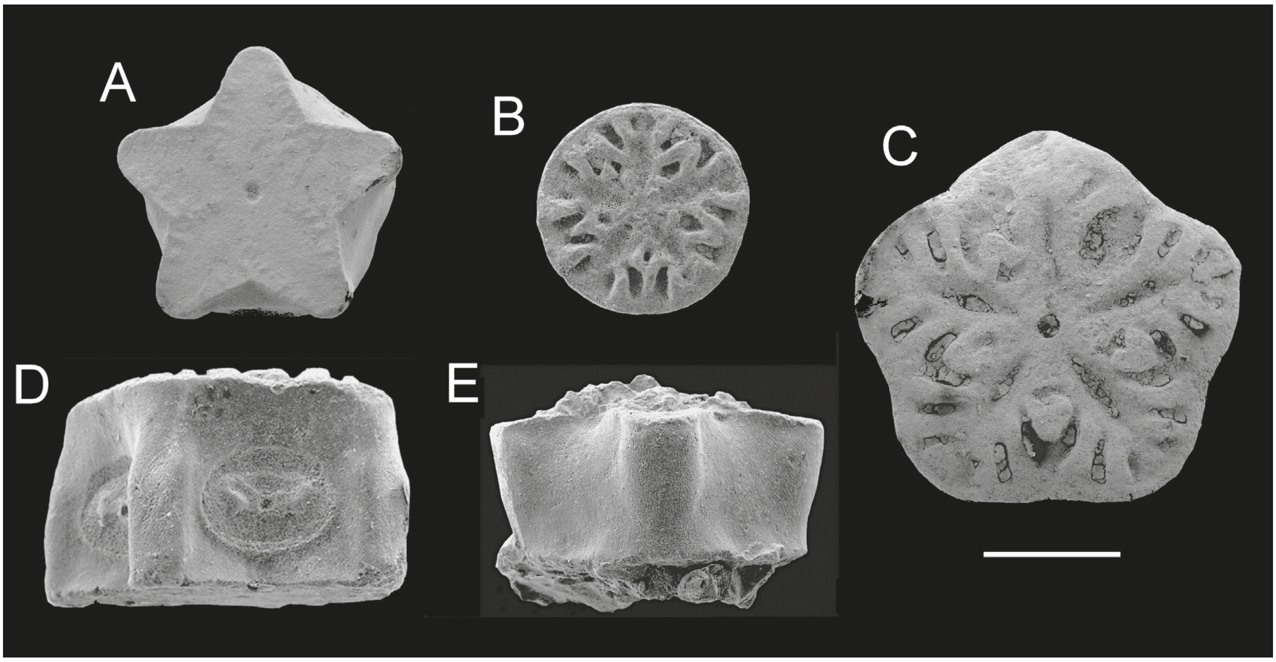

Fig. 11 - *Isocrinus archiaci* Pasotti, columnals. A) MPG-PD 32486, cryptosymplexy of internodal. B) MPG-PD 32488, symplexy of internodal. C) MPG-PD 32489, symplexy of internodal. D) MPG-PD 32483, nodal with cirrus socket in lateral view. E) MPG-PD 32485, internodal in lateral view. The scale bar equals 1 mm.

Type A (Fig. 11D) is very rare; it is of moderate height and has lateral cirrus sockets. Its proximal side is characterized by a pentagonal contour and a symplexy, with a large crenularium consisting of five narrow petals. Each petal consists of up to five oblique culmina. The first two culmina of two adjacent petals are joined together to form oval "sockets". The floor of the petals is oblong and depressed. The lumen of the axial canal is circular; the perilumen is raised.

The distal side of type A has a star-shaped contour and a cryptosymplexy, slightly concave and with very weak crenulae, characterized by five petals. The cirrus sockets are elliptical in shape. They are placed closer to the distal part of the columnal. This articular surface is slightly concave, with a raised transverse part. A central pore and two lateral tubercles are visible within it.

Type B (Figs. 11A, E) is also rare. This type is similar to type A but lacks lateral cirrus sockets. Its distal side is pentagonal in shape and has a symplexy. The proximal side has a star-shaped contour and a cryptosymplexy (Fig. 11A), slightly concave and with very weak crenulae, characterized by five petals. The lumen is circular.

Type C is the most frequent type (Figs. 11B-C) found. Its sides are characterized by a pentagonal or circular contour and by a symplexy, characterized by a wide crenularium consisting of five petals. Each petal has up to five oblique crenulae. The first two crenulae of two adjacent petals are joined together to form oval "sockets". The floor of the petals is oblong, thin, and depressed. The lumen of the axial canal is circular; the perilumen is raised.

Remarks: The symplectial articulation of these columnals features a crenularium the individual petals of which have only three, rarely six, crenulae on either side. Mature specimens (i.e., the largest columnals) have a greater number of crenulae, up to seven, and narrow areola. Cryptosymplexies always have a very weak crenularium, usually not clearly visible.

Discussion: The largest specimens at hand are closely similar to specimens described by Pasotti, whereas the smallest differ from those described by that author especially in the smaller number of crenulae and in the very narrow petals. Moreover, these columnals are also close to those described by Wienberg Rasmussen (1961, Pl. 14, Figs. 3-4) as *Nielsenicrinus fionicus* (Brünnich Nielsen, 1913), but have a narrower areola and usually fewer crenulae; furthermore, each petal has a reduced number of marginal crenulae.

A specimen of *Nielsenicrinus* sp., from the upper Paleocene of Western Australia, described by Milner (1989, Fig. 2), is also very similar to our specimens, but the petals are larger.

Stratigraphical and geographical distribution: Eocene of France and northern Italy.

5. CONCLUSIONS

New species of Eocene crinoids from Cava Boschetto (north-eastern Italy) described herein include *Chiampocrinus lobatus* n. gen., n. sp., *C. conicus* n. gen., n. sp., *Fabianicrinus fusus* n. gen., n. sp. and *Lessinicrinus minutus* n. gen., n. sp. Cups of *Pseudoconocrinus elongatus*, *Conocrinus veronensis* and *Lessinicrinus suessi* have also been identified, as well as remains of holopodids (Manni and Pacioni, 2021). Some crinoid cups are encrusted with bryozoan cheilostoma cribrimorph colonies (Fig. 4A3). This means that these crinoids were already dead and disarticulated on the seafloor when they were encrusted by the bryozoans.

Isocrinids represented include only *Isocrinus archiaci*. The absence of comatulids and other types of isocrinid, which are relatively common in Cenozoic strata elsewhere in northern Italy, is worthy of note. The absence of comatulids was also underlined by Pasotti (1929) for Eocene strata of Gassino. The reason why no comatulid remains are found has not yet been explained.

5.1. EOCENE FAUNAS COMPARISON

Prior to the present record, non-isocrinid Eocene crinoids from strata in Italy included *Conocrinus thorenti*, *C. veronensis*, *C. rovasendai* Pasotti, 1929, *Lessinicrinus suessi*, *Paraconocrinus pyriformis,* and *Holopus spileccense.* The most important areas to yield Eocene crinoids are the hills around Turin (Piedmont) and the Berici Hills (Veneto), with the former area rich in crinoids. Near the town of Gassino, deposits have yielded merely three species of conocrinids (*Conocrinus thorenti*, *Paraconocrinus pyriformis,* and *C. rovasendai*). On the Berici Hills, Eocene levels have produced four genera (*Conocrinus*, *Lessinicrinus* n. gen., *Paraconocrinus,* and *Holopus*), with five species (*Conocrinus thorenti*, *C. veronensis, Lessinicrinus suessi, Paraconocrinus pyriformis,* and *Holopus spileccense*). Moreover, three isocrinids have been described, namely *Isselicrinus diaboli*, *I. subbasaltiformis,* and *Isocrinus archiaci*.

The Cava Boschetto locality in Chiampo is characterized by a well-differentiated fauna, comprising eight genera with ten species. Five bourgueticrinoids [*Chiampocrinus* n. gen. (two species), *Conocrinus* (one species), *Fabianicrinus* n. gen. (one species), *Lessinicrinus* n. gen. (two species), *Pseudoconocrinus* (one species)], two cyrtocrinids (*Holopus* and *Cyathidium*) and one isocrinid (*Isocrinus*). In short, Cava Boschetto has yielded the most diverse non-isocrinid crinoid fauna of Eocene age in northern Italy.

Elsewhere in Europe, and France in particular, Cenozoic sedimentary rocks are rich in crinoids. In particular, the Pyrenees area is characterised by numerous localities with Eocene crinoids. Among these, Biarritz and Miretrain are well known. Biarritz (Pyrénées-Atlantiques, Aquitaine region, south-western France) is the typical site of *Conocrinus*. d'Archiac (1846, 1850), Rouault (1850) and Roux (1978a) described from the upper Lutetian-Bartonian at this locality different species of conocrinids such as *Conocrinus archiaci*, *C. duperrieri*, *C. thorenti*, *Globulocrinus globulosus* (Roux, 1978a), *Pseudoconocrinus elongatus* and *Paraconocrinus handiaensis* (= *P. pyriformis?*). Two species of isocrinid have also been recorded: *Isselicrinus didactylus* and *Isocrinus* (?) *archiaci.* Therefore, the outcrop of Biarritz is characterised by seven genera with eight species (i.e., conocrinids with six species and isocrinids with two species).

Roux et al. (2006) described from Lutetian to upper middle Bartonian strata at Miretrain (near Angoumé, Landes, Aquitaine region, south-western France), several cups of *Conocrinus archiaci*, *C. duperrieri* and *Pseudoconocrinus elongatus*, in addition to columnals of *Isselicrinus diaboli* and *Isselicrinus* spp. and *Cainocrinus* sp. Thus, the outcrop of Miretrain is characterized by four genera with eight species (conocrinids with three species and isocrinids with nine species).

The only genera that Biarritz, Miretrain, and Chiampo have in common are *Conocrinus* and *Pseudoconocrinus*, with only a single species found in all three areas, namely *Pseudoconocrinus elongatus*. The isocrinid fauna is different, as it consists of three different genera (*Cainocrinus* Forbes, 1852, *Isselicrinus* Rovereto, 1914, and *Isocrinus*), with no genus in common.

5.2. PALEOBATYMETRY

The different composition of these faunas might be explained by several ecological factors, including water depth. Unfortunately, it is very difficult to extrapolate ecological data from Cava Boschetto. Fabiani (1915) believed that the crinoid-bearing levels in Veneto were deposited in the deepest neritic zone. P. Mietto (University of Padua, pers. comm., April 2015) considers these levels to have been laid down in deep waters, being made up of ruditic basaltic tuffites (Beccaro et al., 2001). However, these tuffites are not *in situ*, as gravitational re-settlement events coming from an adjacent carbonate ramp can be clearly observed. It should be considered that these remains all belong to sessile benthic crinoids, which underwent *post-mortem* transport. Therefore, these crinoid species probably inhabited different environments and should not be associated directly with the Cava Boschetto depositional environment.

Living conocrinids live at depths between 300 and 2,070 meters (Roux and Montenat, 1977; Roux and Plaziat, 1978) and are probably rheophobic, due to their very delicate structure. As far as Miretrain is concerned, Roux et al. (2006) assumed the depth at which the fossil crinoid fauna had lived would have ranged from over 700 to about 1,000 meters during the middle Lutetian.

Modern holopodids live at depths of 200 to 900 meters (Cherbonnier and Guille, 1972; Heinzeller et al.,1996) and *Holopus* is considered near-rheophobic (Donovan and Pawson, 2008, pag. 36).

In order to gauge the depth at which these crinoids lived, their state of preservation has been analysed. Many of the specimens studied here are moderately abraded, probably as a result of transport, for which reason they cannot be considered to represent *in-situ* biota.

As to holopodids, it should be noted that extant holopodids cement their cup directly to hard substrates. Since these cups are found detached from the original substrates, it is likely that a high-energy event led to these cups being detached (see Manni and Pacioni, 2021).

Perhaps gravitational flows have violently detached the holopodid cups from the substrate.

The abrasion of the specimens studied here is perhaps due to the gravitational flows that occurred along the carbonate ramp. During these flows, the crinoids rolled and were therefore abraded. Increased abrasion could be due to increased transport. But greater transport could also depend on the position of the crinoids along the ramp. The higher they lived, the greater the transport. It can therefore be assumed that the more abraded crinoids are those that lived at a shallower depth and, conversely, the less abraded ones are those that lived at a greater depth.

The cups of *Conocrinus veronensis* and *Pseudoconocrinus elongatus* are considerably more damaged than the others: it can therefore be assumed that these two species, living in shallower marine waters, have undergone greater transport than all the other species studied here. Conversely, as the robust bourgueticrinid columnals are slightly eroded, while those of *Isocrinus* are generally well preserved, it can be assumed that perhaps they lived in deeper waters.

In summary, the conocrinid and holopodids cups and some of the columnals of the bourgueticrinids are more abraded than the cups of *Chiampocrinus* n. gen. and the columnals of the isocrinids.

By also analysing the articular facets of the crinoids studied here, some interesting hypotheses can be drawn.

Chiampocrinus lobatus n. gen., n. sp., with very thin articular surfaces of the arms, were probably unable to survive in turbulent waters and thus were perhaps rheophobic or nearly rheophobic. *Pseudoconocrinus* and *Lessinicrinus* n. gen., having wider radial facets than *Chiampocrinus* n. gen., perhaps could live in less calm waters. *Lessinicrinus suessi* and *L. minutus* n. gen., n. sp., both having large radial facets, perhaps could have lived in slightly turbulent waters, which is consistent with their size. *Conocrinus* and *Fabianicrinus* n. gen., both of which had tiny radial facets and thus delicate arms, were perhaps could not live in turbulent waters. Finally, isocrinids and large bourgueticrinids were perhaps able to live in slightly more turbulent waters due to their larger size.

In summary, *Chiampocrinus* n. gen. and holopodids, with delicate arms, perhaps preferred calm waters, *Conocrinus* and *Fabianicrinus* n. gen., with slightly more robust arms, perhaps slightly more turbulent waters, while *Pseudoconocrinus*, *Lessinicrinus* n. gen. and isocrinids, with more robust arms, perhaps turbulent waters. Therefore, based on anatomical features of these crinoids and on their state of preservation as well as the lithological setting, it is assumed that *Conocrinus*, *Fabianicrinus* n. gen., *Chiampocrinus* n. gen. and the holopodids inhabited a ramp setting, at a depth probably greater than 200 metres, below wave action. In contrast, *Pseudoconocrinus*, *Lessinicrinus* n. gen. and *Isocrinus*, for reasons mentioned above, could also have lived at shallow depths.

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REFERENCES

Albus L., 1930. Nuove ricerche sui crinoidi miocenici della Collina di Torino. Bollettino della Società Geologica Italiana 49, 279-296.

Améziane N., Eléaume M., Roux M., 2021. Ontogeny of non-muscular brachial articultions in Balanocrininae (Echinodermata, Crinoidea): iterative trajectories or phylogenetic significance? Zoomorphology 140, 47-67.

d'Archiac A., 1846. Description des fossiles recueillis par M. Thorent, dans les couches à Nummulines des environs de Bayonne. Mémoires de la Société Géologique de France 2, 189-217.

d'Archiac A., 1850. Description des fossiles du groupe Nummulitique recueillis par M.S.-P. Pratt et M.J. Delbos aux environs de Bayonne et de Dax. Mémoires de la Société Géologique de France 3, 397-456.

Bassi D., Bianchini G.B., Mietto P., Nebelsick J.H., 2008. Southern Alps in Italy: Venetian Pre-Alps. In: McCann T. (Ed.), The Geology of Central Europe, 2. The Geological Society of London, Special volume, 56-62.

Bather F.A., 1899. A phylogenetic classification of the Pelmatozoa. British Association for the Advancement of Science Report 1898, 916-923.

Bayan F., 1870. Sur les terrains tertiaires de la Vénétie. Bulletin de la Société Géologique de France 27, 444-486.

Beccaro L., Fornaciari E., Mietto P., Preto N., 1999. Analisi di facies e ricostruzione paleoambientale dei "Calcari Nummulitici" (Eocene, Monti Lessini orientali, Vicenza): dati preliminari. Studi Trentini di Scienze Naturali, Acta Geologica 76, 3-16.

Beschin C., Busulini A., De Angeli A., Tessier G., 1994. I crostacei eocenici della Cava "Boschetto" di Nogarole Vicentino (Vicenza - Italia Settentrionale). Lavori della Società Veneta di Scienze Naturali 19, 159-215.

Biese W., Sieverts-Doreck H., 1939. Crinoidea caenozoica. In: Quenstedt F.A. (Ed.), Fossilium Catalogus, I: Animalia, parte 80. 's Gravenhage (W. Junk), 1-151.

Brünnich Nielsen K., 1913. Crinoiderne i Danmarks Kridtaflejringer. Danmarks Geologisk Undersøgelse 26, 1-114.

Brünnich Nielsen K., 1915. *Rhizocrinus maximus* n.sp. og nogle Bemaerkninger om *Bourgueticrinus danicus* Br. N. Meddelelser frå Dansk Geologisk Forening 4, 1-391.

Carpenter P.H., 1882. Report on the results of dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-1878) and the Caribbean Sea (1878-1879) by the U.S. Coast Survey steamer "Blake", Lieut. Commander

C.D. Sigsbee, U.S.N. and Commander J.R. Bartlett, U.S.N., commanding. XVIII: The stalked crinoids of the Caribbean Sea. Bulletin of Museum of Comparative Zoology, Harvard University 10, 165-181.

Carpenter P.H., 1884. Part I. The stalked crinoids. In: The Voyage of H.M.S. Challenger. Report upon the Crinoidea collection during the Voyage of H.M.S. Challenger during the years 1873-76. Zoology 11, 1-442.

Cherbonnier G., Guille A., 1972. Sur une espèce actuelle de Crinoïde crétacique de la famille Holopodidae: *Cythidium foresti* nov. sp. Comptes Rendus de l'Académie des Sciences de Paris D274, 2193-2196.

Ciampaglio C.N., Donovan S.K., Weaver P.G., 2007. A new bourgueticrinid (Crinoidea) from the Castle Hayne Formation (Eocene) of southeastern North Carolina, USA. Swiss Journal of Geosciences 100, 243-249.

Clark A.H., 1910. *Proisocrinus*, a new genus of recent crinoids. Proceedings of the United States National Museum 38, 387-390.

Clark A.H., 1917. A revision of the recent genera of the crinoid family Bourgueticrinidae with the description of a new genus. Journal of Washington Academy of Science 7, 388-392.

Di Rovasenda L., 1892. I fossili di Gassino. Bollettino della Società Geologica Italiana 11, 409-424.

Donovan S.K., 1996. Comparative morphology of the stems of the extant bathycrinid *Democrinus* Perrier and the Upper Paleozoic platycrinids (Echinodermata, Crinoidea). Bulletin of the Mizunami Fossil Museum 23, 1-27.

Donovan S.K., Pawson D.L., 2008. A new species of the sessile crinoid *Holopus* d'Orbigny from the tropical western Atlantic, with comments on holopodid ecology (Echinodermata: Crinoidea: Holopodidae). Zootaxa 1717, 31-38.

Fabiani R., 1908. Paleontologia dei Colli Berici. Memorie della Società Italiana delle Scienze (detta dei XL) 15, 45-248.

Fabiani R., 1915. Il Paleogene del Veneto. Memorie dell'Istituto Geologico della Regia Università di Padova 3, 1-336.

Forbes E., 1852. Monograph of the Echinodermata of the British Tertiaries. Palaeontographical Society of London, Monograph 6, 1-36.

Frisone V., Preto N., Pisera A., Agnini C., Giusberti C.A., Papazzoni A., De Angeli C., Beschin C., Mietto P., Quaggiotto E., Monaco P., Dominici S., Kiessling W., Luciani V., Roux M., Bosellini F.R., 2020. A first glimpse on the taphonomy and sedimentary environment of the Eocene siliceous sponges from Chiampo, Lessini Mts., NE Italy. Bollettino della Società Paleontologica Italiana 59, 299-313.

Goldfuss A., 1826-1833. Petrefacta Germaniae, tam ea, quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhelmiae Rhenanae, servantur quam alia quaecunque in Museis Hoeninghusiano Muensteriano aliisque, extant, iconibus et descriptionibus illustrata. Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angränzenden Länder, unter Mitwirkung des Herrn Grafen Georg zu Münster, herausgegeben von Professor Dr. August Goldfuss. Düsseldorf (Arnz and Comp.) 1, 1-242.

Hébert E., Munier-Chalmas E., 1877. Recherches sur les terrains tertiaires de l'Europe méridionale. Deuxième partie: Terrains tertiaires du Vicentin. Comptes Rendus de l'Académie des Sciences des Paris 85, 259-265.

Heinzeller T., Fricke H., Bourseau J.-P., Améziane-Cominardi N., Welsch U., 1996. *Cyathidium plantei* sp. n., an extant cyrtocrinid (Echinodermata, Crinoidea), morphologically identical to the fossil *Cyathidium depressum* (Cretaceous, Cenomanian). Zoologica Scripta 25, 77-84.

Hess H., 2011a. Isocrinida. In: Hess H., Messing C.G., Ausich W.I. (Eds.), Treatise on Invertebrate Paleontology, Part T, Echinodermata 2 (revised), Crinoidea, 3. The University of Kansas, Paleontological Institute, Lawrence, Kansas, 42-69.

Hess H., 2011b. Suborder Bourgueticrinina Sieverts-Doreck, 1953. In: Hess H., Messing C.G., Ausich W.I. (Eds.), Treatise on Invertebrate Paleontology, Part T, Echinodermata 2 (revised), Crinoidea, 3. The University of Kansas, Paleontological Institute, Lawrence, Kansas, 146-158.

ICZN (1999): International Code of Zoological Nomenclature, 4th edition. International Trust for Zoological Nomenclature, London, pp. 306.

Jaekel O., 1891. Ueber Holopocriniden mit besonderer Berücksichtigung der Stramberger Formen. Zeitschrift der deutschen geologischen Gesellschaft 43, 557-670.

Jaekel O., 1894. Entwurf einer Morphogenie und Phylogenie der Crinoiden. Sitzungs-Berichte der Gesellschaft der Naturforschenden Freunde zu Berlin 1894, 101-121.

Jaekel O., 1907. Ueber die Körperform der Holopocriniten. Neues Jahrbuch für Mineralogie, Geologie, Paläontologie, Festband 1907, 272-309.

Jagt J.W.M., 1999. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeastern Netherlands and northeastern Belgium. Part 2: Crinoids. Scripta Geologica 116, 59-255.

Kjaer C.R., Thomsen E., 1999. Heterochrony in bourgueticrinid sea-lilies at the Cretaceous/Tertiary boundary. Paleobiology 25, 29-40.

Klikushin V.G., 1979. [The microstructure of isocrinid columnals]. Paleontologicheskiy Zhurnal 1, 88-96 [in Russian].

Klikushin V.G., 1982. Cretaceous and Paleogene Bourgueticrinina (Echinodermata, Crinoidea) [*sic*] of the USSR. Geobios 15, 811-843.

Loriol P. de, 1879. Monographie des crinoïdes fossiles de la Suisse. Mémoires de la Société Paléontologique Suisse 6, 125-300.

Loriol P. de, 1882-1884. Crinoïdes. In: Paléontologie Française, 1 Série, Animaux invertébrés, Terrain Jurassique 1, 1-627.

Manni R., 2005. The non-isocrinid crinoids of the Michelotti Collection. Bollettino della Società Paleontologica Italiana 44, 211-218.

Manni R., Nicosia U., 1990. Jurassic and Lower Cretaceous crinoids of northern Turkey. METU, Journal of Pure and Applied Sciences 21, 361-375.

Manni R., Pacioni E., 2021. New records of the cyrtocrinid crinoids *Cyathidium gastaldii* (Michelin, 1851) and *Holopus spileccense* (Schlüter, 1878) from Eocene strata in Veneto, north-east Italy. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 301, 65-77.

Meneghini G., 1876. I crinoidi terziari. Atti della Società Toscana di Scienze Naturali 2, 36-59.

Merle D., Roux M., 2018. Stalked crinoids from Gan (Late Ypresian, southwestern France). Exceptional stereom preservation, paleoecology and taxonomic affinities. Swiss Journal of Palaeontology 137, 225-244.

Meyer H. von, 1836. Mittheilungen an Professor Bronn gerichtet. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1836, 55-61.

Meyer H. von, 1847. Mittheilungen an Professor Bronn gerichtet. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1847, 572-580.

Michelotti G., 1847. Description des fossiles des terrains miocènes de l'Italie septentrionale. Société Hollandaise des Sciences, Leiden (Arnz and Co.), 1-408.

Michelotti G., 1861. Description de quelques nouveaux fossiles du terrain miocène de la colline de Turin. Revue et Magazine de Zoologie 13, 353-355.

Milner G.J., 1989. The first record of an isocrinid crinoid from the Tertiary of Australia. Records of the Western Australian Museum 14, 385-389.

Moore R.C., 1967. Unique stalked crinoids from the Upper Cretaceous of Mississippi. University of Kansas Paleontological Contributions, Paper 17, 1-35.

Münster G.G. von, 1839. Beschreibung einiger neuer Crinoideen aus der Übergangsformation. Beiträge zur Petrefactenkunde 1, 1-124.

Nebelsick J.H., Rasser M.W., Bassi D., 2005. Facies dynamics in Eocene to Oligocene circumalpine carbonates. Facies 51, 197-216.

Nicosia U., 1991. Mesozoic crinoids from the north-western Turkey. Geologica Romana 27, 389-436.

Noelli A., 1900. Contribuzione allo studio dei crinoidi terziari del Piemonte. Atti della Società Italiana di Scienze Naturali 39, 19-49.

Oji T., 1985. Early Cretaceous *Isocrinus* from northeast Japan. Palaeontology 28, 629-642.

Oppenheim P., 1902. Revision der tertiären Echiniden Venetiens und des Trentino, unter Mittheilung neuer Formen. Zeitschrift der deutschen geologischen Gesellschaft 54, 159-283.

Orbigny A. d', 1850. Prodrome de Paléontologie Stratigraphique universelle des animaux mollusques et rayonnés faisant suite au cours élémentaire de paléontologie et de géologie stratigraphique. Paris (Masson) II, 1-427.

Papazzoni C.A., Bassi D., Fornaciari E., Giusberti L., Luciani V., Mietto P., Roghi G., Trevisani E., 2014a. Geological and stratigraphical setting of the Bolca area. In: Papazzoni C.A., Giusberti L., Carnevale G., Roghi G., Bassi D., Zorzin R. (Eds.), The Bolca Fossil-Lagerstätten: a window into the Eocene world. Rendiconti della Società Paleontologica Italiana 4, 19-28.

Papazzoni C.A., Carnevale G., Fornaciari E., Giusberti L., Trevisani E., 2014b. The Pesciara-Monte Postale Fossil-Lagerstätte: 1. Biostratigraphy, sedimentology and depositional model. In: Papazzoni C.A., Giusberti L., Carnevale G., Roghi G., Bassi D., Zorzin R. (Eds.), The Bolca Fossil-Lagerstätten: a window into the Eocene world. Rendiconti della Società Paleontologica Italiana 4, 29-36.

Pasotti P., 1929. Di alcuni crinoidi paleogenici con particolare riguardo a quelli di Gassino. Bollettino della Società Geologica Italiana 48, 71-89.

Perrier E., 1883. Sur un nouveau Crinoïde fixé, le *Democrinus parfaiti*, provenant des dragages du "Travailleur". Comptes Rendus de l'Académie des Sciences Paris 96, 450-452.

Perrier E., 1885. Les Encrines vivantes. Revue des Travailles Scientifiques, Paris 35, 690-693.

Rouault A., 1850. Description des fossiles du terrain Éocène des environs de Pau. Mémoires de la Société Géologique de France 3, 457-502.

Roux M., 1970. Introduction à l'étude des microstructures des tiges de Crinoïdes. Géobios 3, 79-98.

Roux M., 1974. Observations au microscope électronique à balayage de quelques articulations entre les ossicules du squelette des Crinoïdes pédonculés actuels (Bathycrinidae et Isocrinina). Travaux du Laboratoire de Paléontologie, Université de Paris, Faculté des Sciences d'Orsay 1974, 1-10.

Roux M., 1977. Les Bourgueticrinina (Crinoidea) recueillis par la Thalassa dans le Golfe de Gascogne: anatomie comparée des pédoncules et systématique. Bulletin du Muséum national d'Histoire naturelle, Zoologie 296, 25-83.

Roux M., 1978a. Les Crinoïdes pédonculés (Échinodermes) du genre *Conocrinus* provenant de l'Éocène des environs de Biarritz. Comptes Rendus de l'Académie des Sciences, Paris (D) 286, 265-268.

Roux M., 1978b. Importance de la variabilité de la forme chez les Bathycrinidae (Echinodermes, Crinoïdes): l'exemple de l'espèce éocène *Conocrinus doncieuxi* nov. sp. Comptes Rendus de l'Académie des Sciences Paris (D) 287, 797-800.

Roux M., Cahuzac B., Sztrákos K., 2006. Les paléoenvironnementes éocènes a crinoïdes pédonculés des marnes de Miretrain (Angoumé, SW France): interprétations paléobathymétriques. Comptes Rendus de Geociences 338, 262-271.

Roux M., Eléaume M., Améziane N., 2019. A revision of the genus *Conocrinus* d'Orbigny, 1850 (Echinodermata, Crinoidea, Rhizocrinidae) and its place among extant and fossil crinoids with a xenomorphic stalk. Zootaxa 4560, 51-84.

Roux M., Martinez A., Vizcaïno D., 2021. A diverse crinoid fauna (Echinodermata, Crinoidea) from the Lower Eocene of the Gulf of Languedoc (Corbières, Aude, southern France). Zootaxa 4963, 201-242.

Roux M., Montenat C., 1977. Sites à Crinoïdes pédonculés et bathymétrie des bassins messiniens dans les Cordillières bétiques orientales (Espagne méridionale). Bulletin de la Société Géologique de France 19, 405-416.

Roux M., Philippe M., 2021. Early Miocene stalked crinoids (Echinodermata) from the southern Rhodanian basin (southeastern France). Paleoenvironments and taxonomy. Zootaxa 5052, 301-331.

Roux M., Plaziat J.-C., 1978. Inventare des Crinoïdes et interprétation paléobathymétrique de gisements du Paléogène pyrénéen franco-espagnol. Bulletin de la Société Géologique de France 20, 299-308.

Rovereto G., 1914. Nuovi studi sulla stratigrafia e sulla fauna

dell'Oligocene Ligure. Genova (Oliviero), pp. 179.
Sacco F., 1905. Les étages et les faunes du bassin tertiaire du Piémont. Bulletin de la Société Géologique de France 5, 893-916.
Sars M., 1868. Mémoires pour servir à la connaissance des Crinoïdes vivants. Christiania (Brøgger and Christie), 1-65.
Schafhäutl K.F.E., 1854A. Beiträge zur näheren Kenntnis der Bayern'schen Veralpen. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1854, 513-559.
Schauroth K. von, 1855. Übersicht der geognostischen Verhältnisse der Gegend von Recoaro im Vicentinischen. Sitzungsberichte der kaiserlichen Akademie der Wissenschaften in Wien. mathematisch-naturwissenschaftliche Classe 17, 481-562.
Schlüter C., 1878. Über einige astylide Crinoiden. Zeitscrift der deutschen geologischen Gesellschaft 30, 28-66.
Schlotheim E.F. von, 1822. Nachträge zur Petrefactenkunde, Teil 1. Becker'sche Buchhandlung, Gotha, pp. 100.
Thomson C.W., 1872. On the crinoids of the "Porcupine" deep-sea dredging expedition. Proceedings of the Royal Society of Edinburgh 7 (1869-1872), 764-773.
Valette A., 1924. Note sur deux espèces de «*Conocrinus*» de l›étage Bartonien des environs de Vence. Bulletin de l›Association des Naturalistes de Nice et des Alpes Maritimes 11, 25-32.
Weber G.F., 1949. Class Echinoidea - sea urchins. Paleogene. Atlas of the guide forms of the fossil faunas of the U.S.S.R. 12, 143-152. [In Russian]
Wienberg Rasmussen H., 1961. A monograph of the Cretaceous Crinoidea. Biologiske Skrifter udgivet af det Kongelige Danske Videnskabernes Selskab 12, 1-428.
Wienberg Rasmussen H., 1978. Articulata. In: Moore R.C., Teichert C. (Eds.), Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, 3, 814-1027. The Geological Society of America, Boulder and The University of Kansas Press, Lawrence.
Zamora S., Aurell M., Veitch M., Saulsbury J., López-Horgue M.A., Ferratges F.A., Arz J.A., Baumiller T.K., 2018. Environmental distribution of post-Palaeozoic crinoids from the Iberian and south-Pyrenean basins, NE Spain. Acta Palaeontologica Polonica 63, 779-794.