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New Eocene species of the crinoid genera *Holopus* and *Cyathidium* (Cyrtocrinida: Holopodidae) from north-eastern Italy

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Abstract

Holopodidae is one of the three families in the order Cyrtocrinida that have extant representatives. Two genera have been described, *Holopus* and *Cyathidium*, both with extant species and fossil representatives dating back to the Cenomanian (Late Cretaceous). Eocene (Lutetian) holopodid material from the Chiampo Valley (north-eastern Italy) has recently been attributed to *H. spileccense*, the type-stratum and locality of which is the Ypresian of the nearby Spilecco Hill, and to *C. gastaldii* known from the Miocene of Turin. Here we describe new holopodid material from both Chiampo and Spilecco, comprising cups and numerous brachials. Using qualitative and quantitative characters, the Chiampo holopodids are deemed to be assignable to two new species: *Holopus fabianii* **sp. nov.** and *Cyathidium chiampoensis* **sp. nov.** The Chiampo material includes the first records of keystone plates and distal brachials for an extinct species of *Holopus*. New proximal brachials are described for *H. spileccense* but no keystone plate was found for this species. Access to the holotype of *Cyathidium gastaldii* has enabled a description of the specimen and a first diagnosis for the species. Formerly described cups, as well as a newly collected one, are attributed to *Cyathidium* sp. due to the lack of diagnostic characters. The affinities between *H. spileccense*, *H. fabianii* **sp. nov.** and the extant Indo-Pacific *H. alidis* suggest that these three species might share a common Gondwanan origin.

Key words: Ypresian, Lutetian, type-locality, Gondwana, Cengio dell'Orbo, Cava Boschetto, Chiampo, Spilecco Hill, Veneto region, keystone plate

Introduction

The Holopodidae is one of the three families in the order Cyrtocrinida (the others being the Sclerocrinidae and Eudesicrinidae) that have extant representatives (Hess & Messing 2011). Holopodids are stemless and directly attach to hard substrates with their aboral cup which has classically been considered to be composed only of the fused radials. Two genera are described within the family: *Cyathidium* and *Holopus*. In both genera, extant species possess the ability to roll up their arms to form a tight vault covering their distal arm segments and the tegmen (e.g., Améziane *et al.* 1999). Their general morphology thus resembles that of barnacles which is very peculiar among the Echinodermata. The tight vault made from the retracted crown is preserved only in a few fossil specimens of *Cyathidium* (e.g., Donovan & Jakobsen 2004). Usually, fossil holopodid remains comprise aboral cups and isolated brachials (see references listed in Manni & Pacioni 2021). For a long time, the sole fossil aboral cup attributable to the genus *Holopus* was *Cyathidium spileccense* Schlüter, 1878 from the Ypresian of north-eastern Italy (Spilecco

Hill). The discovery of an aboral cup of a second fossil representative of *Holopus* in the upper Campanian of northern Germany (Jagt *et al.* 2010) moved back the appearance of *Holopus* by some 20 Ma. This species has not been formally named and illustrated to date, but work is under way (J.W.M. Jagt, pers. comm., July 2024). The oldest holopodid species known is *C. depressum* Sieverts, 1932 from the upper Cenomanian of western Germany. Most recently, crinoidal material comprising cups and numerous brachials belonging to both holopodid genera has been reported from the lower Lutetian of north-eastern Italy (Frisone *et al.* 2020). Having studied a smaller number of specimens from the same Lutetian outcrop and level, Manni and Pacioni (2021) attributed brachials to *H. spileccense* and three cups to the Miocene species *C. gastaldii* (Michelin, 1851). Brachials from the lower Ypresian of Corbières in southern France were described as a new species, namely *H. plaziati* Roux, Martinez & Vizcaïno, 2021.

The aim of the present paper is to discuss the validity of taxonomic attributions of recently described Eocene holopodid material from north-eastern Italy to previously erected species. Did *H. spileccense* have a wider stratigraphic distribution (lower to middle Eocene) than previously thought? Is the same true for *C. gastaldii* (middle Eocene to Middle Miocene)? What are the possible relationships with extant species and what is their palaeogeographical context? To answer these questions, here we report on aboral cups and brachials of the rare *H. spileccense* newly collected from Ypresian strata at the type locality. We also describe in detail the relatively abundant Lutetian holopodid ossicles mentioned by Frisone *et al.* (2020) and attribute them to two new species, *Holopus fabianii* **sp. nov.** and *Cyathidium chiampoensis* **sp. nov.** Finally, we present a redescription of *Cyathidium gastaldii* based on the holotype.

Material and methods

A good understanding of the morphology of extant species is fundamental to identify ossicles in the washed fossil material. Therefore, to attribute the present fossil holopodid brachials we first studied the brachials in extant species of the family housed in the collections of the Muséum national d'Histoire naturelle, Paris (MNHN) (Table 1). The extant specimens were studied by scanning electron microscopy (SEM).

TABLE 1. Material of extant taxa examined.

Collection number	Taxon	Provenance	Material	Figures	Remarks
MNHN-IE-2013-11946	<i>Holopus rangii</i>	Guadeloupe	Whole organism	Fig. 6	
MNHN-IE-2013-10012	<i>Holopus alidis</i>	New Caledonia	Whole organism	Figs. 4A, D, E, 5	Paratype 4
MNHN-IE-2014-2185	<i>Holopus alidis</i>	New Caledonia	Whole organism	Fig. 4B, C	Juvenile

Since fossil crinoids are usually found disarticulated, it is difficult to attribute isolated ossicles to a nominal species. Therefore, the sampling location and specially the use of topotypical material become crucial for assigning ossicles with more confidence. For this reason, we searched for new material at the type-locality of *H. spileccense*. A sample of 10 kg of crinoidal calcareous red marl was collected at Spilecco in September 2019, washed and sieved on a 500 µm mesh. Residues were then sorted under a stereomicroscope and about 10,000 crinoid ossicles were identified. In a sub-sample of 3500 crinoid ossicles only 0.74% (25 ossicles) could be attributed to *Holopus*, and 84% were columnals belonging to xenomorphic stalks of Rhizocrinidae.

For holopodids from the Chiampo Valley, ossicles were handpicked under the stereomicroscope from the residues of the > 500 µm fraction obtained from the fossiliferous tuffite horizon (“*Lophoranina* tuff”) at the Cengio dell’Orbo quarry (residues of the Lovato Collection). Most of the specimens (more than one hundred ossicles) were obtained from the residues labelled MCZ 1, 6 and 7, originally housed at the Museo di Archeologia e Scienze Naturali “G. Zannato” of Montecchio Maggiore (Vicenza, Italy).

The fossils obtained from the MCZ residues, described herein, are now housed in the Museum of Nature and Humankind of the University of Padua (MGP-PD), Section of Geology and Palaeontology (Table 2). The holotype of *Cyathidium gastaldii* (Michelin, 1851) is housed in the palaeontological collection of the MNHN.

TABLE 2. Cenozoic Holopodidae examined. MGP-PD: Museum of Nature and Humankind of the University of Padua; MNHN: Muséum national d’Histoire naturelle, Paris. Spilecco Hill: near Bolca, lower Ypresian; Chiampo: Cengio dell’Orbo quarry, Chiampo Valley, lower Lutetian; Superga Hill: near Turin, Miocene (Serravallian); Man21: Manni & Pacioni, 2021.

Collection number	Taxon	Provenance	Material	Figures	Remarks
MGP-PD 33229	<i>C. chiampoensis</i>	Chiampo	1 cup	Fig. 8A–B	Holotype
MGP-PD 33230	<i>C. chiampoensis</i>	Chiampo	1 cup	Fig. 8C	Paratype
MGP-PD 33231	<i>Cyathidium</i> sp.	Chiampo	1 cup	Not fig.	
MGP-PD 31469, 31471	<i>Cyathidium</i> sp.	Chiampo	2 cups	Fig. 8D–E	Man21 Fig. 3A, C
MGP-PD 31470	<i>Cyathidium</i> sp.	Chiampo	1 cup	Not fig.	Man21 Fig. 3B
MNHN-F-R68284	<i>C. gastaldii</i>	Superga Hill	1 cup, 2 casts	Fig. 8F–G	Holotype
MGP-PD 33232	<i>H. fabianii</i>	Chiampo	1 cup	Fig. 8H–I	Holotype
MGP-PD 33233	<i>H. fabianii</i>	Chiampo	1 cup	Fig. 8J	Paratype 1
MGP-PD 33234	<i>H. fabianii</i>	Chiampo	6 cups	Not fig.	Paratypes 2–7
MGP-PD 33235	<i>H. fabianii</i>	Chiampo	12 IBrax	Fig. 10A–L	Paratypes 8–19
MGP-PD 33236	<i>H. fabianii</i>	Chiampo	5 IIBr	Fig. 11A–H	Paratypes 20–24
MGP-PD 33237	<i>H. fabianii</i>	Chiampo	14 IBrax	Not fig.	Paratypes 46–59
MGP-PD 33238	<i>H. fabianii</i>	Chiampo	21 IIBr	Not fig.	Paratypes 25–45
MGP-PD 33239	<i>H. fabianii</i>	Chiampo	17 IBrax	Not fig.	Supp. Table 1
MGP-PD 33385	<i>H. fabianii</i>	Chiampo	8 IIBrax	Not fig.	Supp. Table 2
MGP-PD 33240	<i>H. fabianii</i>	Chiampo	57 IIBr	Not fig.	Wp<2.8 mm
MGP-PD 33241	<i>H. fabianii</i>	Chiampo	14 IIBr	Not fig.	Wp>2.8 mm
MGP-PD 31438– 31442	<i>H. fabianii</i>	Chiampo	5 IBrax	Not fig.	Man21 Fig. 4
MGP-PD 33242	<i>H. spileccense</i>	Spilecco Hill	3 cups	Fig. 12D–G	
MGP-PD 33243	<i>H. spileccense</i>	Spilecco Hill	6 cups	Not fig.	
MGP-PD 33244	<i>H. spileccense</i>	Spilecco Hill	6 IBrax	Fig. 13A–F	
MGP-PD 33245	<i>H. spileccense</i>	Spilecco Hill	1 IBr	Fig. 12C	bivium?
MGP-PD 33246	<i>H. spileccense</i>	Spilecco Hill	5 IBrax	Not fig.	
MGP-PD 33247	<i>H. spileccense</i>	Spilecco Hill	2 IIBr	Fig. 12A–B	
MGP-PD 33248	<i>H. spileccense</i>	Spilecco Hill	2 IIBr	Not fig.	

Quantitative measurements on fossils were done using callipers, stereomicroscope or SEM views following the measurement points described in figure 1. Prior to SEM observations, crinoid ossicles were cleaned ultrasonically, and platinum coated. Observations were done under a Hitachi SU3500 SEM (15kV) at the MNHN’s technical platform for electron microscopy. The holotype of *C. gastaldii* was photographed using focus-stacking on a Zeiss Axio Zoom V16 microscope. The samples MGP-PD 31469–71 were photographed using focus-stacking with an Olympus OM-D E-M10 Mark II camera and Olympus M.Zuiko Digital ED 60mm macro lens.

For terminology of qualitative and quantitative characters reference is made to figure 1. Additional terms may be found in Hess and Messing (2011) and Roux *et al.* (2021).

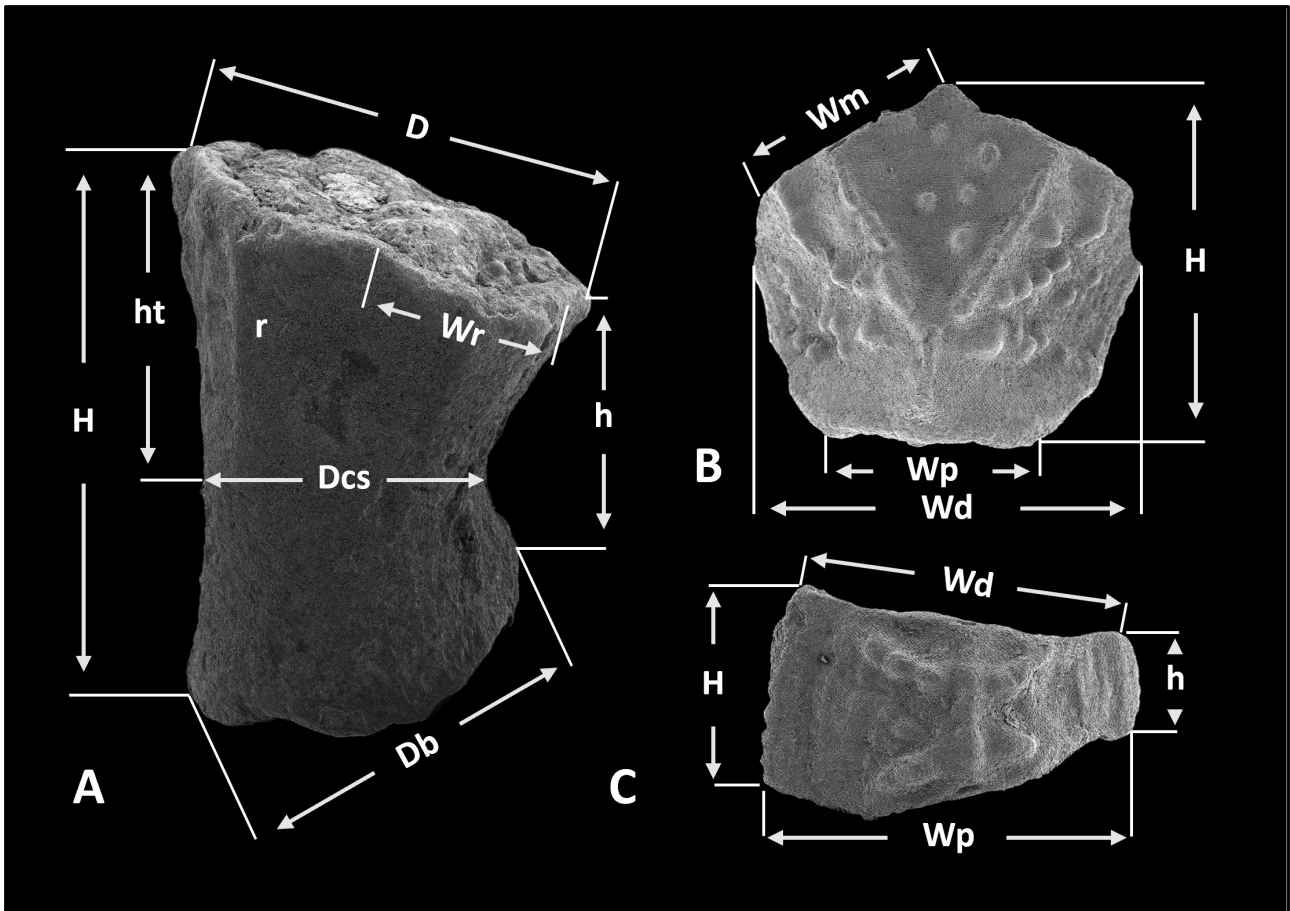


FIGURE 1. Characters measured in ossicles of fossil Holopodidae. A. Aboral cup, D: adoral diameter, Db: attachment disk diameter, Dcs: minimum diameter (constriction), H: maximum height, h: minimum height, ht: maximum height of adoral part, r: radial ridge, Wr: width of the radial articulation. B. Axillary primibrachial (IBrax), H: maximum height, Wd: maximum (distal) width, Wm: width of distal synarthry, Wp: minimum (proximal) width. C. Secundibrachial (IIBr) of proximal series, H: maximum lateral height, h: minimum lateral height, Wd: distal width, Wp: proximal width.

Geological Setting

The two studied sites with holopodids are located in two parallel valleys within the eastern Lessini Mountains (Southern Alps, Verona and Vicenza provinces, Veneto region, north-eastern Italy) (Fig. 2) and belong to the South Alpine foreland. Palaeogeographically, the Lessini Mountains were part of a structural high (the Trento Plateau, characterized by pelagic sedimentation) belonging to the Adriatic Plate initially derived from Gondwanaland. Starting in the late Paleocene, active tectonics associated with magmatic activity developed extensional structures in this area in response to active convergence between the European and Adriatic plates (e.g., Barbieri *et al.* 1991; Beccaluva *et al.* 2007; Brombin *et al.* 2019; Zampieri 1995; Fig. 2). Both magmatism and tectonism had a marked impact on the sedimentation in the Lessinian area that, at least since the early Eocene, was characterized by carbonate shallow-water sedimentation with uplifted blocks and grabens inducing various unstable environments. Eventually, the Trento Plateau was partly transformed into a carbonate platform, the so-called “Lessini Shelf” that persisted until the Oligocene (e.g., Bosellini 1989; Bosellini & Papazzoni 2003; Luciani 1989). The eastern Lessini Mountains area belongs to an extensional structure called the Alpone-Agno or Alpone-Chiampo semigraben (e.g., Barbieri *et al.* 1991; Zampieri 1995), bounded to the west by the Castelvevo normal fault (Fig. 2). This fault was active during the Eocene, controlling the accumulation of volcanics, their reworked products as well as interlayered carbonates (Barbieri & Zampieri 1992). Several magmatic pulses were separated by periods of magmatic inactivity during which marine sedimentation took place (De Vecchi & Sedeà 1995).

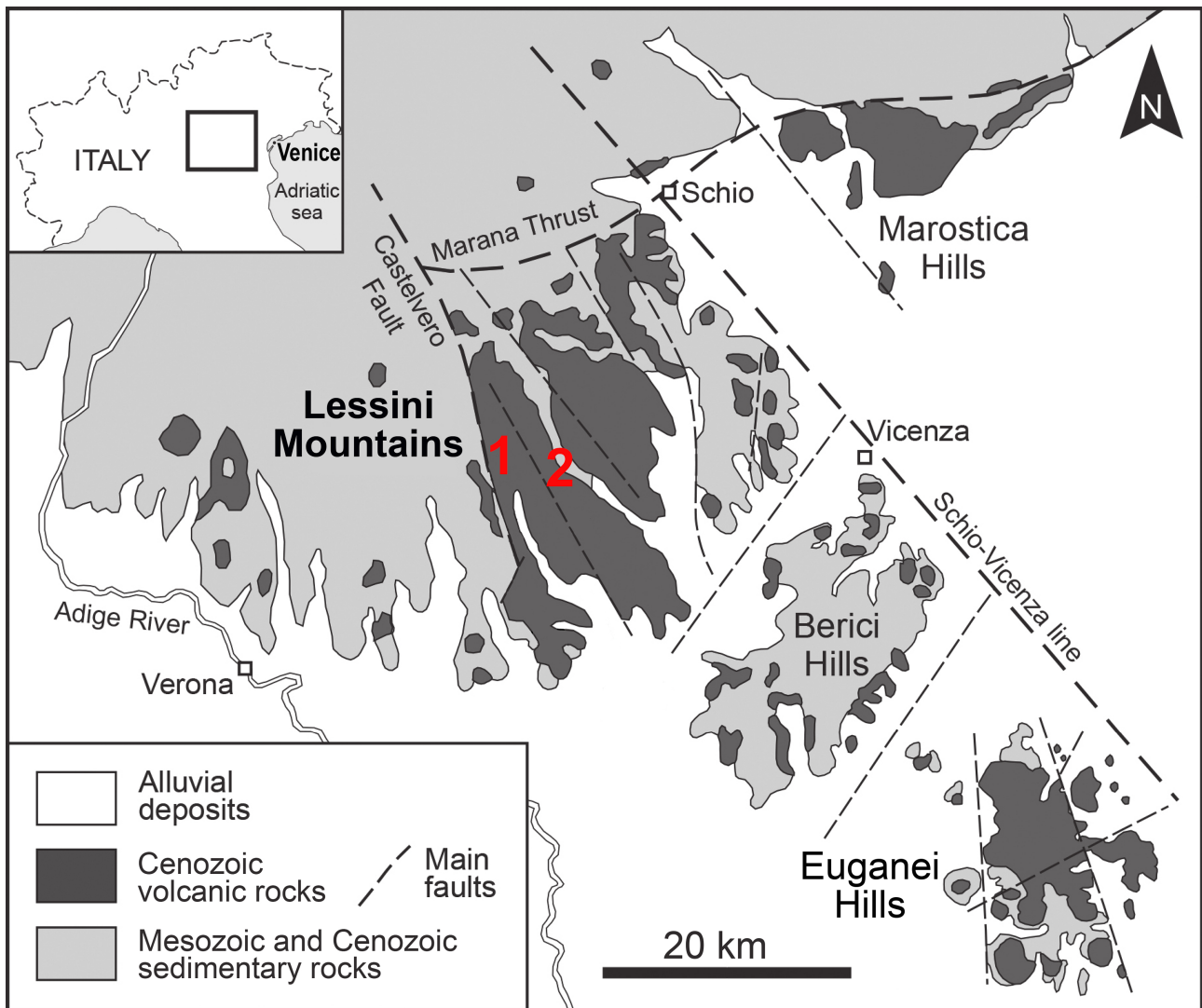


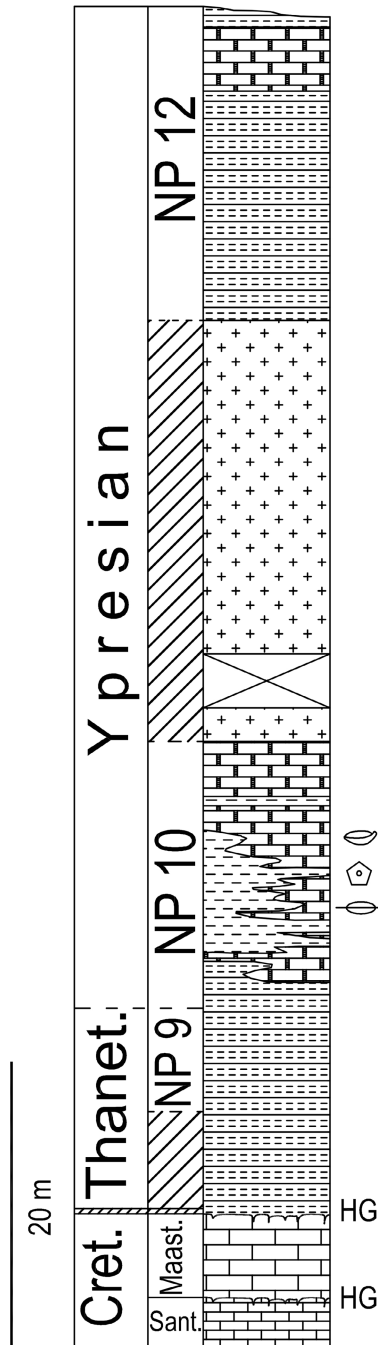
FIGURE 2. Simplified geologic map of the study area showing the Spilecco Hill site (1), close to Bolca (Verona province), and (2) Cengio dell’Orbo quarry (known also as “Boschetto di Chiampo” quarry), close to Chiampo (Vicenza province), Lessini Mountains of Veneto region, north-eastern Italy (modified from Mattioli *et al.* 2016).

The older site is the Spilecco Hill, in the Alpone Valley, less than half a kilometre north-west of the village of Bolca (Fig. 2). Its fossiliferous reddish and greyish marls and limestones are mainly characterized by the presence of larger foraminifera, crinoids, bryozoans, brachiopods and shark teeth (e.g., Massalongo 1850; Medizza 1980; Papazzoni *et al.* 2014; Fig. 3). These beds have been dated as early Ypresian (calcareous nannofossil Zone NP10 of Martini 1971 and SB Zone 7 of Serra-Kiel *et al.* 1998; see Papazzoni *et al.* 2014; Fig. 3) and represent periplatform deposits resedimented in a basinal setting, attesting to nearby initiation of shallow-water sedimentation (Papazzoni *et al.* 2014; Trevisani & Papazzoni 2003). Spilecco has yielded an abundant crinoid fauna, dominated by taxa with xenomorphic stalks and is the type-locality of *H. spileccense*.

The main site investigated herein is located on the western side of the Chiampo Valley in the Cengio dell’Orbo quarry (45° 32’ 25.56” N, 11° 15’ 44.47” E, referred to as “Cava Boschetto di Chiampo” in Beccaro *et al.* 2001 and Beschin *et al.* 1991; Fig. 2). Along the Chiampo Valley, building stone was extracted from the so-called “Chiampo limestone” in several quarries until the 1990s (now closed and mostly inaccessible). This is a local informal unit belonging to the so-called lower-middle Eocene “Nummulitic limestones”, widespread in the western Veneto region (Frisone *et al.* 2020). Many volcanoclastic horizons with limited lateral extension and belonging to different stratigraphical levels are intercalated in the “Nummulitic limestones” and some of them are very fossiliferous, such as the so-called “*Lophoranina* tuff” in the Chiampo Valley which is particularly rich in crustaceans (see Beschin *et al.* 1991, 2016).

Spilecco Hill

(A)(B)



Cengio dell'Orbo

(A)

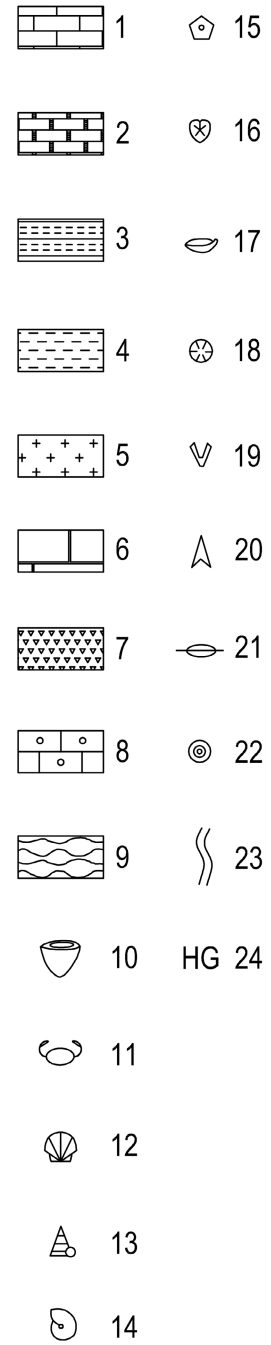
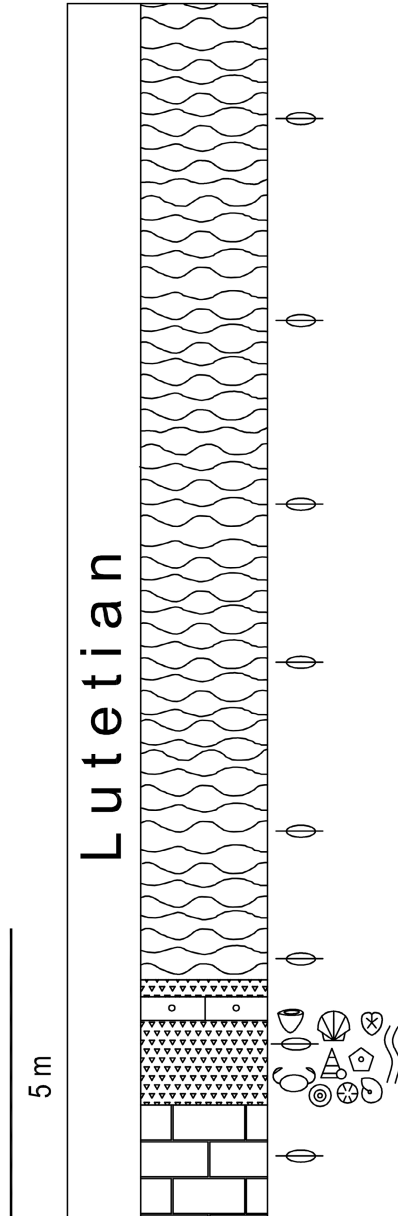


FIGURE 3. Simplified stratigraphic log of the Spilecco succession, Bolca (modified and redrawn from Medizza, 1980 and Papazzoni *et al.* 2014) and stratigraphic log of the Cengio dell'Orbo quarry, near Chiampo, Lessini Mountains of Veneto region, north-eastern Italy (modified and redrawn from Beccaro *et al.*, 2001 and Beccaro, 2003). A) Chronostratigraphy, B) Calcareous nannofossil zones of Martini (1971). Legend. 1) pelagic limestones (Scaglia Rossa); 2) limestones, marly limestones and calcareous marls; 3) bedded volcanoclastic rocks; 4) clayey marls and volcanic clays; 5) hyaloclastites and volcanic rocks; 6) fossiliferous packstones/grainstones with planar stratification; 7) fossiliferous ruditic tuffites and hyaloclastites ("Lophorantina tuff" Auct.); 8) arenaceous limestones; 9) fossiliferous subnodular packstones/grainstones; 10) sponges; 11) crabs; 12) bivalves; 13) gastropods; 14) cephalopods; 15) crinoids; 16) echinoids; 17) brachiopods; 18) corals; 19) bryozoans; 20) shark teeth; 21) larger foraminifera; 22) calcareous algae; 23) bioturbations; 24) hardgrounds. Cret.=Cretaceous; Sant.=Santonian; Maast.=Maastrichtian; Thanet.=Thanetian.

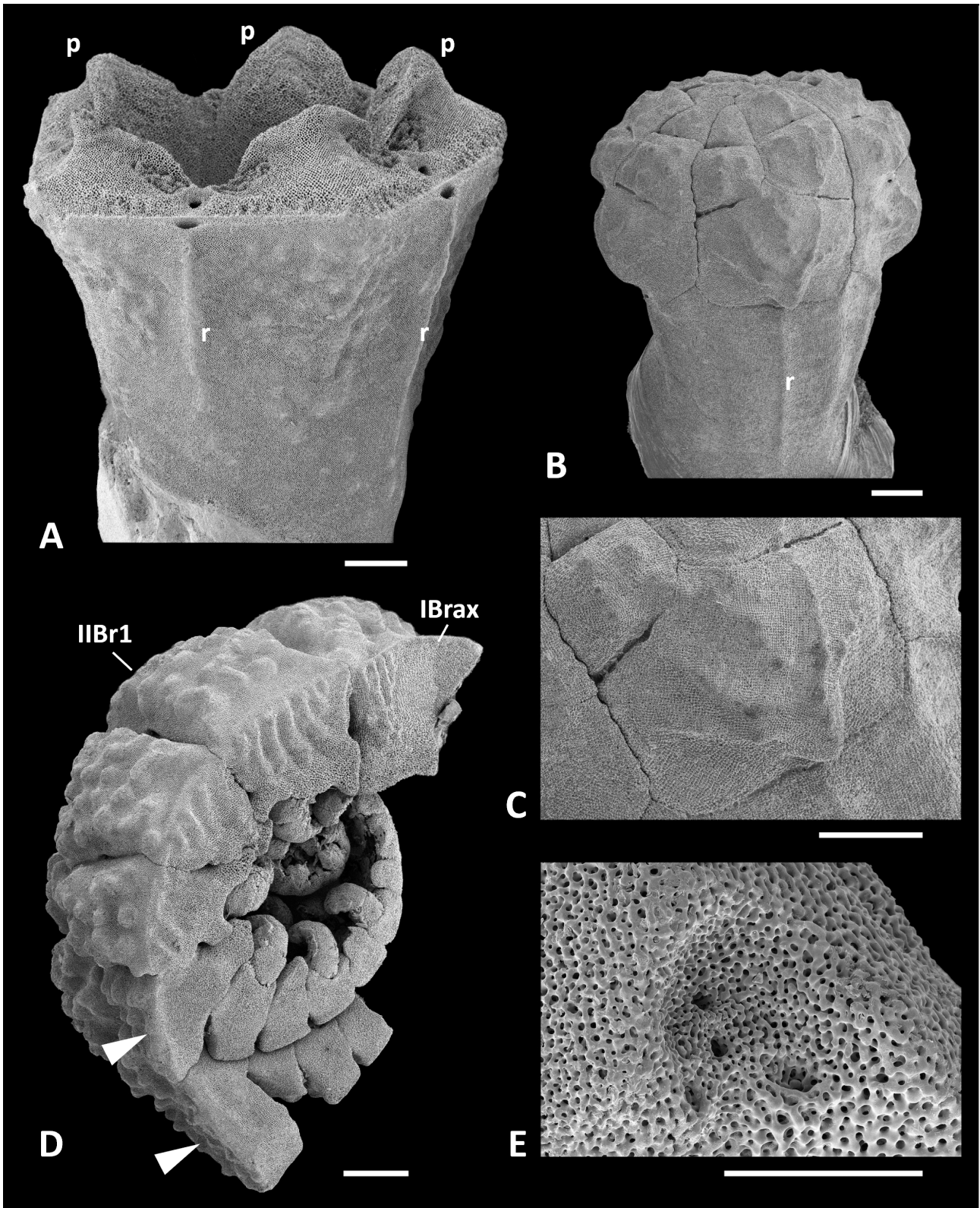


FIGURE 4. *Holopus alidis*. A: lateral distal view of paratype 4 without its arms (MNHN-IE-2013-10012); B: lateral distal view of a juvenile specimen with closed crown (MNHN-IE-2014-2185), C: close-up of IBrax of B; D: lateral oblique view of rolled arm attached to IBrax (arrow heads: keystone plates (IIBr4) of the two arms of the same ray) (MNHN-IE-2013-10012), E: pinnule socket on IIBr1 of Fig. 5B (adoral part at bottom with two small muscular pits); p: interradial process, r: thin radial ridge. Scale bars: 0.5 mm in E, 1.0 mm in all others.

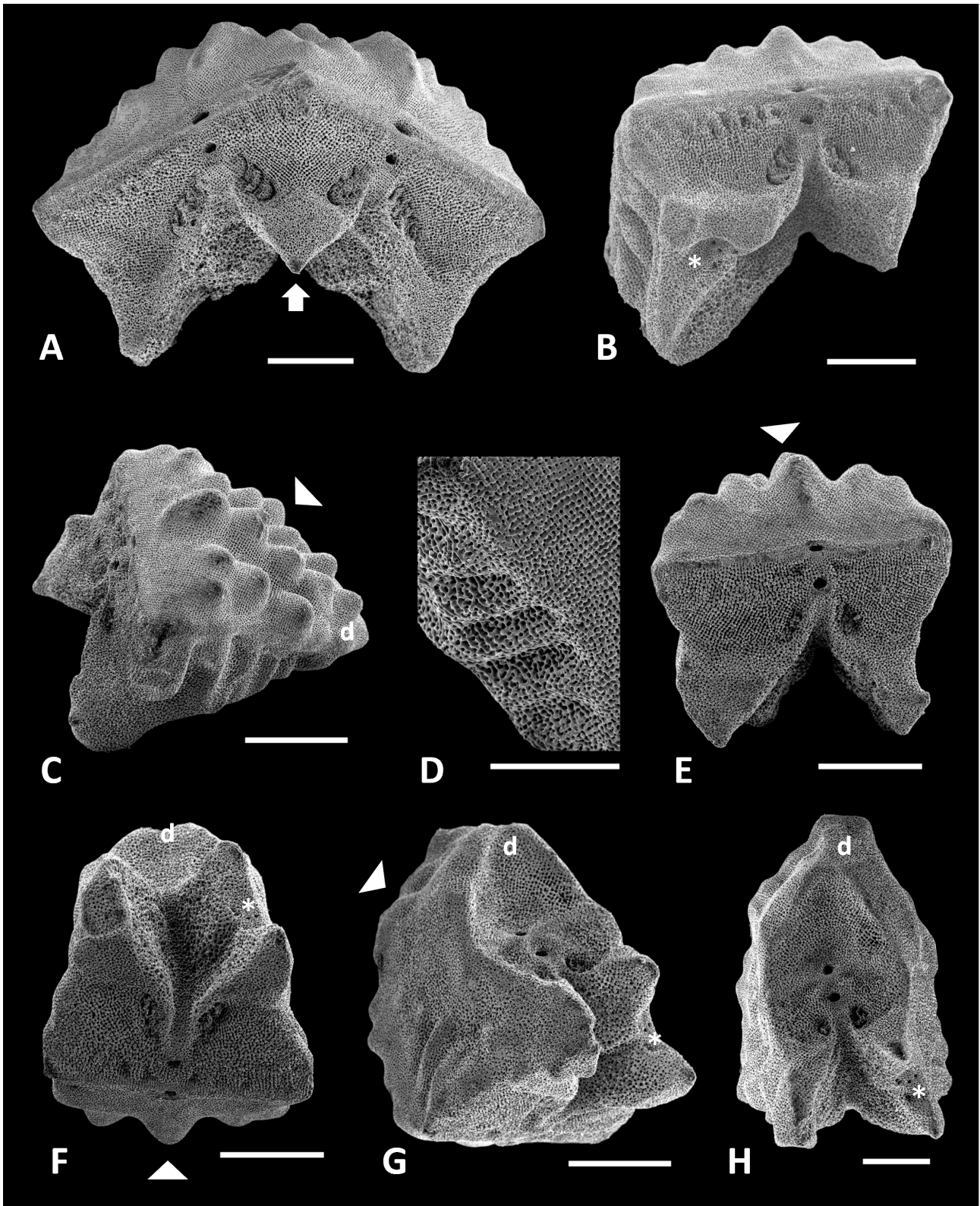


FIGURE 5. *Holopus alidis* (MNHN-IE-2013-10012). A: distal view of IBrax; B: adoral distal view of IIBr1; C–H: keystone plate (IIBr4) ending proximal brachial series (e.g., see arrow head in Fig. 4D), C: outer proximal side view (proximal muscular synarthrial articulation to IIBr3 at left), D: close-up of lateral crenulation, E: proximal muscular synarthry, F: proximal adoral view, G: oblique distal lateral view, H: distal muscular synarthry (articulation to distal brachial series) at opposite side of external surface; arrow: adoral process, arrow heads: location of external triangular surface shown in C; d: distal tip of the keystone plate; *: pinnule insertion. Scale bars: 0.5 mm in D, 1.0 mm in all others.

At the Cengio dell'Orbo quarry such a horizon, a tuffite composed of rounded volcanic fragments, calcareous bioclasts and calcitic cement, yielded an assemblage representing a mixture of shallow and deep marine organisms such as larger foraminifera, decapod crustaceans, molluscs, sponges, echinoderms (crinoids and echinoids), bryozoans, rare corals, and calcareous algae (Fig. 3). Siliceous sponges represent the most characteristic macrofaunal element of this tuffite (Frisone *et al.* 2016, 2020) whose calcareous nannofossil content suggests a lower Lutetian age (zones CNE8–CNE9 of Agnini *et al.* 2014, likely correlative with the upper part of NP14–lower part of NP15 zones of Frisone *et al.* 2016, 2020; Martini 1971). According to Beccaro *et al.* (2001) and Frisone *et al.* (2020) the site represents a distal oligophotic to aphotic part of a distally steepened carbonate ramp at a water depth below 200 m. The crinoids from the fossiliferous tuffite horizon of the Cengio dell'Orbo quarry were recently investigated by Frisone *et al.* (2020), Manni and Pacioni (2021) and Manni (2022).

Outline of extant Holopodidae morphology

To date, three extant species have been described in the genus *Cyathidium*. *Cyathidium foresti* Cherbonnier & Guille, 1972 (north-central Atlantic Ocean) is the largest species with an aboral cup diameter (D) of up to 20 mm and a height (H) below 13 mm. *Cyathidium plantei* Heinzeller, Fricke, Bourseau, Améziane-Cominardi & Welsch, 1996 (south-western Indian Ocean) is of medium size (D up to 9.6 mm, H very variable). *Cyathidium pourtalesi* Améziane, Bourseau, Heinzeller & Roux, 1999 (tropical western Atlantic Ocean) is the smallest extant described species (D up to 6.3 mm, H < 1.5 mm). Before 2008, two extant *Holopus* species had been described. *H. rangii* Orbigny, 1837 (tropical western Atlantic Ocean) is the largest with a total height of up to 40 mm (including retracted crown). Its aboral cup has a maximum D of *c.* 25 mm and a maximum H of *c.* 30 mm. *Holopus alidis* Bourseau, Améziane-Cominardi, Avocat & Roux, 1991 (south-western Pacific Ocean) has a more moderate size with a total height of up to 22 mm and the aboral cup's maximum D and H are *c.* 9 mm and 13 mm, respectively. A third *Holopus* species, closely related to *H. rangii* in morphology and size has since been described from the Caribbean based on a single specimen: *H. mikihe* Donovan & Pawson, 2008. Heinzeller *et al.* (1997) demonstrated that in Holopodidae the two primibrachials (IBr1+IBr2ax) fuse during early postlarval ontogeny. We here designate this fused IBr observed in adults as IBrax. According to Améziane *et al.* (1999), comparative anatomy in extant holopodid species shows a continuum of forms due to various heterochronic processes from *C. pourtalesi* to *H. rangii*. Table 3 lists some of the main morphological characters that discriminate between *Cyathidium* and *Holopus*.

TABLE 3. Main qualitative characters differentiating *Cyathidium* and *Holopus* modified from Roux *et al.* (2021).

	Characters	<i>Cyathidium</i>	<i>Holopus</i>
Closed crown	Outer convexity	Weak to moderate	Strongly marked
	Number of IIBr visible	1, rarely 2	usually more than 3
	Maximum diameter	Radial or Ibrax circlet	IIBr1–3 circlet
	Maximum Ibrax width	Proximal facet (Wp)	Distal third (Wd)
	H/Wd of Ibrax	<0.7	>0.7
	Ibrax shape	Subtrapezoidal, very obtuse distal angle	Subpentagonal, marked distal angle
	IIBr1 shape	Trapezoidal to triangular	Subrectangular
Aboral cup	Constriction of radial ring	Variable or absent	Usually marked
	Growth rings on external surface	Usually conspicuous	Usually absent
	Outer interradian process on adoral face	Small but usually present	Absent or inconspicuous

Holopus alidis (Figs. 4, 5) shares with species of *Cyathidium* a pronounced differentiation of the arms into two segments. The proximal arm segments form a protective vault that is tightly assembled when the crown retracts thanks to lateral symplexial crenulations (Fig. 3B). The distal arm segments curl under this vault (Fig. 4D) (Améziane *et al.* 1999; Bourseau *et al.* 1991). In *H. alidis* the proximal segment contains 3 to 4 IIBr, exceptionally 5, whereas

it is reduced to 1 IIBr, exceptionally 2, in *Cyathidium*. This proximal arm part ends in a specialized secundibrachial that we refer to as the keystone plate. It usually presents a triangular or subrectangular external face and peculiar muscular synarthries (Fig. 5C–H). This type of differentiated ossicle does not exist in the Caribbean *H. rangii* and *H. mikihe* (e.g., Donovan 1992; Donovan & Pawson 2008).

Both Caribbean species have an aboral cup with an adoral diameter (D) usually between 12 and 24 mm, the largest specimen reaching 31.2 mm (Carpenter 1884; Syverson *et al.* 2015), and a ratio $H/D < 1.1$. *Holopus alidis* has an aboral cup that is markedly constricted in the aboral quarter, usually taller than wide ($H/D > 1$) and the largest known specimen is smaller in size ($D = 9.4$ mm) than the Caribbean species (Bourseau *et al.* 1991). Donovan and Pawson (2008) considered that the three species are distinguished mainly by their ornamentation and depth distribution. They described *H. mikihe* as having a smooth aboral cup with a pentagonal cross section, and presenting very faint radial ridges, as well as smooth primibrachials, and each secundibrachial bearing a single, coarse aboral tubercle. In *H. rangii* the ornamentation varies greatly (Donovan & Pawson 2008). However, the aboral cup often shows well-marked radial ribs accompanied by a few scattered tubercles, and more or less marked interrachial depressions, while the arms are covered with multiple tubercles more or less aligned, sometimes forming almost a radial ridge (Agassiz & Pourtalès 1874; Carpenter 1884; Donovan 1992). In *H. alidis*, the aboral cup displays narrow, often prominent, radial ribs (Fig. 4A, B), sometimes formed by an alignment of small tubercles. The primibrachials have fine radial ridges that are more or less distinct and sometimes branch forming a Y-shaped ridge (Fig. 4C). The proximal IIBr are densely covered with prominent tubercles (Fig. 5C) and display one or two radial ridges on the most proximal brachials (Bourseau *et al.* 1991, present paper).

In the present study of Eocene holopodids, for *Cyathidium* we only have identified aboral cups, whereas for *Holopus* we have found both aboral cups and brachials. To compare brachial variations within the genus *Holopus*, it is useful to discuss in detail some morphological characters observed in extant species. In *H. rangii* the axillary primibrachials are more robust (Fig. 6A, B) than in *H. alidis* (Fig. 5A), with an outer surface sometimes almost hemispherical. The two adjacent half-synarthries along the axillary's plane of symmetry form a very prominent adoral process framed by the ramifications of the feeding groove. The strongly oblique distal articulations of the single primibrachial results in a highly asymmetrical appearance of the first secundibrachials (Figs. 5B, 6D, 10D). This asymmetry is usually restricted to or disappears beyond IIBr2 (Fig. 6F). The fulcral ridge is as long as the maximum brachial width axis (W) (Figs. 5B, 5E, 6D). The width of the muscular synarthries of the proximal brachials exceeds their height. They have a very narrow aboral ligament area without galleried stereom (Fig. 6C). The latter is sometimes difficult to distinguish and may appear restricted to the central pit (Fig. 4A) (Améziane *et al.* 1999). The fulcral ridge is bordered by an irregular adoral crenularium, better developed in *H. alidis* (Fig. 5A, B) than in *H. rangii* (Fig. 6A–D) which tends to disappear in more distal brachials (Fig. 5E). The surface of the adoral areas, concave and widely developed, shows labyrinthic stereom that does not allow to discern a boundary between the inner ligaments and the muscles. The joints of the distal brachials from the proximal arm series are taller than wide, with facets separated into two parts by a discrete fulcral ridge (Fig. 5H).

The pinnule sockets show very rudimentary symmetric synarthries, with the axial nerve canal surrounded by three pits that are likely related to the innervation of the two muscle areas and the aboral ligament (Figs. 4E, 6E). This articulation pattern is also observed in the brachials of early post-larval specimens of isocrinids (Améziane *et al.* 2023, fig. 9). Symplexial crenulations develop on the lateral faces of the proximal brachials and disappear beyond the keystone plate in *H. alidis* and *Cyathidium* (Figs. 4D and 5D). In *H. rangii*, which do not possess differentiated keystone plates, this crenulation is present mainly on the proximal part of the arm (Carpenter 1884, pl. 5a, fig. 3; Donovan 1992, figs. 5, 12).

Environment of extant Holopodidae

At a depth of 420–500 m off the Açores, Wisshak *et al.* (2009) observed *in situ* *Cyathidium foresti* closely associated with the large oyster *Neopycnodonte zibrovii* in particularly high densities on steep submarine cliffs including bedrock overhangs. *Cyathidium foresti* occurs directly attached to the oysters as well as the bedrock. Its depth range is from 420 m to 843 m, possibly 900 m (Améziane *et al.* 1999). Cherbonnier and Guille (1972, figs. B and H) figured juveniles of this species nested inside the calycinal cavity of dead individuals, allowing three generations to overlap. The other two species of *Cyathidium* are known only from relatively shallower depths in similar environments, without association with oysters. *Cyathidium plantei* is known to live between 196–203 m off the Comoros inside

caves in steep basaltic drop-offs (Heinzeller *et al.* 1996), and *Cyathidium pourtalesi* between 171–249 m off the Bahamas and Jamaica (Améziane *et al.* 1999). The latter species may also occur at greater depths (430–600 m) but is difficult to distinguish from alleged *Holopus* juveniles (Syverson *et al.* 2015).

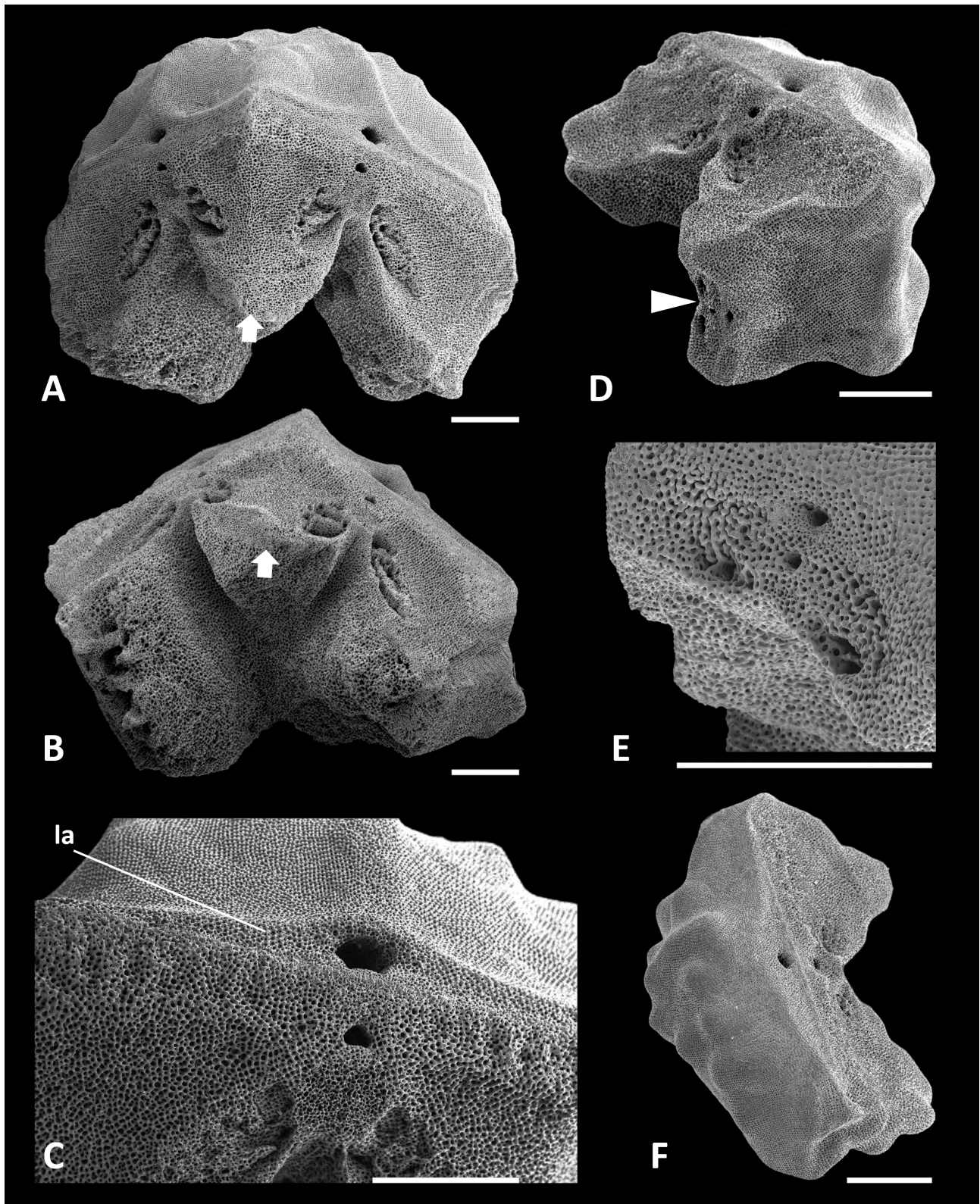


FIGURE 6. *Holopus rangii* (MNHN-IE-2013-11946). A–C: IBrax, A: oblique view of distal muscular synarthries, B: adoral view, C: close-up of fulcral ridge and outer ligament area (la) of proximal muscular synarthry, D–E: IIBr1, D: oblique distal view, E: close-up of pinnule socket, F: oblique aboral view of IIBr2 with proximal synarthrial facet; arrow: adoral interradial process, arrow head: pinnule socket. Scale bars: 1 mm.

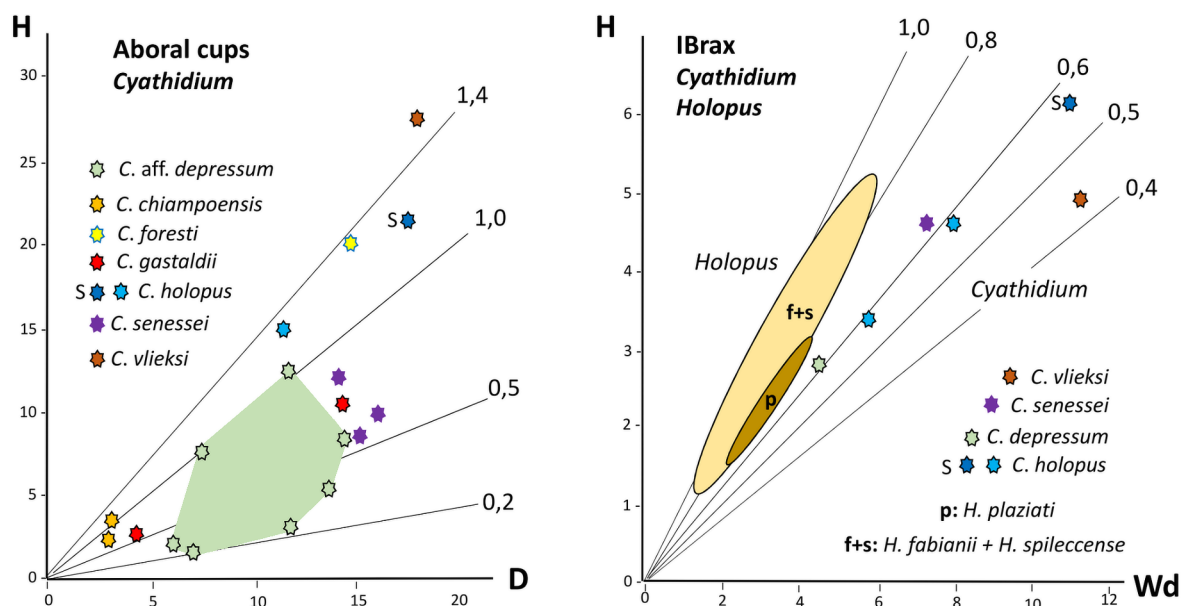


FIGURE 7. Main quantitative characters of aboral cup and IBrax in fossil Holopodidae. S: *Cyathidium holopus* from Seymour Island. Straight lines: values of H/D and H/Wd. Other values in mm.

Since the first *in situ* observations of *H. rangii* off Jamaica (Macurda & Meyer 1974), *Holopus* has been encountered on numerous occasions during dives in the Caribbean Sea off Bahamas and Honduras at depths from 100 m to 758 m (Donovan & Pawson 2008; Syverson *et al.* 2015). Specimens were invariably attached to hard rock, usually under overhangs, similar to *Cyathidium*. The holotype of *H. mikihe* was collected at a depth of 758 m yet Syverson *et al.* (2015) recorded a population of this species with numerous specimens from depths of 430 m to 640 m. *Holopus rangii* occurs at depths ranging from 100 m to 654 m (Donovan & Pawson 2008; Meyer *et al.* 1978) with dense populations at a depth range of 274–305 m off Jamaica (Macurda & Meyer 1974). In the southwestern Pacific, *H. alidis* was first collected off New Caledonia at a depth range of 375–470 m (Bourseau *et al.* 1991). New investigations around New Caledonia have sampled 10 new specimens at depths of 300–437 m, one of which is a juvenile (Martinez-Soares *et al. in prep*). One individual has also been trawled on a seamount of the Tonga Islands at depths between 664–781 m, nearly doubling this species' depth range.

Taxonomy

Family Holopodidae Zittel, 1879

Remarks. Sieverts-Doreck (1951) believed that some ossicles and deformed *Eugeniocrinus* cups figured by Remeš (1902: pl. 19, figs. 11 a–c, 12–15) from the Štramberg Tithonian could belong to an Upper Jurassic species of *Cyathidium*. However, the figure is too imprecise to confirm an attribution to Holopodidae. The mere inclusion of *Cyathidium depressum* in a long list of cyrtocrinids cited from Lower Cretaceous Štramberg-type limestones (Salamon & Gorzelak 2010: 871) cannot be taken into account without a critical analysis of the material concerned. Moreover, the attribution to *C. senessei* (Valette *in* Lambert & Valette, 1934) of a very poorly preserved axillary from the Santonian of Poland by Salamon and Gorzelak (2011: 311, fig. 2C, D) is highly questionable. Here, we consider that the appearance of Holopodidae prior to the Cenomanian has not been demonstrated.

It appears that the H/Wd ratio of IBrax is the best quantitative character to discriminate between the two genera in the family (>0.7 in *Holopus*, <0.7 in *Cyathidium*) (Fig. 7).

Stratigraphic distribution. Upper Cenomanian–Recent.

Genus *Cyathidium* Steenstrup in Michaelis & Scherk, 1847

Type-species. *Cyathidium holopus* Steenstrup in Michaelis & Scherk, 1847, by monotypy.

Synonymy. *Cyathidium* (Steenstrup 1847) in Michaelis & Scherk, 1847: 119, 150; *Micropocrinus* Michelin, 1851: 93; Sieverts, 1931:173; *Pseudocupressocrinus* Valette in Lambert & Valette, 1934: 59; *Cyathidium* Sieverts-Doreck, 1938: 29; *Micropocrinus* Biese & Sieverts-Doreck, 1939: 117; *Cyathidium* Rasmussen, 1961: 238–239; 1978: T839.

Remarks. Žitt *et al.* (2014) thoroughly described the wide range of shape variation in a lower Turonian population of 136 aboral cups attributed to *Cyathidium* aff. *depressum*. The ratio H/D varies from 0.2 to *c.* 1.0 and usually increases during growth (Fig. 7). The cup curvature is also greatly variable with H/h from 1 to 2.7. Details of characters discriminating the extant species such as interradial morphology and fulcral ridge arrangement (Améziane *et al.* 1999) are only preserved in a few specimens, and only parts of the external surface show growth lines and peculiar ornamentation. Therefore, attribution to a new species or to previously described species merely based on aboral cups requires well-preserved specimens and discriminating qualitative characters. Intact fossil specimens with a retracted crown are known exclusively in *C. holopus* (Baumiller & Gaździcki 1996; Donovan & Jakobsen 2004; Hess & Messing 2011; Nielsen 1913; Rasmussen 1961). The vault covering the distal arm series is composed solely of IIBr1, their height being substantially greater than their width. IIBr have not yet been described from the large species *Cyathidium vlieksi* Jagt, 1986, but are known (Jagt pers. comm.). This species has an aboral cup seemingly very similar to some specimens of *C. holopus*. Intraspecific variation of the aboral cup in *C. holopus* and *C. vlieksi* show two extreme morphotypes: one very depressed, like in *C. depressum*, and another as high or taller than wide with conspicuous growth lines. The lower Santonian species, *C. senessei*, differs from all other known congeners in having a stout and tumid curved IBrax, with relatively small distal articular facets facing inwards and subperpendicular to the upper plan of the IBr circle (Améziane *et al.* 1999; Heinzeller *et al.* 1996; Rasmussen 1961). The central space provided by the IBrax circle (Rasmussen 1961, pl. 34 fig. 7c) probably houses IIBr1 keystone plates, but these have not yet been described. Žitt *et al.* (2014) figured the main discriminating characters of dissociated brachials of *C. aff. depressum* from the lower Turonian. Unfortunately, IIBr were not available in the original description of *C. depressum* from the upper Cenomanian but IBr1 were illustrated (Rasmussen 1961). The presence of granulation on the aboral cup appears highly variable among fossil assemblages and cannot be used as a specific discriminating character except when there are sufficient ossicles to demonstrate the stability of this trait. Another early Campanian form from southern England and north-west France will be published soon (Gale & Jagt, in press).

Included fossil species and occurrence. *Cyathidium chiampoensis* sp. nov. (lower Lutetian of Chiampo valley, north-eastern Italy), *C. depressum* including *C. aff. depressum* first described by Žitt 1996 (upper Cenomanian–lower Turonian, Germany and Bohemia), *C. gastaldii* (Middle Miocene near Turin, northwestern Italy), *C. holopus* (upper Maastrichtian of Netherlands, Danian of Denmark and Sweden, lower Eocene of Seymour Island, Antarctica), *C. senessei* (lower Santonian of Bugarach, southern France), *C. vlieksi* (Maastrichtian of Belgium, Netherlands), *C. sp. nov.* (Gale & Jagt, in press; lower Campanian, north-western France and southern England).

Stratigraphic distribution. Upper Cenomanian–Recent.

Cyathidium chiampoensis sp. nov.

Figures 8A–C; Table 4

Synonymy. *Cyathidium* sp. Frisone *et al.*, 2020: 306.

Type material. Two aboral cups including the holotype (MGP-PD 33229, Fig. 8A–B), one well-preserved paratype (MGP-PD 33230, Fig. 8C).

Etymology. From Chiampo valley, Vicenza province, north-eastern Italy.

Diagnosis. Small species (D < 3 mm), aboral cup shape more or less depressed (H/D 0.42 to 1.03), conspicuous growth lines interrupting numerous perpendicular ridges, subcircular adoral face with coarse, short interradial processes. Brachials unknown.

Type stratum. Lower Lutetian tuffite horizon.

Type locality. Cengio dell’Orbo quarry (Cava Boschetto) in the Chiampo Valley, north-eastern Italy.

Description of type series. Aboral cups belonging to small specimens with cup diameter up to 2.72 mm, H equal or substantially lower than D (H/D 0.42), usually D greater than Db. Quantitative characters of the type series listed in Table 4. The holotype, which is the largest specimen, has a curved aboral cup and an external surface showing 8–9 conspicuous parallel growth lines interrupting numerous perpendicular ridges; base smaller than D straight on one side (Fig. 8A) and displaying a coarse groove on the other side probably corresponding to the attachment on an irregular substrate (Fig. 8B); subcircular adoral face without asymmetry despite the marked cup curvature, external border wide and rounded having coarse outer interradiial processes; wide central calycinal cavity. Main characters similar in paratype 1, except cup base more regular than in holotype.

Remarks. The ornamentation consisting of regular growth bands and perpendicular ridges is unknown in congeners. *Cyathidium depressum* and *C. aff. depressum* both differ in usually having granulation and more irregular growth bands (Sieverts 1931; Žitt 1996; Žitt *et al.* 2014). *Cyathidium holopus* differs in having variable growth banding either with relatively wide bands (Rasmussen, 1961: pl. 35, fig. 6) or only numerous very serrated lines (Donovan & Jakobsen, 2004: fig. 2 f, h), granulation (Donovan & Jakobsen, 2004: fig. 2 d) or an almost smooth external surface in the specimen from Seymour Island (Baumiller & Gaździcki 1996). The two latter species and *C. vlieksi* (Jagt, 1986: fig. 1) do not show ridges perpendicular to growth lines.

Occurrence. Chiampo Valley (north-eastern Italy), lower Lutetian.

TABLE 4. Main quantitative characters of aboral cups in *Cyathidium chiampoensis* **sp. nov.** Abbreviations: see Fig. 1A. D used as growth index. Values in mm except ratios. Holotype: MGP-PD 33229; Paratype: MGP-PD 33230.

Specimen	Figure	D	H	h	Db	Dcs	Wr	H/D	H/h	D/Db	D/Dcs
Paratype	8C	2.59	2.10	1.17	2.17	1.65	1.30	0.42	1.79	1.19	1.57
Holotype	8A–B	2.72	2.80	1.26	2.10	1.71	1.40	1.03	2.22	1.29	1.59

Cyathidium sp.

Figures 8D–E, Table 5

Synonymy. *Cyathidium gastaldii* Manni & Pacioni, 2021: 68–69, fig. 3 (*non* Michelin, 1851).

Material examined. Four aboral cups from Cengio dell’Orbo quarry (Cava Boschetto) in the Chiampo Valley, north-eastern Italy: three (MGP-PD 31469 to 71) figured by Manni & Pacioni (2021, fig. 3) (Fig. 8D–E) and one (MGP-PD 33231) not figured.

Description of the specimens. All specimens without ornamentation and with very variable cup shape from depressed (H/D 0.36) to taller than wide (H/D 1.15), H/h 1.10 to 3.67, D/Db 0.54 to 1.19, D/Dcs 0.79 to 1.38 (Table 5). Three bioeroded and worn aboral cups with $Db > D$ from MGP-PD collection described in Manni and Pacioni (2021) with only adoral faces figured. Additional data on quantitative characters listed in Table 5 and side views illustrated in Fig. 8D–E. Two cups MGP-PD 31469 (D 3.9 mm) and MGP-PD 31470 (D 3.5 mm) larger than holotype of *C. chiampoensis* **sp. nov.**, strongly depressed, showing one thin growth band above attachment surface (Fig. 8D). Cup MGP-PD 31471 is smaller (D 2.2 mm) with adoral face poorly preserved and two thick growth bands without marked ornamentation (except for short, faint granules) above attachment surface (Fig. 8E). Smallest specimen MGP-PD 33231 with $Db < D$, bioeroded and slightly worn without growth line, slight constriction (D/Dcs 1.38), two interradiial processes preserved, and cup base broken just above attachment surface.

Remarks. Do all *Cyathidium* cups from the Cengio dell’Orbo quarry belong to the same species? The four specimens described here resemble *C. championensis* **sp. nov.** except for the absence of ornamentation and growth lines and appear to fall within the range of variation of quantitative characters. Bioerosion and wear may have erased the fine wrinkles on the cups’ surface, perpendicular to the growth lines, that characterize *C. chiampoensis* **sp. nov.** In the absence of ornamentation, and given their intraspecific morphological plasticity, the different *Cyathidium* species cannot be easily distinguished based solely on the external morphology of the aboral cup (see above). The presence of short, faint granules on the cup MGP-PD 31471 led Manni and Pacioni (2021) to attribute these specimens to *C. gastaldii*, although this character, which develops variably in different species of Holopodidae, is not a discriminating feature (see below and above). Moreover, it seems unlikely that two *Cyathidium* species would

cohabit in the same biotope. However, the fossil association of the Chiampo deposit includes both well-preserved specimens and others that are biocorroded or worn, suggesting a mixture of ossicles from different biotopes, possibly with reworked elements (see Taphonomy below). Thus, the existence of two *Cyathidium* species cannot be ruled out, one living in the depositional environment (*C. chiampoensis* **sp. nov.**), the other from a different ecological niche. As a result, we leave these specimens that lack observable discriminating characters in open nomenclature.

Occurrence. Cengio dell’Orbo quarry (Cava Boschetto) in the Chiampo Valley, north-eastern Italy, lower Lutetian.

TABLE 5. Main quantitative characters of aboral cups in *Cyathidium* sp. Abbreviations: see Fig. 1A. D used as growth index. Values in mm except ratios. *: figures of specimens attributed to *C. gastaldii* by Manni and Pacioni (2021).

Specimen	Figure	D	H	h	Db	Dcs	Wr	H/D	H/h	D/Db	D/Dcs
MGP-PD 33231	-	2.06	1.73	1.57	1.71	1.49	0.96	0.81	1.10	1.19	1.38
MGP-PD 31471	8E, 3C*	2.2	2.5	1.9	4.1	2.8	1.1	1.15	1.32	0.54	0.79
MGP-PD 31470	3B*	3.5	2.2	0.6	4.2	3.6	1.9	0.63	3.67	0.83	0.97
MGP-PD 31469	8D, 3A*	3.9	1.4	1.1	5.0	4.2	2.2	0.36	1.27	0.78	0.93

Cyathidium gastaldii (Michelin, 1851)

Figures 8F, G; Table 6

Synonymy. *Micropocrinus gastaldii* Michelin, 1851: 93–94; Michelotti, 1861: 354; Jaekel, 1891: 621; Sieverts, 1931: 173; Biese & Sieverts-Doreck, 1939: 11; *Cyathidium gastaldii* Manni, 2005: 214, pl. 1 fig. 8, text fig. 4
Non *Cyathidium gastaldii* Manni & Pacioni, 2021: 68–69, fig. 3.

Type material. A single aboral cup (holotype) from the Miocene of the Superga Hill near Turin and two plaster casts are housed in the palaeontological collection of the MNHN in Paris (MNHN-F-R68284). Several casts of this holotype were sent to collections outside of France. Two of them are housed in the Palaeontological Museum of Turin University (Manni & Pacioni 2021). The cast of an aboral cup (MPURLS NS 6/800) having nearly the same size and belonging to the Palaeontological Museum of Rome (Manni 2005) is also a cast of the holotype.

Emended diagnosis. Aboral cup rounded subpentagonal, diameter up to 14.2 mm, ratio of height to diameter 0.7, dense regular granulation developed especially on upper part of external surface, interradial processes conspicuous, no marked growth bands.

Description of the holotype. Aboral cup rounded subpentagonal, with granulated external surface as indicated in Michelin’s diagnosis. Quantitative characters listed in Table 6. Wall relatively thick (2.5–2.7 mm); interradial processes conspicuous but irregularly preserved; synarthrial articulation of radials worn, aboral ligament pit inconspicuous (Fig. 8G). Lateral view asymmetrical (H/h 1.6); side of maximum height with a convex subconical growth discontinuity of smooth surface related to the undulating attachment surface (Fig. 8F). Dense regular granulation especially well developed on the upper part of the external surface and extended very close to the fulcral ridge of radial articulation, no marked growth bands.

Other specimen. Manni (2005) figured a small aboral cup (quantitative characters listed in Table 6) with a granulated external surface belonging to the Michelotti Collection housed in the Museum of Palaeontology of “La Sapienza” University of Rome (MPURLS 2534). He attributed it to a juvenile of *C. gastaldii* corresponding to the specimen cited by Michelotti (1861) from the Miocene near Turin.

Remarks. Jaekel (1891) considered *Micropocrinus gastaldii* to be very similar to the Cretaceous *C. holopus* and deemed that the difference in granulation was a result of better preservation. Rasmussen (1961, p. 246) pointed out that *C. gastaldii* is “very similar to large specimens of *C. depressum* and to specimens of *C. holopus* with low theca and a broad base”. Manni and Pacioni (2021) attributed to *C. gastaldii* three poorly preserved specimens from Cava Boschetto (= Cengio dell’Orbo quarry, Chiampo Valley, Lutetian), specimens here maintained in open nomenclature (see above). However, at the species rank, all these presumed affinities are not well supported by discriminating characters. Additional new material is required to confirm the validity of *C. gastaldii*.

Occurrence. Serravallian (Middle Miocene) of Superga Hill near Turin, northwestern Italy.

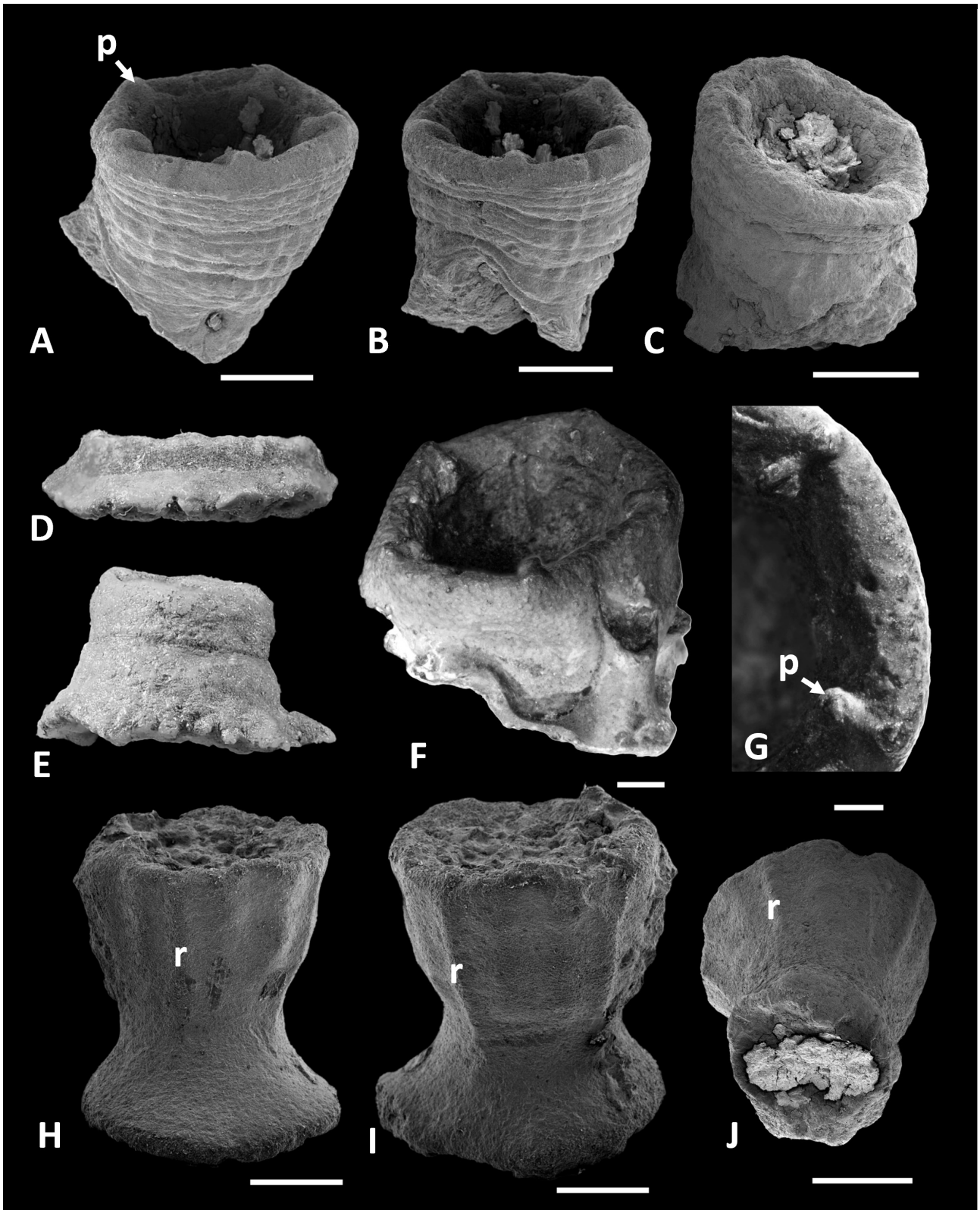


FIGURE 8. Holopodid aboral cups from Chiampo. A–C: *Cyathidium chiampoensis* **sp. nov.**, A–B: holotype (MGP-PD 33229), A: oblique lateral view, B: opposite side, C: paratype 1 oblique lateral view (MGP-PD 33230), D–E: *Cyathidium* sp., D: lateral view MGP-PD 31469, E: lateral view MGP-PD 31471; F–G: holotype of *Cyathidium gastaldii* (MNHN-F-R68284), F: lateral adoral view, G: close-up of one arm articulation; H–J: aboral cups of *Holopus fabianii* **sp. nov.**, H–I: holotype (MGP-PD 33232), H: oblique lateral view, I: opposite side; J: lateral aboral view of juvenile paratype 1 (MGP-PD 33233); p: interradial process, r: radial ridge. Scale bars: 1 mm.

TABLE 6. Quantitative characters of the aboral cups of *Cyathidium gastaldii*. Measurements of MPURLS 2534 are based on text and figures in Manni (2005: fig. 4 and pl. 1 fig. 8). Abbreviations see Fig. 1A. D used as growth index. Values in mm except ratios. Holotype: MNHN-F-R68284.

Specimen	Figure	D	H	h	Db	Wr	H/D	H/h	D/Db
Holotype	8F–G	14.22	10.05	6.27	13.27	6.8–7.1	0.71	1.6	1.07
MPURLS 2534		4.6	2.4	~0.9	5.4	~2.2	0.52	2.7	0.86

Genus *Holopus* Orbigny, 1837

Type-species. *Holopus rangii* Orbigny, 1837, by monotypy.

Remarks. For main discriminating characters between *Holopus* and *Cyathidium*, see Table 3. *H. fabianii* **sp. nov.** and *H. spileccense* are the only fossil species of *Holopus* for which both the aboral cup and brachials are described. *H. plaziati* is known only from brachials, and the Campanian species in Jagt *et al.* (2010) is known exclusively from a single aboral cup. We here present the first description of well-differentiated keystone plates as well as distal brachials in a fossil *Holopus* species.

Included fossil species and occurrences. *Holopus fabianii* **sp. nov.** (lower Lutetian of Chiampo Valley, north-eastern Italy), *H. plaziati* (lower Ypresian, Corbières, southern France), *H. spileccense* (lower Ypresian, Spilecco Hills near Bolca, north-eastern Italy), *Holopus* sp. in Jagt *et al.* (2010) (upper Campanian, Krons Moor, northern Germany).

Stratigraphic distribution. Upper Campanian–Recent.

Holopus fabianii **sp. nov.**

Figs. 7, 8H–J, 9–11; Tables 7–10

Synonymy. *Holopus spileccense* Manni & Pacioni, 2021: 69–73, figs. 4–6; Frisone *et al.*, 2020: 306 (*non* Schlüter 1878).

Type material. Eight aboral cups including the holotype (Fig. 8H–I), one figured paratype (paratype 1, Fig. 8J), six non-figured paratypes (paratypes 2–7); 17 figured brachials including 12 IBrax (paratypes 8–19, Fig. 10A–L) and five IIBr (paratypes 20–24, Fig. 11A–H); 14 non-figured IBrax (paratypes 46–59), 21 non-figured IIBr (paratypes 25–45) including three keystone plates and three IIBr from distal series.

Other material examined. 17 IBrax, 58 IIBr of $W_p < 2.8$ mm, 21 IIBr of $W_p > 2.8$ mm.

Etymology. Species dedicated to Ramiro Fabiani (1879–1954) for his contributions to stratigraphy and palaeontology of the Paleogene from north-eastern Italy.

Diagnosis. Cup with conspicuous constriction in the lower half; upper part of cup with rounded pentagonal cross-section; pronounced radial ribs and marked interradial ribs; adoral face without external interradial process; calycinal cavity unknown; estimated maximum cup size: H 21.0 mm, D 14.8 mm; IBrax about as high as wide, with Y-shaped ridge, upper part of ridge (V-shape) irregularly doubled, usually with outer branches reaching angles of maximum brachial width (Wd) and inner branches corresponding to radial axis of brachial ramifications; small IBrax with only a few tubercles or none at all; large IBrax with several tubercles especially in the proximal half; external ornamentation of proximal IIBr consisting of X-shaped positioned tubercles, muscular synarthries with fulcral ridge shorter than maximum brachial width axis, adoral border forming an obtuse angle giving relatively narrow V-shape section; keystone plates with distal muscular synarthry roughly triangular and rounded, proximal synarthry symmetrical with fulcral ridge as long as W_p , external face smooth, shaped like an isosceles triangle, four conspicuous parallel symplectial crenulations on each side; distal IIBr series higher than broad, muscular synarthries with inconspicuous fulcral ridge, marked aboral ligament pit and axial nervous canal, conspicuous adoral muscle pits.

Type stratum. Lower Lutetian, tuffite horizon.

Type locality. Cengio dell’Orbo quarry in the Chiampo Valley, north-eastern Italy.

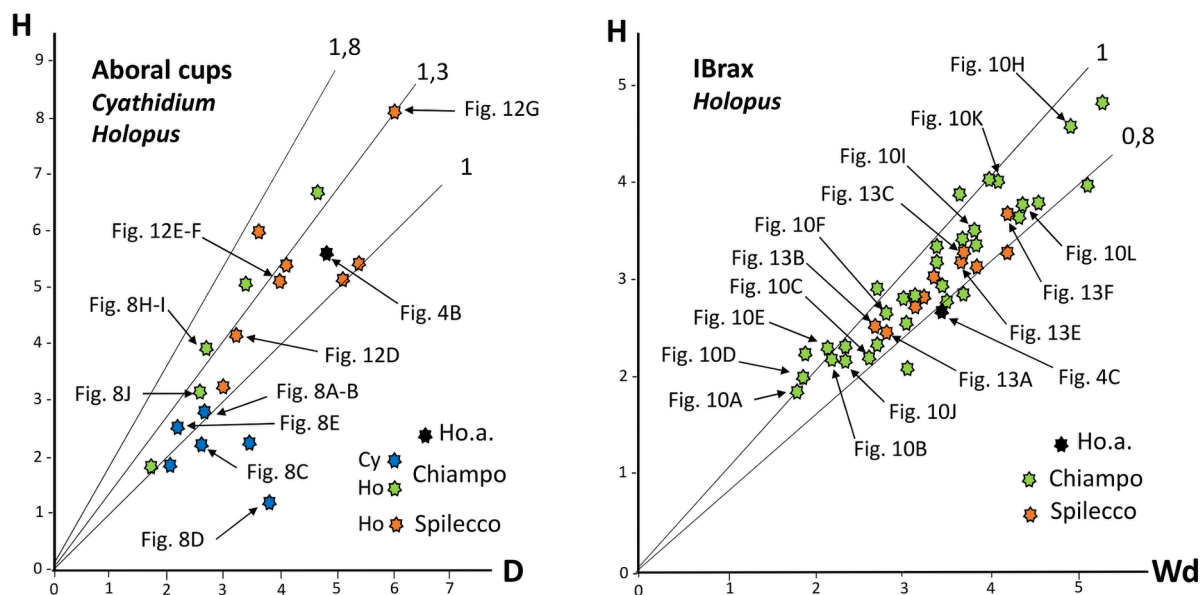


FIGURE 9. Main quantitative characters of Holopodidae from the Eocene of north-eastern Italy. Cy: *Cyathidium*, Ho: *Holopus*, Ho.a.: juvenile of *H. alidis* (MNHN-IE-2014-2185). Straight lines: values of H/D and H/Wd. Other values in mm.

Description of type series. Among the 8 aboral cups of the type series (quantitative characters listed in Table 7), the holotype was selected as the best preserved aboral cup (Fig. 8H, I). Holotype medium sized (H 3.83 mm, D 2.75 mm), with a strong constriction (Db/Dcs 1.68) located in the aboral half and separating adoral two-thirds of cup from a broad basal part with flat attachment surface with a greater diameter than the adoral side (D/Db 0.88); adoral part with rounded pentagonal cross-section demarcated by five conspicuous radial ribs with intermediate ribs more pronounced on one side (Fig. 8H) than on the other (Fig. 8I); adoral face without external interradial process, calycinal cavity filled with recrystallized sediment making it impossible to identify any possible internal interradial processes, if present. Other aboral cups of type series are of variable sizes (H 1.72 to 6.55 mm, D 1.76 to 4.62 mm), usually height greater than adoral diameter (H/D 1.21 to 1.48) except in small paratype 7 (H/D 0.98), H/D increasing from nearly 1 to more than 1.4 with size (Fig. 9), similar characters as the holotype, more or less conspicuous, attachment surface often smaller than adoral diameter and very irregular, sometimes appearing as a mold of a subcylindrical substrate (Fig. 8J), cup with moderate curvature (H/h~1.3) only in paratype 3.

Type series of IBrax (paratypes 8 to 19) illustrate changes in form and ornamentation with size (Fig. 10, Table 8). Smallest IBrax nearly as high as wide; external surface (Fig. 10A–E) with a more or less thick Y-shaped ridge, distal part of ridge (V-shape) irregularly doubled with usually outer branches reaching angles of maximum brachial width (Wp) and inner branches corresponding to radial axis of brachial ramifications; proximal external surface without tubercles on either side of axial ridge. Larger IBrax about as wide as high except paratypes 10 and 18 which show H/Wd 0.82 and 0.84, respectively; external ornamentation (Fig. 10I–L) showing Y-shaped ridge composed of a short lower segment and predominantly longer V-shaped segments corresponding to radial axis of brachial ramifications, 10 to 20 large tubercles developed irregularly over the entire external surface, sometimes transforming former ridges into rows of tubercles (Fig. 10K–L). Asymmetric paratype 17 possibly belongs to a lateral trivium plate (Fig. 10J). Aboral interradial process moderately developed.

Type series of IIBr, proximal series to keystone plate (paratypes 20 to 23 and 25 to 39) with external ornamentation predominantly X-shaped, always with a more or less marked axial ridge and few tubercles (Fig. 11D–E). Ratios H/h, H/Wp and Wp/Wd independent of size (Table 9). Height asymmetry mostly due to oblique articulation with IBrax, 12 cases with $H/h < 1.3$, 4 cases with $1.5 < H/h < 1.7$ (Fig. 11E) and 3 cases with $1.95 < H/h < 2.05$ (Fig. 11D). Lateral faces with 4 to 6 parallel symplexial crenulations, sometimes restricted to the highest one. Muscular synarthries with fulcral ridge shorter than maximum brachial width (W). Two types of muscular synarthries: one symmetrical with equal fulcral ridge segments parallel to W (Fig. 11A), another asymmetrical with unequal fulcral ridge segments oblique to W (Fig. 11B); most IIBr with one synarthry asymmetrical and the other symmetrical (IIBr1 or IIBr2?),

other IIBr with two articular facets asymmetrical (IIBr1) or symmetrical (IIBr2 or 3?). Four IIBr nearly as high as wide and asymmetrical, assigned to IIBr1 of a bivium (Fig. 11E). Articulations with adoral border forming an obtuse angle, ambulacral groove shallow, giving the whole ossicle a relatively flat V-shaped section.

Keystone plates of type series (paratypes 24 and 40–42, Table 10) with distal muscular synarthry roughly triangular and rounded (Fig. 11F); proximal synarthry symmetrical, with fulcral ridge as long as Wp (Fig. 11H); external face smooth, shaped as an isosceles triangle (Fig. 11G), four conspicuous parallel symplectial crenulations on each side (Fig. 11F).

A few brachials from the distal IIBr series (paratypes 43–45, Table 10) higher than broad, muscular synarthries similar to the distal articulation of the keystone plates with inconspicuous fulcral ridge, marked aboral ligament pit and axial nervous canal, conspicuous adoral muscle pits.

Complementary data from material not included into the type series. The additional material allows us to investigate in more detail the range of variation of quantitative characters (Supplementary Tables 1–2) and ratios in the main types of brachials. All material examined including the types-series: 8 aboral cups, 43 IBrax, 46 IIBr of the proximal series (including 14 with Wp > 2.8 mm) and 60 IIBr with Wp < 2.8 mm (distal series plus a few keystone plates poorly preserved). Ratio of IBrax to aboral cups 5.4, very close to expected ratio of 5; ratio of IBrax to proximal IIBr 1.07, far from the expected ratio of 4 or 6 indicating a high IIBr deficit. Height asymmetry (H/h) of the proximal IIBr is independent of their size. In 50% of the proximal IIBr $1.1 < H/h < 1.3$ (possibly IIBr2 or IIBr3), in 34.6% $1.4 < H/h < 1.75$ (possibly IIBr1 or IIBr2) and in 15.4% $1.75 < H/h < 2.3$ (possibly IIBr1). Quantitative characters of IBrax attaining maximum values with H 4.78 mm, Wd 5.30 mm, Wp 4.15 mm and Wm 3.25 mm (Appendix Table 1).

Remarks. The high number of isolated ossicles of *Holopus fabianii* sp. nov. from the type locality provides a unique insight into intraspecific character variation in the genus *Holopus*. To date, no comparable data have been published for extant species. However, the absence of a crown preserved with connected brachials makes it impossible to establish the precise number of IIBr in the arm's proximal series. The combination of H/h asymmetry, which appears to increase proximally in extant species, and the fact that 50% of the IIBr have a H/h close to 1 suggest that there might have been at least 2–3 IIBr preceding the keystone plate. Like in the extant species *H. alidis*, the position of the keystone plate could have varied depending on the arm and the developmental stage (Bourseau *et al.* 1991).

The recrystallized sediment within the calycinal cavity masks possible inner interradial processes, whose presence and characters would have been useful to describe and compare to extant species. These structures might have been absent as in *H. spileccense* (see below).

The maximum size of the aboral cup and IBrax of *H. fabianii* sp. nov. can be estimated by comparing the greatest width of the facets corresponding to the same articulation joining two adjacent ossicles. The proximal articulation of the largest IIBr (paratype 20) is 1.6 times wider (Wp 5.06 mm) than the largest distal articulation of IBrax (Wm 3.25 mm). The largest proximal articulation of IBrax is 2 times wider (Wp 4.15 mm) than the largest distal articulation of the available aboral cups (paratype 2, Wr 2.03 mm). Thus, the estimated size of the individual to which paratype 20 brachial belonged was 3.2 times larger than paratype 2. Therefore, the aboral cup of *H. fabianii* sp. nov. could possibly be as large as H 21.0 mm and D 14.8 mm, a size intermediate between the known maximum aboral cup sizes of *H. alidis* (H 13 mm, D 9 mm) and *H. rangii* (H 30 mm, D 25 mm).

Holopus fabianii sp. nov. displays closer affinities with *H. alidis* than with *H. rangii*, as both possess a differentiated keystone plate beyond IIBr2 separating proximal and distal arm series (Figs. 5C–H and Fig. 11F–H). Both species also have an aboral cup with rather marked radial ribs. Yet, *H. alidis* differs in having a distinctly granulated external cup and brachials, including the keystone plates, with a predominantly tuberculated ornamentation unlike the nearly smooth keystone plates found for *H. fabianii* sp. nov. (Fig. 5C, Fig. 5G, Bourseau *et al.* 1991, pl. 12). However, judging from our observation on *Cyathidium*, the relevance of the latter character might be called into question. The IBrax ornamentation with Y- or V-shaped ridges common in *H. fabianii* sp. nov. is restricted to juveniles of *H. alidis* (Fig. 4B, C) and tends to disappear under the tuberculate ornamentation in older specimens. Moreover, the adoral side of the fulcral ridge of the proximal-most brachials often conspicuously crenulated in *H. alidis* (Fig. 5A–B) is not found in more distal synarthries (Fig. 5E). This character appears to be absent in *H. fabianii* sp. nov. (Fig. 11A–B). Furthermore, the IIBr fulcral ridges in *H. alidis* (Fig. 5B) and *H. rangii* (Fig. 6D, F) are as long as the brachial is wide, which contrasts significantly with what is observed in *H. fabianii* sp. nov. (Fig. 11A–C). This appears to be due to a lateral aboral displacement of the adoral surfaces of the synarthries, “opening” the articulation and thus giving the brachial a rather flat V-shape. The brachials of *H. alidis* (and *H. rangii*) are thus far thicker than those of *H. fabianii* sp. nov., and, in IBrax, exhibit a more pronounced distal interradial process.

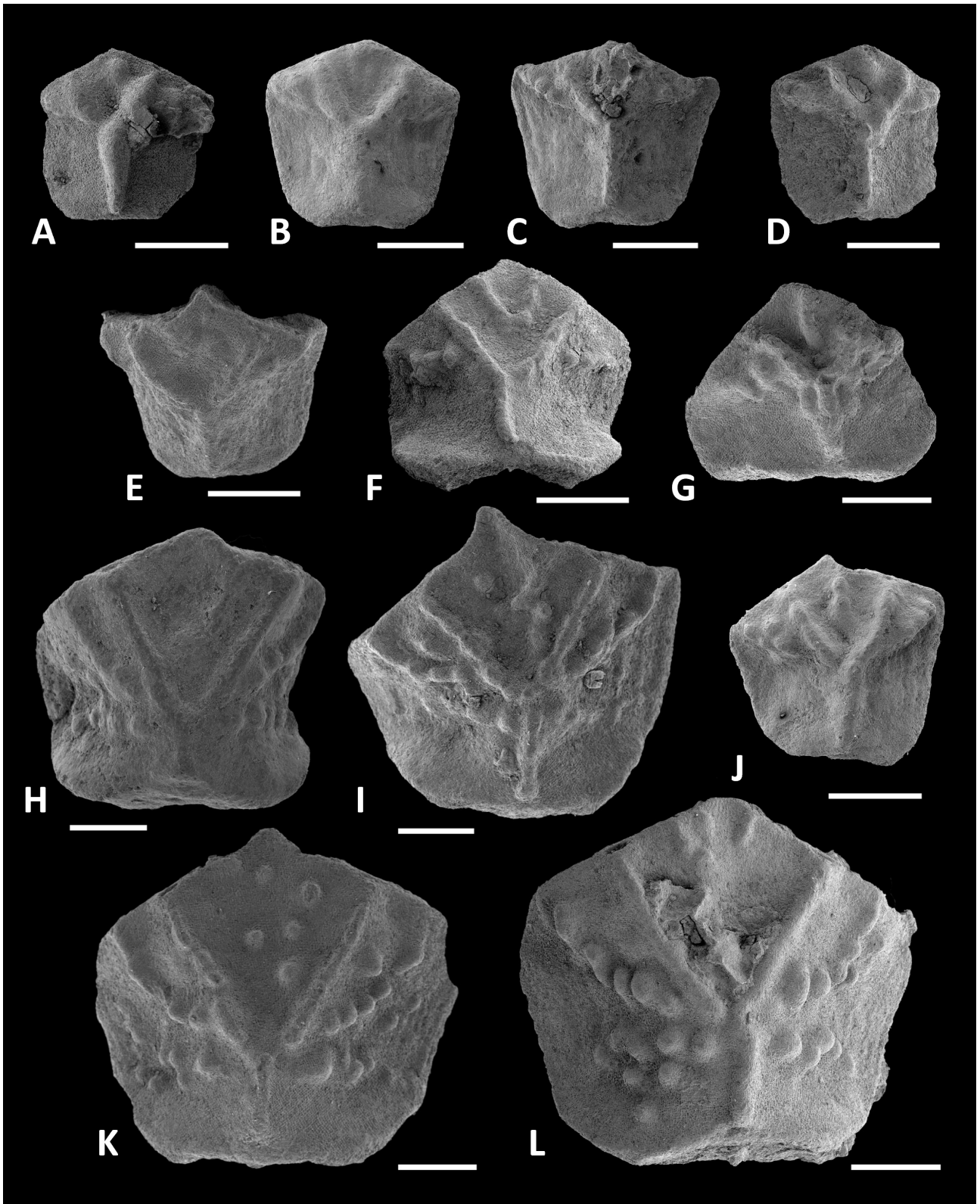


FIGURE 10. Variation in primibrachial ornamentation in *Holopus fabianii* **sp. nov.** from Chiampo (MGP-PD 33235). A–G, J: small specimens, A: paratype 8, B: paratype 9, C: paratype 10, D: paratype 11, E: paratype 12, F: paratype 13, G: paratype 14, J: paratype 15, H, I, K, L: large specimens, H: paratype 16, I: paratype 17, K: paratype 18, L: paratype 19. Scale bars: 1 mm.

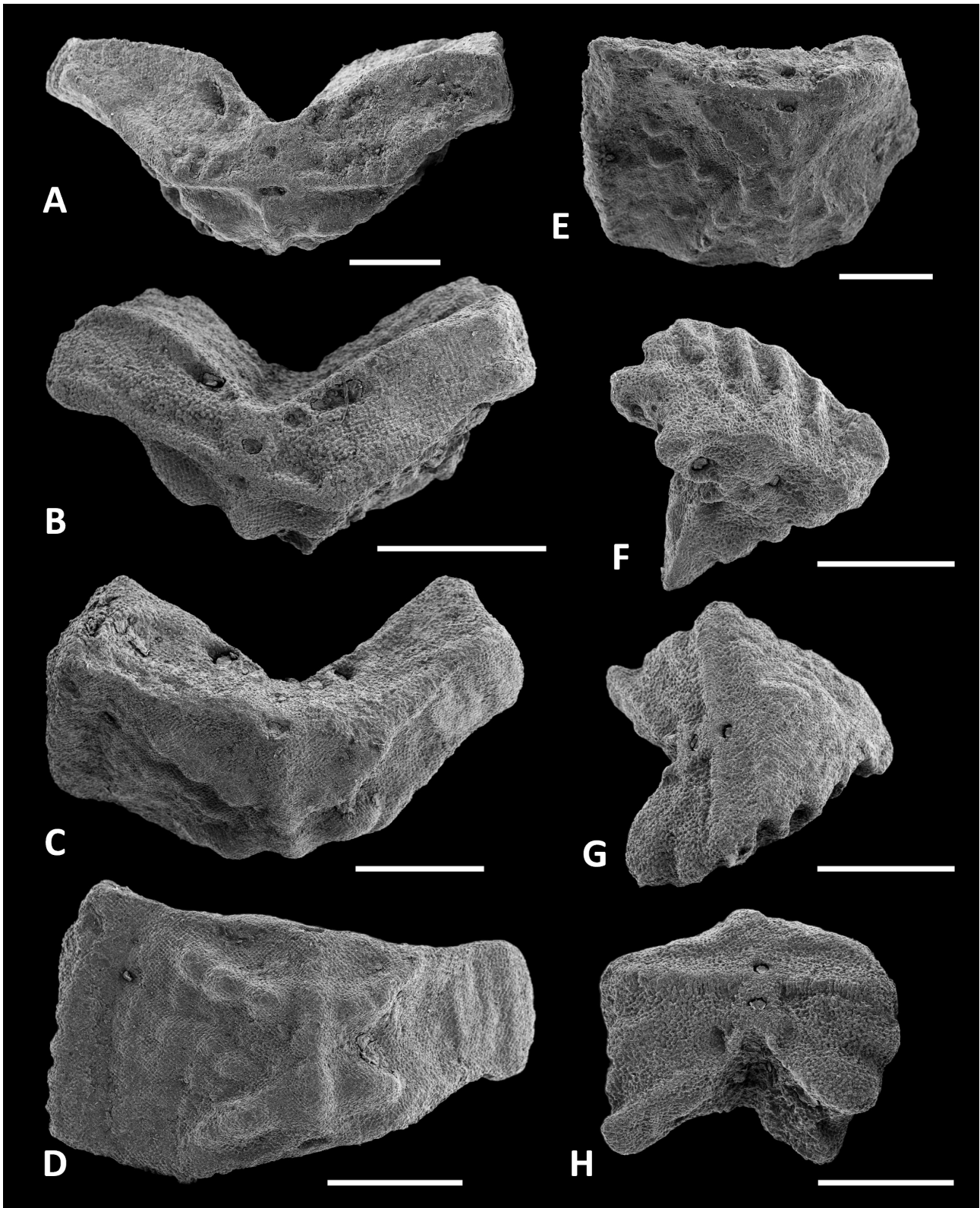


FIGURE 11. Secundibrachials of *Holopus fabianii* sp. nov. from Chiampo belonging to proximal series (MGP-PD 33236); A–E: IIBr from proximal part of proximal series, A: symmetrical muscular synarthry from a small specimen (paratype 20), B: asymmetrical muscular synarthry (paratype 21), C–D: proximal-most IIBr of a large specimen (paratype 22), C: oblique distal view, D: external face, E: IIBr of a bivium (paratype 23), F–H: keystone plate, distalmost IIBr of proximal series (paratype 24), F: oblique view of distal muscular synarthry, G: oblique view showing triangular external face and proximal muscular synarthry at left, H: proximal muscular synarthry. Scale bars: 1 mm.

Holopus plaziati, known exclusively from isolated brachials (7 IBrax + 1 proximal IIBr), comes from the lower Eocene of the Corbières in southern France (Roux *et al.* 2021). Its IBrax differ from those of *H. fabianii* **sp. nov.** and *H. spileccense* in being generally smaller with a smaller H/Wd (Fig. 7), and in having muscular synarthries with usually conspicuous crenulation on the adoral side of the fulcral ridge and sometimes on the adoral border of the muscular area. While syntype 2 of *H. plaziati* appears similar to the IBrax of *H. fabianii* **sp. nov.**, IBrax of syntypes 3 and 7 have adoral articulation facets larger than in *H. fabianii* **sp. nov.** In *H. plaziati* this increases the size of the distal interrarial process and the general thickness of the brachial, resulting in an ambulacral groove that is more deeply carved into the ossicle. The conspicuous lateral symplexial crenulations in *H. plaziati* are variable (parallel to undulated or branched). Its aboral surface displays irregular tuberculate ornamentation without formation of interrarial or Y-shaped ridges.

TABLE 7. Quantitative characters of the eight aboral cups in the type-series of *Holopus fabianii* **sp. nov.** Abbreviations: see Fig. 1A. *: estimated value (broken ossicle). D used as growth index. Values in mm except ratios. Holotype: MGP-PD 33232; Paratype 1: MGP-PD 33233; Paratypes 2–7: MGP-PD 33234.

Specimen	D	H	h	ht	Db	Dcs	Wr	H/D	H/h	H/ht	D/Dcs
Paratype 7	1.8	1.7	1.7	0.8	1.2–1.7	1.6	1.2	0.98	1.00	2.07	1.13
Paratype 1	2.5	3.0	2.8	1.6	1.7–2.3	1.7	1.4	1.21	1.06	1.83	1.49
Holotype	2.7	3.9	3.7	2.5	3.1	1.8	1.7	1.39	1.02	1.53	1.49
Paratype 6	>3*	4.4	-	2.1	3.2–4.1	3.1	-	<1.4*	-	1.35	1.06
Paratype 3	3.3	4.9	3.8	2.8	5.0	3.2	-	1.48	1.29	1.74	1.03
Paratype 5	>4*	5.1	-	3.7	>2.7*	2.4	-	<1.4*	-	1.35	>1.5*
Paratype 4	-	>5*	>3*	-	4.5–5.3	-	-	-	1.6*	-	-
Paratype 2	4.6	6.5	6.5	4.5	7.3–8.1	3.9	2*	1.42	1.00	1.44	1.17

TABLE 8. Quantitative characters of IBrax of *Holopus fabianii* **sp. nov.** belonging to figured paratypes. Abbreviations: see Fig. 1B. Wd used as growth index. Values in mm except ratios. Paratypes 8–19: MGP-PD 33235.

Specimen	Figure	Wd	H	Wp	Wm	H/Wd	H/Wp	Wp/Wm	Wp/Wd
Paratype 8	10A	1.8	1.8	1.0	1.1	1.02	1.78	0.93	0.57
Paratype 11	10D	1.9	1.9	1.0	1.0	1.03	1.90	0.97	0.54
Paratype 12	10E	2.2	2.2	1.5	1.3	1.01	1.46	1.16	0.69
Paratype 9	10B	2.2	2.1	1.1	1.3	0.96	1.96	0.85	0.49
Paratype 15	10J	2.3	2.2	1.2	1.2	0.95	1.82	0.98	0.52
Paratype 10	10C	2.6	2.1	1.2	1.3	0.82	1.76	0.96	0.46
Paratype 14	10G	2.7	2.4	-	1.8	0.89	-	-	-
Paratype 13	10F	2.8	2.6	2.6	1.7	0.92	1.01	1.51	0.91
Paratype 16	10H	3.8	3.4	3.4	2.0	0.90	1.02	1.64	0.88
Paratype 17	10I	4.1	4.0	2.9	2.4	0.97	1.35	1.24	0.72
Paratype 18	10K	4.4	3.7	3.1	2.4	0.84	1.18	1.30	0.71
Paratype 19	10L	4.9	4.5	3.9	2.4	0.92	1.17	1.58	0.78

Manni and Pacioni (2021) attributed 30 brachials from Cava Boschetto (= Cengio dell’Orbo quarry, the type-locality of *H. fabianii* **sp. nov.**) to *H. spileccense* (Schlüter), a taxon known only from cups found in the Ypresian strata of Spilecco Hill (see below). These 30 brachials are housed in the MGP-PD collections. Manni and Pacioni

(2021) figured the ornamentation of 5 IBrax and 6 IIBr from the proximal series but did not identify keystone plates. The variation of X-shaped ridges on IIBr was well-illustrated and corresponds to the range observed in the material here ascribed to *H. fabianii* **sp. nov.** The quantitative characters of these brachials also fall within the variation range of those of *H. fabianii* **sp. nov.** (except IBrax MGP-PD 31442 which presents the largest Wd, 5.3 mm) and they should thus be attributed to this species.

Occurrence. Middle Eocene (Lutetian) of Chiampo Valley, north-eastern Italy.

TABLE 9. Main quantitative characters of IIBr from the proximal arm series (except keystone plates) of *Holopus fabianii* **sp. nov.** belonging to the type-series. Abbreviations: see Fig. 1C. Wp used as growth index. Values in mm except ratios. Paratypes 20–23: MGP-PD 33236; Paratypes 25–39: MGP-PD 33238.

Specimen	Figure	Wp	H	h	Wd	H/h	H/Wp	Wp/Wd
Paratype 25	-	2.1	1.5	1.3	2.1	1.15	0.78	0.99
Paratype 26	-	2.3	2.2	1.8	2.1	1.22	0.95	1.12
Paratype 27	-	2.5	1.8	1.5	2.0	1.22	0.73	1.22
Paratype 28	-	2.7	1.6	1.3	2.7	1.26	0.60	1.00
Paratype 29	-	2.7	2.5	1.4	2.3	1.70	0.91	1.17
Paratype 30	-	2.7	2.2	1.9	2.6	1.15	0.79	1.04
Paratype 31	-	2.8	2.0	1.6	2.8	1.25	0.72	1.00
Paratype 21	11B	2.9	1.5	1.3	2.9	1.17	0.52	1.00
Paratype 32	-	3.1	1.5	0.7	2.6	2.05	0.50	1.20
Paratype 23	11E	3.3	2.9	1.7	2.9	1.67	0.90	1.11
Paratype 22	11C–D	3.6	2.0	1.0	3.6	2.03	0.57	1.00
Paratype 33	-	3.6	2.3	1.4	3.5	1.64	0.65	1.03
Paratype 34	-	3.9	2.5	2.3	3.8	1.08	0.65	1.03
Paratype 35	-	3.9	2.4	1.9	3.9	1.22	0.60	1.01
Paratype 36	-	4.0	2.6	2.0	3.7	1.28	0.64	1.07
Paratype 37	-	4.2	3.1	2.0	4.1	1.53	0.74	1.00
Paratype 38	-	4.3	2.2	1.7	4.3	1.24	0.51	1.00
Paratype 39	-	4.4	4.0	3.1	3.6	1.27	0.91	1.20
Paratype 20	11A	5.1	2.4	1.4	4.6	1.97	0.48	1.10

TABLE 10. Main quantitative characters of distal IIBr and keystone plates of *Holopus fabianii* **sp. nov.** belonging to the type-series. Abbreviations: see Fig. 1C. H for keystone plates: height of triangular external face. Wp used as growth index. Values in mm except ratios. Paratypes 24: MGP-PD 33236; Paratypes 40–45: MGP-PD 33238.

Specimen	Place in arm	Wp	H	h	Wd	H/h	H/Wp	Wp/Wd
Paratype 43	Distal arm series	1.3	1.2	1.1	1.3	1.04	0.86	1.04
Paratype 44	Distal arm series	1.5	1.2	1.2	1.3	1.00	0.84	1.08
Paratype 45	Distal arm series	1.5	-	-	-	-	-	-
Paratype 24	Keystone plate	2.0	1.2	0.0	1.8	-	0.59	1.11
Paratype 40	Keystone plate	2.1	1.7	0.0	1.9	-	0.83	1.08
Paratype 41	Keystone plate	2.4	2.5	0.0	2.1	-	1.05	1.12
Paratype 42	Keystone plate	2.1	2.1	0.0	-	-	0.98	-

Holopus spileccense (Schlüter, 1878)

Figs. 7, 9, 12–14; Tables 11–13

Synonymy. *Cyathidium spileccense* Schlüter, 1878: 54, 65, pl. 3, figs. 11–15; Carpenter, 1884: 212; Jaekel, 1891: 614–616, fig. 14; Jaekel, 1907: 293; *Holopus* (*Cyathidium*) *spileccense* Jaekel, 1891: 567, *Holopus spileccense* Jaekel, 1891: 607, 615–616; *Holopus* (*Cyathidium*) *spileccensis* Jaekel, 1891: 592; *Holopus spileccensis* Jaekel, 1891: 591, 619–620; *Cyathidium spileccense* Nielsen, 1913: 17, 40, 58; Wanner, 1929: 319; *Holopus spileccensis* Sieverts, 1931: 174–175; *Holopus spileccense* Biese & Sieverts-Doreck, 1939: 117; Manni, 2005: 216–217, pl. 1 figs. 9–10, text-fig. 5a–b. Non *Holopus spileccense* Manni & Pacioni, 2021: 69–73, figs. 4–6.

Material examined. Nine aboral cups, 12 IBr, 4 IIBr

Diagnosis. Cup with strong constriction in the aboral half; adoral part with markedly pentagonal cross-section; marked radial ridge without other ornamentation; frequently slight interrarial depression; calycinal cavity without inner interrarial process; measured maximum cup size: H 8.1 mm, D 6 mm; IBrax wider than high; Y-shaped ridge coarse, usually simple (not doubled) with branches corresponding to radial axis of brachial ramifications; no other ornamentation; small IBrax with more marked and doubled ridge; external ornamentation of proximal IIBr with coarse X-shaped and discrete mid-radial ridge; articular facets with fulcral ridge slightly shorter than maximum brachial width; no prominent muscular or ligament pits; more distal IIBr and keystone plates unknown.

Type stratum. Lower Ypresian.

Type locality. Spilecco Hill near Bolca, north-eastern Italy.

Description of material examined. Quantitative characters of aboral cup relatively variable (Table 11), H/D from 1.02 to 1.63 independent of size (D used as growth index; Fig. 9). Constriction at mid-height conspicuous (D/Dcs up to 1.73), upper adoral cup and adoral face markedly pentagonal with each angle forming a radial ridge (Fig. 12E), no additional ridges or granulation on external surface, no trace of interrarial process and inner process masked by recrystallized sediment (Fig. 12D), attachment surface flat to slightly concave (Fig. 12F), cup curvature usually marked, especially in the two largest specimens (H/h 1.5 to 1.6) (Fig. 12G).

Primibrachials pentagonal except for a single anomalous quadrangular specimen MGP-PD 33245 Br7 (Fig. 12C). Pentagonal IBrax broader than high ($0.75 < H/Wd < 0.86$), in smallest (youngest) specimens nearly as wide as high (Fig. 13A–B), external face showing coarse Y-shaped ribs, no other ornamentation (Fig. 13A–B), Y-pattern more conspicuous in small specimen (Fig. 13A) than in larger ones (Fig. 13E–F) (quantitative characters listed in Table 12). The coarse Y-shaped rib identifies the quadrangular specimen MGP-PD 33245 Br7 as a primibrachial (probably corresponding to a bivium). Articulations poorly preserved.

TABLE 11. Main quantitative characters of the nine aboral cups of *Holopus spileccense* housed at the MGP-PD and lectotype from Schlüter (1878). Abbreviations: see Fig. 1A. D used as growth index. Values in mm except ratios.

Specimen	Figure	D	H	h	ht	Db	Dcs	Wr	H/D	H/h	H/ht	D/Dcs
MGP-PD 33243 CD9	-	3.0	3.2	2.9	1.5	4.1	2.8	-	1.06	1.11	2.17	1.09
MGP-PD 33242 A7	12D	3.3	4.1	3.5	2.1	2.1	1.9	1.9	1.25	1.17	1.89	1.73
MGP-PD 33243 A4	-	3.5	>4	>3	2.6	-	3.1	2.2	>1.0	-	>1.4	1.16
MGP-PD 33243 A5	-	3.6	5.9	5.2	3.0	3.9	2.9	2.2	1.63	1.15	1.96	1.26
MGP-PD 33242 A6	12E–F	4.0	5.1	4.4	3.0	3.2	2.6	2.2	1.27	1.16	1.69	1.54
MGP-PD 33243 A3	-	4.0	5.3	3.0	2.5	4.4	3.7	-	1.32	1.79	2.13	1.09
MGP-PD 33243 A1	-	>4	5.6	-	2.5	3.9	3.1	2.7	<1.3	-	2.17	-
MGP-PD 33243 CD8	-	5.0	5.1	3.4	2.6	4.5	4.1	-	1.02	1.50	1.96	1.23
MGP-PD 33242 A2	12G	6.0	8.1	5.1	4.5	5.0	3.8	4.0	1.36	1.58	1.79	1.58
Lectotype	14	5.8	7.7	4.3	6	4.5	3	3.2	1.3	1.8	1.3	1.9

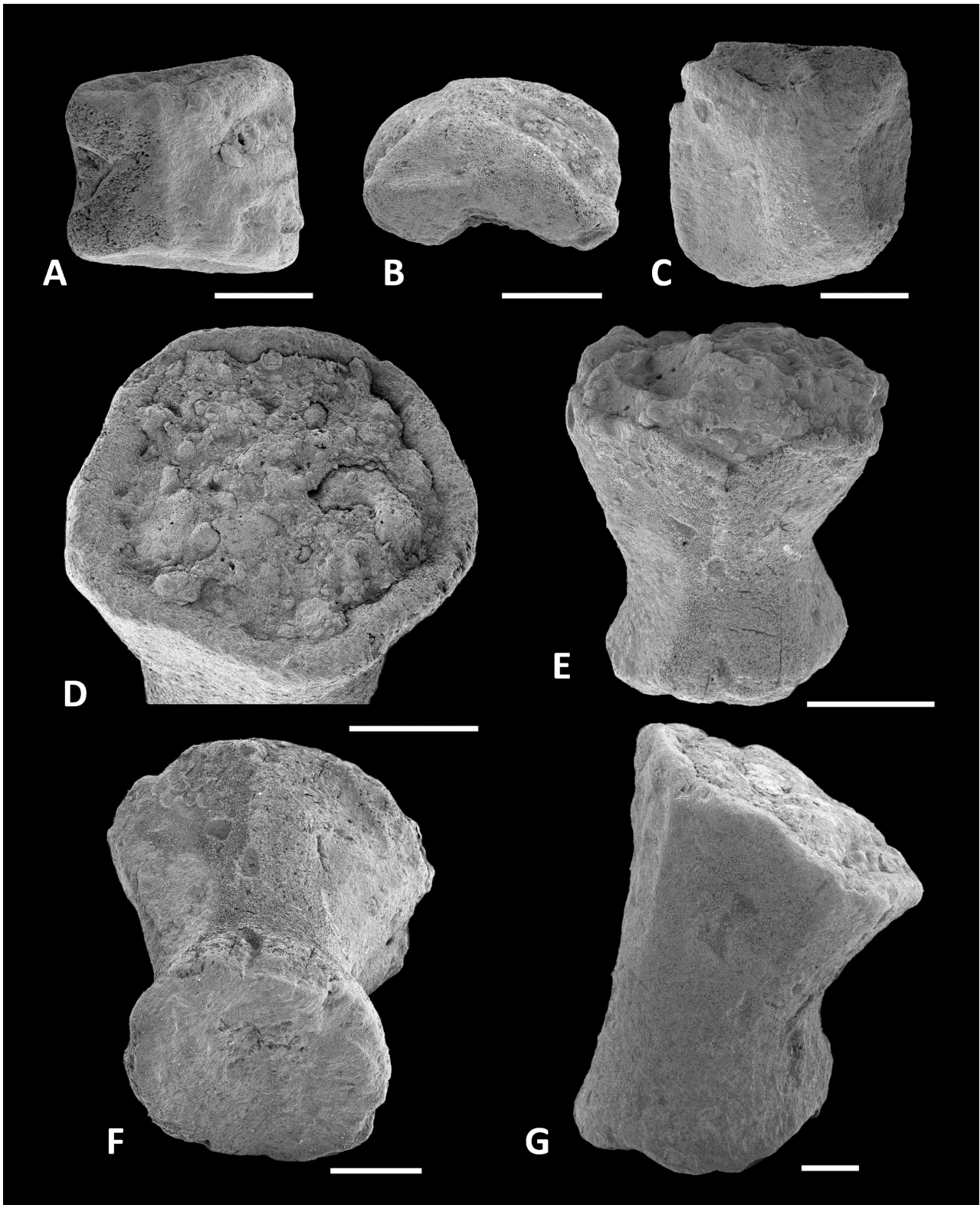


FIGURE 12. *Holopus spileccense*, Spilecco. A–B: secundibrachials, A: external surface (MGP-PD 33247 Br8), B: distal facet (MGP-PD 33247 Br4), C: non-axillary IBr, external surface (MGP-PD 33245 Br7), D–G: aboral cups (MGP-PD 33242), D: adoral face (A7), E–F: A6, E: oblique lateral adoral view, F: oblique aboral view, G: lateral view, A2. Scale bars: 1 mm.

IIBr belonging to proximal series slightly wider than high with H/h 1.12 to 1.42 (Table 13), no keystone plate identified possibly due to the small number of IIBr found; external face showing a coarse X-shaped rib with a discrete mid-radial ridge (Fig. 12A). Distal IIBr articulations rather symmetrical (Fig. 12B). The articular facets

appear to present a fulcral ridge that is slightly shorter than the maximum brachial width and there are no prominent muscular or ligament pits.

Remarks. The maximum sizes of the aboral cup and IBrax of *H. spileccense* have been estimated using the same method as for *H. fabianii* **sp. nov.** (see above) and are nearly the same as the maximum sizes measured. However, this estimation might be biased due to the small number of brachials available.

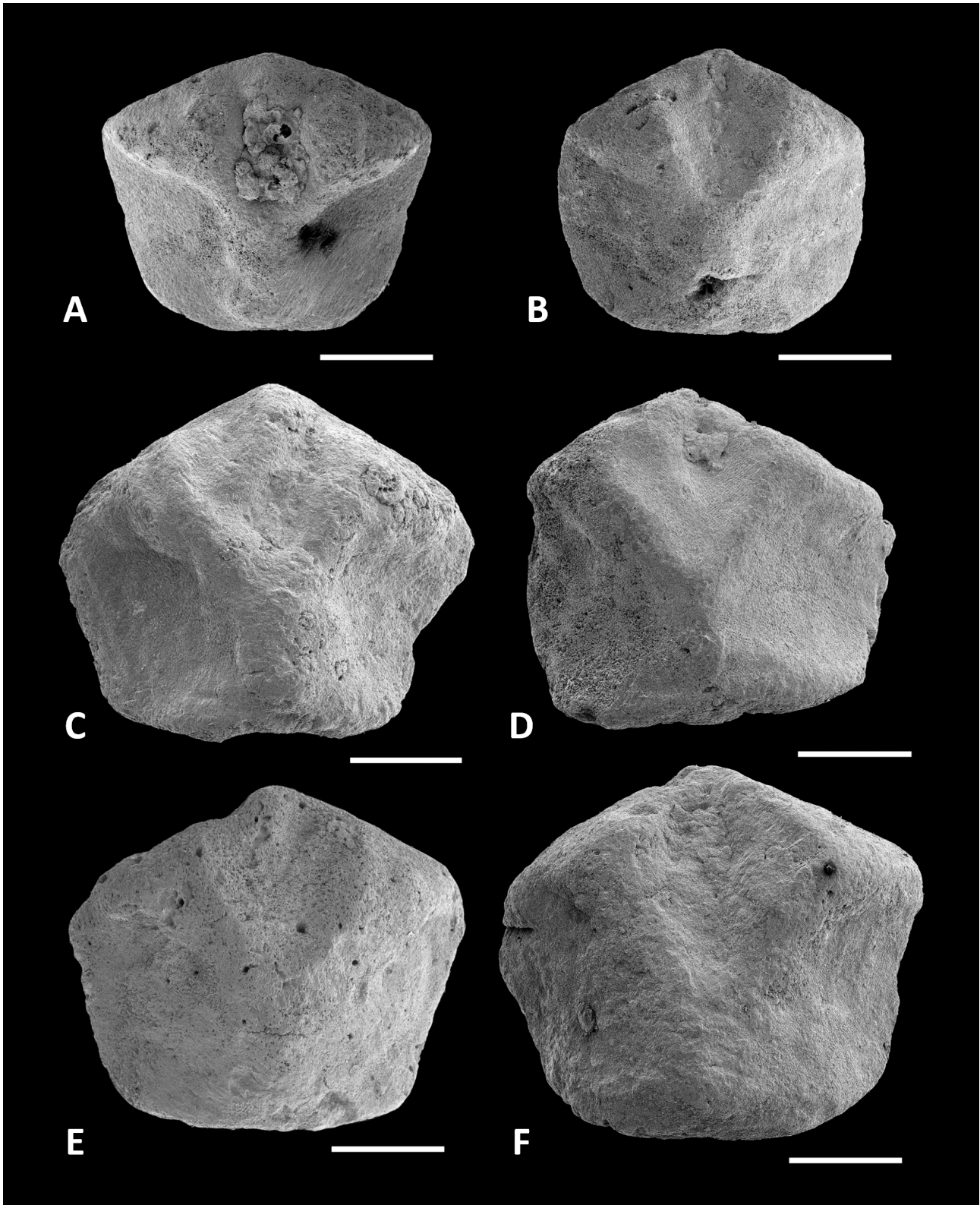


FIGURE 13. *Holopus spileccense*, Spilecco, IBrax, variation in external ornamentation (MGP-PD 33244). A–B: small specimens, A: Br12, B: Br9, C–E: medium-sized specimens, C: Br14, D: Br13, E: largest specimen, Br1, F: Br16. Scale bars: 1 mm.

Schlüter (1878) figured four aboral cups without describing them in the text. The current whereabouts of these are unknown to us. Three of the four are rather straight without significant curvature. The fourth is markedly curved (H/h 1.56). It also appears to be the best-preserved specimen and its adoral face and side view are figured enlarged, showing the main characters of the species (Fig. 14; Schlüter 1878, pl. 3, figs 11, 12). Its cup is pentagonal, higher than wide (H/D 1.22), with a conspicuous constriction (D/Dcs 2.09) in the lower part (H/ht 1.33), marked radial ribs, slight interradial depressions with an outer interradial process, and symmetric, rounded muscular synarthries. While not explicitly shown in the drawing, the calycinal cavity is described in the text as being partly filled with sediment. We here designate this drawn aboral cup as the lectotype of *H. spileccense*. The side views of the three paratypes show variable general shape ($1.37 < H/D < 1.78$, $1.4 < D/Dcs < 2.0$). Jaekel (1891: 616, fig. 14) figured an aboral cup (sent to him by Schlüter) that is very similar to the lectotype except that it is not curved (H/D 1.26, H/h 1.03, H/ht 1.45, D/Dcs 1.98). As Schlüter (1878) and Jaekel (1891) do not give precise measurements, we can only deduce ratios with some confidence from the figures. Measures taken from a printed copy of Schlüter (1878) are listed in Table 11. Manni (2005) described and figured a single aboral cup from the Michelotti Collection (H/D 1.0, H/h 1.04, H/ht 1.92, D/Dcs 1.29). With the 9 additional aboral cups described here, we now have 15 cups from *Spilecco* allowing us to assess the variation of quantitative and qualitative characters in *H. spileccense*. A comparison with data for *H. fabianii* **sp. nov.**, based on eight aboral cups, indicates a similar range of variation in the two species (Table 14). *Holopus spileccense* differs in having the adoral part of the cup more markedly pentagonal and having five usually well-marked radial ribs as well as interradial depressions that can be more or less pronounced.

TABLE 12. Main quantitative characters of IBrax in *Holopus spileccense*. Abbreviations: see Fig. 1B. Note that MGP-PD 33245 Br7 is a non-axillary IBr (see text). Wd used as growth index. Values in mm except ratios.

Specimen	Figure	Wd	H	Wp	Wm	H/Wd	H/Wp	Wp/Wm	Wp/Wd
MGP-PD 33244 Br9	13B	2.7	2.5	1.9	1.4	0.92	1.30	1.34	0.70
MGP-PD 33245 Br7	12C	2.8	2.8	2.2	-	1.00	1.24	-	0.81
MGP-PD 33244 Br12	13A	2.9	2.5	1.8	1.6	0.86	1.38	1.16	0.63
MGP-PD 33246 Br5	-	3.2	2.7	2.3	2.0	0.85	1.17	1.18	0.72
MGP-PD 33246 Br15	-	-	2.7	2.2	1.6	0.84	1.24	1.38	0.68
MGP-PD 33244 Br13	13D	>3	3.1	2.9	2.0	<0.91	1.06	1.45	<0.85
MGP-PD 33246 Br10	-	3.5	3.0	2.4	2.1	0.86	1.22	1.17	0.70
MGP-PD 33244 Br1	13E	3.8	3.2	2.7	2.1	0.84	1.18	1.29	0.71
MGP-PD 33244 Br14	13C	3.8	3.2	2.3	2.0	0.86	1.40	1.17	0.61
MGP-PD 33246 Br11	-	3.9	3.1	3.8	2.7	0.78	0.82	1.39	0.95
MGP-PD 33246 Br2	-	4.2	3.2	3.5	2.2	0.76	0.94	1.59	0.81
MGP-PD 33244 Br16	13F	4.2	3.6	2.8	2.3	0.85	1.28	1.25	0.67

TABLE 13. Main quantitative characters of IIBr in *Holopus spileccense*. Abbreviations: see Fig. 1C. Wp is used as growth index. Values in mm except ratios.

Specimen	Figure	Wp	H	h	Wd	H/h	H/Wp	Wp/Wd
MGP-PD 33248 Br17	-	2.0	1.9	1.7	1.8	1.12	0.98	1.10
MGP-PD 33248 Br6	-	2.4	2.3	1.6	2.3	1.42	0.95	1.06
MGP-PD 33247 Br8	12A	2.3	2.2	1.8	1.9	1.20	0.92	1.22
MGP-PD 33247 Br4	12B	2.7	2.2	1.9	2.7	1.15	0.81	1.01

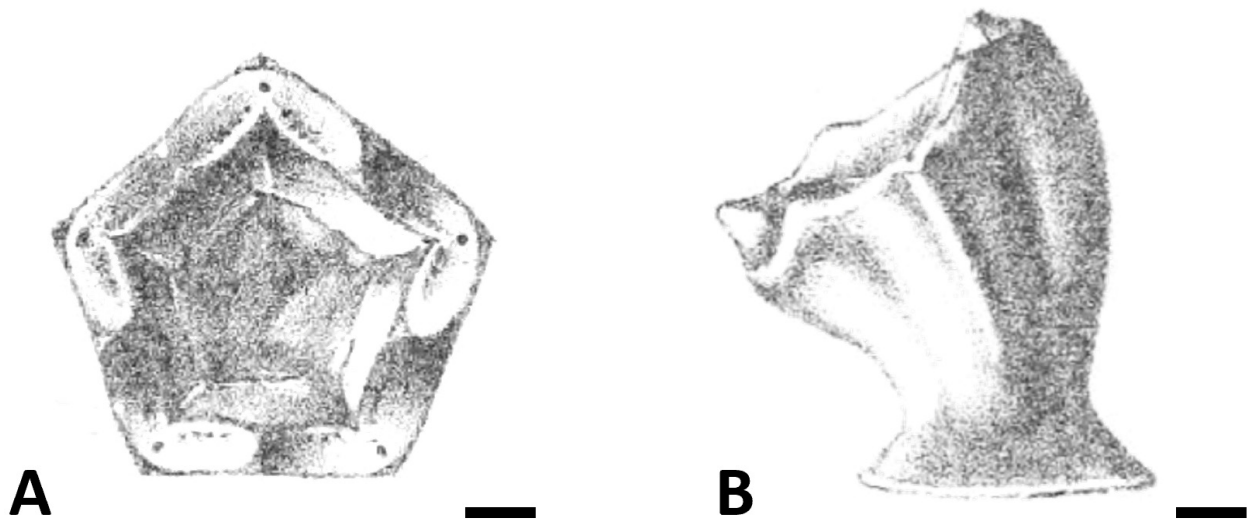


FIGURE 14. Lectotype of *Holopus spileccense* (modified from Schlüter 1878, pl. 3, figs. 11–12). A: adoral face, B: side view. Scale bars: 1 mm.

A comparison of the quantitative characters of the brachials of *H. spileccense* and *H. fabianii* **sp. nov.** reveals further differences (Tables 15 and 16). The former species differs in having IBrax that are wider than high (H/Wd up to 0.93, mean 0.84) and IIBr are less asymmetrical (H/h up to 1.43, mean 1.19) tending to be almost as high as wide (mean H/Wp 0.91). The brachials of both species differ further in their ornamentation. While the number of brachials available is limited, the ornamentation patterns remain consistent: coarse ribs without granulation in *H. spileccense* versus finer ridges with pronounced derived granulation in *H. fabianii* **sp. nov.** Nevertheless, both species share the same Y-shaped ridge pattern in IBrax and X-shaped ridges in IIBr. The two species are likely closely related as both might lack the inner interradial processes in the aboral cup and share keystone plates, which have not yet been found in *H. spileccense*. The presence of a well-developed keystone plate would put both these species closer to the extant *H. alidis* than to the Carribean congeners. However, if the drawings of *H. spileccense* by Schlüter are accurate, its rounded radial articulations with an interradial depression and the outer interradial process are reminiscent of *H. rangii*.

The brachials from the Lutetian of the Chiampo Valley attributed to *H. spileccense* by Manni and Pacioni (2021) are instead here referred to *H. fabianii* **sp. nov.** (see above). Thus, to date, the stratigraphic distribution of *H. spileccense* appears confined to the Ypresian.

Occurrence. Lower Eocene (lower Ypresian) of Spilecco Hill near Bolca, north-eastern Italy.

TABLE 14. Comparison of main quantitative characters of aboral cups in *H. fabianii* **sp. nov.** and *H. spileccense*. Abbreviations: see Fig. 1A. Values in mm except ratios.

Taxon		H	h	ht	D	Db	Dcs	H/D	H/h	H/ht	D/Dcs
<i>Holopus fabianii</i>	Max	6.5	6.5	4.5	4.6	8.1	3.9	1.48	1.29	2.07	1.49
	Min	1.7	1.7	0.8	1.8	1.2	1.6	0.98	1.00	1.35	1.03
<i>Holopus spileccense</i>	Max	8.1	5.1	4.5	6.0	5.0	4.1	1.78	1.79	2.17	1.98
	Min	3.2	2.9	1.5	3.0	2.1	1.9	1.00	1.11	1.45	1.09

TABLE 15. Comparison of main quantitative characters of IBraX in *H. fabianii* **sp. nov.** and *H. spileccense*. Abbreviations, see Fig. 1B. Values in mm except ratios.

Species		H	Wd	Wp	Wm	H/Wd	H/Wp	Wp/Wd	Wp/Wm
<i>Holopus fabianii</i> N = 43	Max	4.78	5.30	4.15	3.25	1.16	2.14	0.91	1.64
	Min	1.83	1.80	1.02	1.05	0.66	0.95	0.43	0.74
	Mean	2.94	3.26	2.25	1.87	0.91	1.41	0.68	1.18
<i>Holopus spileccense</i> N = 11	Max	3.63	4.25	3.76	2.70	0.93	1.40	0.95	1.59
	Min	2.49	2.75	1.81	1.45	0.76	0.82	0.61	1.16
	Mean	2.99	3.56	2.60	1.99	0.84	1.18	0.71	1.31

TABLE 16. Comparison of main quantitative characters of IIBr in *H. fabianii* **sp. nov.** and *H. spileccense*. Abbreviations, see Fig. 1C. Values in mm except ratios.

Species		H	h	Wp	Wd	H/h	H/Wp	Wp/Wd
<i>Holopus fabianii</i> N = 31	Max	4.00	3.15	5.06	4.59	2.25	1.03	1.87
	Min	1.19	0.75	1.62	1.45	1.08	0.48	0.99
	Mean	2.28	1.64	3.33	3.01	1.46	0.71	1.11
<i>Holopus spileccense</i> N = 5	Max	2.78	2.60	2.74	2.77	1.43	0.98	1.22
	Min	1.95	1.62	1.99	1.81	1.07	0.81	1.01
	Mean	2.27	1.94	2.35	2.30	1.19	0.91	1.10

TABLE 17. Composition of the crinoid fauna of Cengio dell'Orbo quarry based on MCZ residues (585 ossicles). br: brachial, Nid: number of individuals, Nid/T': ratio of number of individuals for each taxon to total number of individuals, No: number of ossicles, No/T: ratio of number of ossicles for each taxon to total number of ossicles, T: total number of ossicles (585) in the sample examined, T': total number of individuals (98) in total crinoid assemblage. Sizes given relatively to the usual range in the genus (sm: smaller size, us: usual size). Our identifications are based on the discriminating characters adopted by Roux *et al.* (2019) and Améziante *et al.* (2023) for extant and fossil taxa, *Cainocrinus* sp. = *Isocrinus archiaci* in Manni (2022), *Conocrinus fusus* = *Fabianicrinus fusus* **n. gen. sp. nov.** in Manni (2022). See text for explanations.

Taxa	No	No/T	Nid	Nid/T'	Preservation	Ossicles	size
<i>Cyathidium</i>	3	0.5%	3	3.1%	usually good	aboral cups	sm
<i>Holopus fabianii</i> sp. nov.	129	22%	8	8.2%	usually good	aboral cups, br	us
<i>Chiamprocrinus lobatus</i>	47	8%	47	48.0%	good	aboral cups	sm
<i>Cainocrinus</i> sp.	153	26%	~4	~4%	usually good	columnals	sm
<i>Conocrinus fusus</i>	11	2%	11	11.2%	variable to worn	aboral cups	us
<i>Conocrinus veronensis</i>	4	0.7%	4	4.1%	variable to worn	aboral cups	us
<i>Paraconocrinus</i> sp.	10	1.7%	10	10.2%	variable to well	aboral cups	sm
Bourgueticrinina	221	38%	~6	~6%	variable to worn	columnals	us
Indetermined	3	0.5%	3	3.1%	variable to good	encrusted discs	sm

Taphonomy and palaeoenvironment

Crinoid fauna of Spilecco (lower Ypresian).

In the sediments from the Spilecco site, aboral cups and brachials of *H. spileccense* account for only 0.74% of crinoid ossicles. About 9% of the remaining ossicles are isocrinid columnals, three-quarters of which are of small diameter (<3 mm) and have characters similar to those of the genus *Cainocrinus* (Balanocrininae); 89% are isolated columnals from xenomorphic stalks belonging to Rhizocrinidae; 1% are cups attributable to the rhizocrinid genera *Conocrinus* and *Pseudoconocrinus*. Aboral cups of *Conocrinus* (*sensu stricto*; Roux *et al.* 2019) belong to the species *C. suessi* Oppenheim, 1902 described and figured from a single aboral cup found at Spilecco, the type-locality of the species (Oppenheim 1902; 280, pl. 9, fig. 7). *Bourgueticrinus suessi* Munier-Chalmas in Hébert & Munier-Chalmas, 1877 is a *nomen nudum*. It was used and transferred to the genus *Conocrinus* (*sensu lato*) by Loriol (1879, pl. 19, figs. 33-34) for Eocene aboral cups from Switzerland showing characters very close to the genus *Paraconocrinus* and to the species *Lessinocrinus minutus* Manni, 2022 from the lower Lutetian of Chiampo. The latter two taxa were not found in our washings of Spilecco sediments. *Pseudoconocrinus* was identified from aboral cups and typical IBr2ax. The adoral face of the radial ring suggests a different species than *P. doncieuxi* (Roux, 1978) from the lower Ypresian of southern France (Roux *et al.* 2021). *Pseudoconocrinus* sp., the most abundant form, is represented by ossicles from various parts of the skeleton: rhizoids, distal, median and proximal columnals, aboral cups and axillary brachials. Exceptionally, pluricolumnals of two or three columnals were found. This diversity of *Pseudoconocrinus* ossicles indicates little or no *post-mortem* hydrodynamic sorting. The state of preservation of the ossicles is variable, most often marked by biocorrosion and with blunt angles indicative of attrition. Bite marks are frequent, particularly on aboral cups. Ossicles of all sizes are scattered in the sediment without any particular orientation. The fossil assemblage is a mixture of species attached to a rocky substrate (*Holopus*) and others attached by rhizoids penetrating soft sediment (*Conocrinus*, *Pseudoconocrinus*). The absence of sorting according to ossicle shape or size, and the presence of moderately rheophilic species (Rhizocrinidae, small Balanocrininae) suggest an environment with low to moderate current velocity that would not lead to a significant bioclast movement. The wear observed on certain columnals can be explained by a prior biocorrosional phase that weakened the ossicle angles, making them highly vulnerable to attrition during transport (Améziane-Cominardi & Roux 1987; Merle & Roux 2018). The sediment they were buried in may have been displaced by gravity on a slope with local rocky substrate outcrops. The holopodid and the *Cainocrinus* ossicles are usually the best-preserved, suggesting they were buried close to their biotope.

Crinoid fauna of Chiampo (lower Lutetian).

The complexity of the full fossil assemblage including crinoids at Cengio dell'Orbo quarry and the difficulties with its interpretation had already been pointed out by Frisone *et al.* (2020). The material in the Lovato Collection obtained from screen-washing, which is in a better state of preservation and more abundant, allows a revision of this fauna including a quantitative analysis of the crinoid assemblage (Table 17). The lower Lutetian fauna of the Chiampo Valley differs from that of the lower Ypresian of Spilecco in having a significantly greater taxonomic diversity, a smaller relative quantity of rhizocrinid ossicles (42%), and a great number of holopodid ossicles (22.5%). The most frequent ossicles are columnals from xenomorphic stalks (38%) mostly rhizocrinids, and *Cainocrinus* columnals (26%). The frequency of each taxon in the fossil assemblage can be used to estimate the number of individuals (e.g., Améziane-Cominardi 1989). Each rhizocrinid or cyrtocrinid aboral cup represents one individual. Assuming a mean number of *c.* 37 fossilized columnals per stalk for small *Cainocrinus* and bourgueticrinins, in spite of their great number, columnals belonging to these taxa represent only a few individuals (4% and 6% of total crinoid individuals, respectively).

The species *Chiampocrinus lobatus* Manni, 2022 (which, based on the aboral articular facets of its aboral cup, is possibly a Cyrtocrinida rather than a Bourgueticrinina) is represented by the greatest relative number of individuals (48%), most of which are well preserved. It clearly represents the dominant species of the crinoid community inhabiting in (or near) the depositional environment. Based on the best-preserved specimens and the absence of sorting, this community could have comprised *Chiampocrinus lobatus*, *Cyathidium chiampoensis* **sp. nov.**, *Holopus fabianii* **sp. nov.**, *Cainocrinus* sp. and *Paraconocrinus* sp. It was composed solely of small crinoids dominated by Cyrtocrinida (3 species out of 5, including *Chiampocrinus* as the most abundant taxon). Like the extant species, *H. fabianii* **sp. nov.** must have lived on rocky outcrops (see above), while the two specimens of *C. chiampoensis*

sp. nov. were attached to irregular substrate (maybe bioclasts or gravels lying on a sediment area). Similar to extant Isocrinida, *Cainocrinus* sp. could have settled on a variety of rocky or loose substrates (Tunncliffe *et al.* 2016). However, this genus was mostly found in muddy environments (Rasmussen 1972; Roux *et al.* 2006). Since rhizocrinids are usually rooted in the sediment, such an association suggests a heterogeneous substrate, consisting of both hard (rocky) and soft sediment, with a weak current. The other crinoid taxa, more or less bioeroded or worn, are interpreted as having been transported by gravity flows from shallower biotopes to the foot of the slope (see also depth estimations below). The taxonomic richness of the deposit is therefore the result of the accumulation of ossicles coming from different crinoid faunas and niches, distributed on a slope, mixed and buried together with autochthonous specimens inhabiting the depositional environment.

Depth estimation

Except for a single rhizocrinid specimen found at a depth of 66 m (Meyer *et al.* 1978), extant stalked crinoids occur at depths greater than 100 m. It is between 100 and 200 m depth (depths classically included into the usual term "shallow-water") that dense populations of large isocrinids and rhizocrinids have been collected or observed off southern China (Chang & Liao 1963), Japan (Fujita *et al.* 1987) and Australia (Shortis *et al.* 2007). They appear to belong to sciaphilic benthos living below the euphotic zone. Using an actualistic approach, Roux (1987) suggested that the absence of extant stalked crinoids at depths shallower than 100 m is mainly due to their feeding posture and not to a hypothetical migration from shallow to deep environment. They lift up their crown above the seafloor to filter food in moderate laminar currents, which implies morphofunctional constraints incompatible with storm wave turbulences common in shallower waters. Extant stalked crinoids show a bathymetric zonation of assemblages including more or less stenobathic species (Tunncliffe *et al.* 2016) and some morphological characters related to depth which may be used to estimate environment palaeodepth (e.g., Bourseau *et al.* 1988 for Isocrinida and Merle & Roux 2018 for Bourgueticrinina).

Although stalkless Holopodidae do not appear to be constrained by the hydrodynamic tolerance threshold of stalked crinoids, they have never been collected from depths shallower than 100 m (see above) presumably because they are sciaphilic. The genera and species are relatively eurybathic: *Holopus* from 100 to 758 m (Syverson *et al.* 2015) with *H. rangii* (100–654 m) and *H. mikihe* (430–758 m), *H. alidis* (c. 300–700 m), *Cyathidium* from 171 to 1,140 m (Wisshak *et al.* 2009) with *C. foresti* (420–1,140 m). However, *Holopus* has been found in numbers only below 274 m (*H. rangii*) or below 400 m (*H. mikihe*). Morphological characters related to depth are unknown in holopodids. Consequently, depth estimates can only be made with the help of associated stalked crinoids and other known crinoid assemblages of the same age.

The Ypresian fauna at Spilecco, dominated by Rhizocrinidae and particularly *Pseudoconocrinus*, is similar to one of the same age described from the Gulf of Languedoc in southern France, including *Holopus plaziati*. The latter biotope is thought to have lain between 100 and 140 m (Roux *et al.* 2021). It differs in the absence of *Cainocrinus*. This isocrinid genus occurs in the London Clay (lower Ypresian), which may correspond to depositional depths between 150 and 300 m (see discussion in Merle & Roux 2018). The biotope from which the Spilecco fossil assemblage originates could therefore have been at a depth greater than 150 m.

The Lutetian fauna from Chiampo is an assemblage of species from several biotopes at different depths on a slope (Frisone *et al.* 2020). The crinoid community likely to represent the biotope closest to the depositional environment comprises three genera of cyrtocrinids, with *Chiampocrinus lobatus* as the dominant species. Its small size suggests a much deeper environment than that reflected by the Spilecco fauna. The aboral cup of *Conocrinus veronensis* (Jaekel, 1891) develops long interradial spines, similar to the Bartonian species *C. cahuzaci* Roux, Eléaume & Améziane, 2019, the biotope of which is thought to have lain between 200 and 300 m (level C6a of Roux *et al.* 2006). These fragile spines, which are sometimes well preserved, suggest that the displacement of the specimens along the slope to the site of their burial must have been moderate. The latter could have reached or exceeded a depth of 300 m. The absence of large isocrinids of the genus *Isselicrinus* recently described from the Lutetian of Monte Baldo to the west of the Lessini Mountains, which are common in sedimentary substrates for which similar depths have been estimated (Roux *et al.* 2006, 2024), is possibly due to a low sedimentation rate in the original biotope and environmental instability linked to tectonic and magmatic activity.

To the west of the Alpone-Chiampo semigraben, another type of Lutetian crinoid-bearing deposit is known at Ciupio, Croce Grande, Contrada Gecchelina, San Giovanni Ilarione and Pozza (Merle & Roux 2018). In this area, phrynocrinid columnals of the genus *Eocenocrinus* Merle & Roux, 2018 are present within a faunal mixture rich in molluscs and large benthic foraminifera. The depositional environment inhabited by *Eocenocrinus* seems to have corresponded to an outer platform edge located at a depth of *c.* 150 m depth. In the eastern Lessini Mountains, during the Eocene, extensive tectonics thus created a complex submarine topography with crinoid biotopes ranging from the platform edge to depths equal to or greater than 300 m.

Palaeobiogeography and evolution

During the Eocene, the Lessini Mountains were part of the northern margin of the Gondwanan Adria microplate, which had not yet collided with the European margin. Iberia, Corsica, and Sardinia remained attached to the Pyrenean-Provençal domain prior to the opening of the Ligurian Basin and, more generally, the western Mediterranean Sea, which did not start until the Oligocene (Angrand & Mouthereau 2021). There was no marine connection between the Alpine and Atlantic domains to allow large faunal exchanges, particularly for circalittoral to bathyal benthos. The maximum extension of the Eocene Sea from the Atlantic occurs in the Ypresian in the French-Spanish Pyrenean domain and stops to the east in Catalonia and the Corbières (Plaziat 1981; Roux *et al.* 2021). The Nummulitic transgression of the Alpine Sea from Italy to the west and north-west during the middle-late Eocene stopped at the subalpine ranges of south-eastern France (Cavelier 1984).

Both holopodid genera described herein are known from western Eurasia as early as the Late Cretaceous. The discovery of *Cyathidium* in the Antarctic Eocene illustrates the wide geographic distribution, including the Gondwanan margin, from this period onwards (Baumiller & Gaździcki 1996). New Caledonia, where *H. alidis* now lives, is also a microplate of Gondwanan origin. The affinities between *H. alidis*, *H. spileccense* and *H. fabianii* **sp. nov.** suggest that these three species have the same origin and may belong to the same lineage. *Holopus plaziati* from the Ypresian of the Corbières may belong, together with the extant Caribbean *Holopus*, to another lineage of Laurasian origin. All rhizocrinid species associated with Holopodidae in Spilecco and Chiampo belong to genera described in the European Eocene but are rooted in the Upper Cretaceous (Roux *et al.* 2019). They appear to differ markedly from those of the Pyrenean domain (e.g., Roux *et al.* 2021). In the current state of knowledge, it is not possible to determine whether this difference was the consequence of the geographic isolation during the Eocene between the Pyreneo-Atlantic province to the west and the Alpine marine domain to the east, or between the Gondwanan margin to the south and the Laurasian margin to the north.

Conclusions

The study of ossicles from the type locality of *H. spileccense* and a quantitative comparison with ossicles found in outcrops of younger strata in Chiampo allowed us to identify two closely related species of *Holopus* and two species of *Cyathidium* in the Chiampo Valley, separated by some 10 Myr. This adds to the known morphological diversity and variation of Holopodidae and *Holopus* in particular for which it is the first in-depth study of morphological variation. Interestingly, the study of extant species has allowed us to identify the first fossil records of brachials from the arm's distal series as well as keystone plates in *H. fabianii* **sp. nov.** These findings prove that at least some Eocene *Holopus* species could roll up their arms forming a tight vault. The differentiated keystone plates are a shared character between the fossil *H. fabianii* **sp. nov.** and the extant *H. alidis*, connecting thereby the Tethyan fauna on the Gondwanan margin to today's Indo-Pacific fauna. However, the fact that *H. fabianii* **sp. nov.** lacks the prominent inner interradial processes seen in *H. alidis* raises questions about this character's origin. Further investigations and new samples might add support for a Gondwanan origin. Based on Schlüter's (1878) drawing of *Cyathidium spileccense* this species has rounded radial articulations with slight interradial depressions and outer interradial processes, not visible in our samples. As drawn, this character set is reminiscent of the extant Atlantic species *H. rangii*. Furthermore, small *H. fabianii* **sp. nov.**, *H. spileccense*, and young *H. alidis* share a similar IBrax ornamentation with a Y-shaped ridge that is more or less lost in larger specimens depending on the species. As such, in addition to the apparent character mosaic, morphological characters seem to present substantial plasticity in Holopodidae which is likely to present

problems for evaluating evolutionary hypotheses. Since Holopodidae are quite rare in the fossil record (awaiting the description of the upper Campanian *Holopus* as the oldest representative), it might be the study of the ontogeny of the arms and cups in extant species that brings further insights into the evolution of this crinoid family.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

Supp. Table 1. Main quantitative characters of non-figured IBr and IBrax of *Holopus fabianii* **sp. nov.**

Supp. Table 2. Main quantitative characters of non-type-series IIBr in *Holopus fabianii* **sp. nov.**