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EOCENE STALKED CRINOIDS IN THE GENUS *ISSELICRINUS* (ECHINODERMATA, CRINOIDEA, ISOCRINIDA) FROM NORTHEASTERN ITALY

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Abstract. Long fragments of isocrinid stalks belonging to the stalked crinoid genus *Isselicrinus* (Isocrinida, Isselicrininae) were found at Cambrigar, near Ferrara di Monte Baldo (Verona province, northeastern Italy) in the strata called "*Harpactocarcinus punctulatus* and *Pentacrinus diaboli* horizon", traditionally ascribed to the lower Eocene (Ypresian). Morphometric analysis of this material allowed us to identify two distinct species filtering their food at different levels of the water column. The first species, characterized by a mostly pentagonal stalk section, is ascribable to *Isselicrinus diaboli* (Bayan), a taxon frequently cited from the lower Eocene of northeastern Italy but until now poorly known. The other species has a marked star-shaped stalk section presenting a combination of pedomorphic characters and is ascribed to the new taxon *Isselicrinus baldoensis* n. sp. A detailed analysis of numerous columnals and pluricolumnals of *Isselicrinus diaboli* from the type-locality of San Pancrazio near Mossano (Berici Hills, Vicenza province, northeastern Italy) allowed us to propose a revised and more complete diagnosis of this taxon. The particular burial conditions and the ecology of these two species are discussed as well as a reappraisal of the age of the "*Harpactocarcinus punctulatus* and *Pentacrinus diaboli* horizon". Based on new calcareous nannofossil data, and confirmed by the larger foraminiferal assemblages, the isocrinids from Cambrigar are firmly assigned to the Lutetian (middle Eocene). Calcareous nannofossils identified in the matrix of historical hand specimens from the classical locality of San Pancrazio indicate a similar age.

INTRODUCTION

The isocrinid genus *Isselicrinus* Rovereto, 1914 is known from the Upper Cretaceous up to the Miocene (Hess 2011). A closely related extant genus *Panglaocrinus* has recently been discovered off the Philippine Islands (Améziane et al. 2023). *Isselicrinus* attains a worldwide distribution during the Eocene (Klikushin 1992; Fujiwara et al. 2005; Mulumian & Olivero 2005; Hess 2011; Donovan et al. 2019) in offshore environments, especially on upper bathyal slopes (Roux et al. 2006). The different species are only distinguished based on columnal or pluricolumnal characters. Well-preserved crowns

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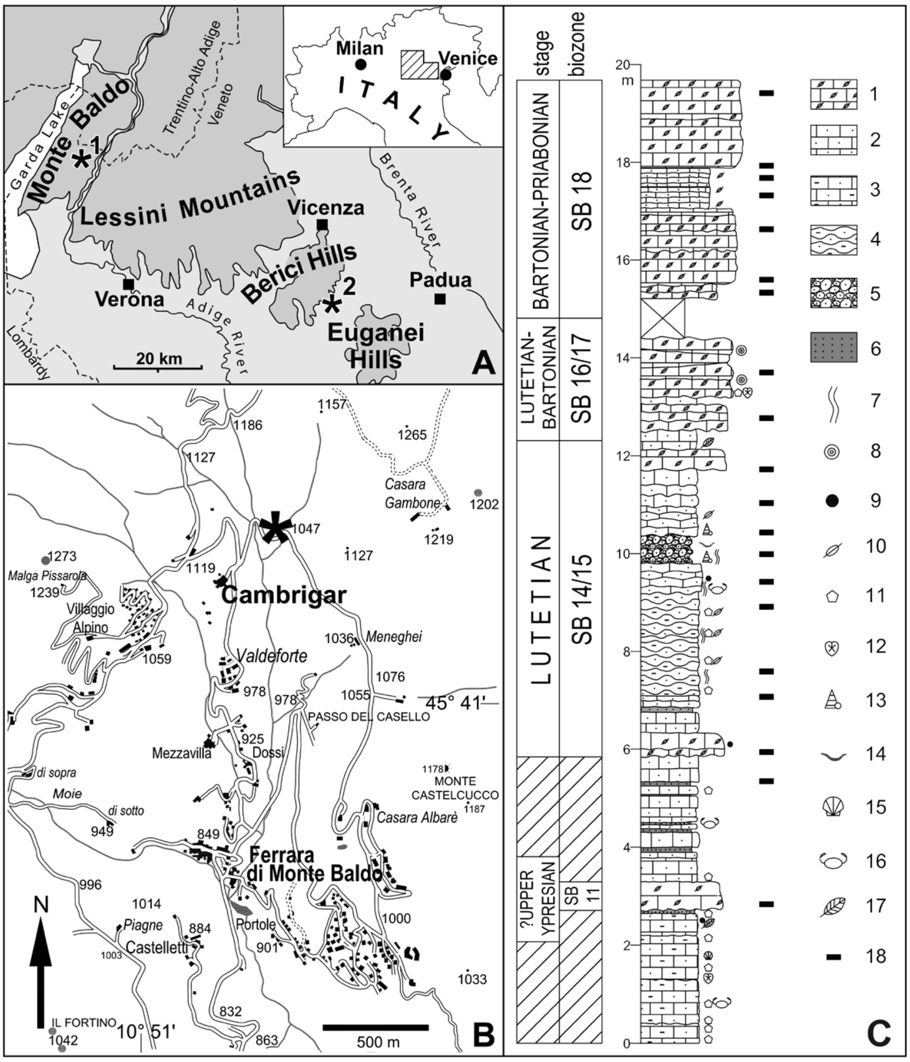


Fig. 1 - A) General map with the location of the *Isselicrinus* sites studied (asterisks): 1, Ferrara di Monte Baldo/Cambrigar; 2, Mossano/San Pancrazio; B) detailed map of the area north of Ferrara di Monte Baldo (Verona) with the location of the Eocene section of Cambrigar (asterisk); C) stratigraphic log of the "upper Cambrigar section", larger benthic foraminiferal biozonation (SB) according to Serra-Kiel et al. (1998). Legend: 1, larger foraminiferal calcirudites, locally glauconitic; 2, calcarenites, locally glauconitic; 3, marly calcarenites, locally glauconitic; 4, subnodular marly calcarenites; 5, synsedimentary fossiliferous breccia with calcarenitic clasts; 6, calcarenitic marls; 7, bioturbation; 8, calcareous algae; 9, iron sulfide nodules; 10, larger foraminifera; 11, crinoids; 12, echinoids; 13, gastropods; 14, ostreids; 15, undetermined bivalves; 16, crabs; 17, plant remains; 18, samples studied for larger foraminifera analysis.

are only known in the lower Eocene species *I. subbasaltiformis* (Miller, 1821) from the boreal province (Rasmussen 1972). *Isselicrinus diaboli* (Bayan, 1870) is a species widely reported from the lower Eocene of northeastern Italy but at present it remains poorly described and without clear identification of discriminating characters. Within the genus *Isselicrinus*, conspicuous discriminant stalk characters are lacking at the species rank. Numerous species were introduced simply from differences in external stalk morphology. These differences might correspond to either intraspecific variations or ecophenotypic convergences.

With the help of biometric studies and a detailed analysis of the articulations, in this paper we describe long stalk fragments of *Isselicrinus* which show morphological changes that can be related to the ossicle position along the stalk (from proximal to distal). These specimens were collected at Cambrigar, near Ferrara di Monte Baldo (west of Lessini Mountains, Verona province, northeastern Italy) (Fig. 1A-B), in Eocene strata usually named «*Harpactocarcinus punctulatus* and *Pentacrinus diaboli* beds» (HPB). Crinoid columnals have long been known from Eocene deposits cropping out in the area of Monte Baldo and have been usually referred to *Pentacrinus diaboli* Bayan (e.g., Fabiani 1915; Luciani 1989), *Pentacrinus* cf. *diaboli* (e.g., Garassino et al. 2009; Beschin & Checchi 2020) or *Isselicrinus diaboli* (Marramà et al. 2021). Given the uncertainty surrounding Bayan's taxon, numerous columnals and pluricolumnals of *Isselicrinus diaboli* coming from the type-locality of the species at San Pancrazio, near Mossano (Berici Hills, south of Vicenza; Fig. 1A), are also examined here and compared with the material from Cambrigar. This study allows to give a more complete diagnosis of *I. diaboli* and to describe a new species, *I. baldoensis* n. sp., associated with *I. diaboli* at Cambrigar. New micropalaeontological data refining the age attribution of the HPB horizon from both localities are also presented.

Historical framework

The area between Ferrara di Monte Baldo and Cambrigar (Fig. 1B) is historically known for its Eocene crab-bearing beds since the second half of XIX century (but probably before; see Beschin et al. 2011) when Nicolis (1882) cited therein the occurrence of rocks with "*Cancer punctulatus*" associated with algae and "*Pentacrinus*". These fossiliferous beds, containing the brachyuran *Harpactocarcinus* and the crinoid "*Pentacrinus*" *diaboli*, have been referred since Fabiani (1915) to the lower Eocene (e.g., Garassino et al. 2009). A recent study on a short section cropping out at Cambrigar ("lower Cambrigar section") based on larger foraminiferal content, however, showed for the first time the presence of isocrinid columnals in firmly dated Lutetian beds (Marramà et al. 2021). The classical locality for the Eocene isocrinids of the Veneto region is the southern portion of the Berici Hills (surroundings of Mossano; Fig. 1A), the type locality of *Pentacrinus diaboli* Bayan, 1870. The type horizon, represented by a few meters of marls and limestones resting on a hard ground surface of the Upper Cretaceous Scaglia Rossa, have been traditionally referred to the lower Eocene by Fabiani (1905; 1908; 1915), but such an attribution is so far unsupported by modern stratigraphic data. A third locality historically known for Eocene "pentacrinids" is the Albettone Hill, located between the Euganei and the Berici Hills, whose source beds have been referred by De Zigno (1879) and Fabiani (1915) to the lower Eocene. De Zigno (1861, 1879) originally ascribed the specimens from Albettone to "*Pentacrinites didactylus*" d'Orbigny, later ascribed to *Pentacrinus diaboli* (e.g., Fabiani 1908; 1915). Specimens of "*Pentacrinus*" *diaboli* and other related "pentacrinids" have been also reported from several Eocene localities of the Veneto, Trentino-Alto Adige, and Friuli-Venezia Giulia regions of northeastern Italy (e.g., Fabiani 1915; 1922; Dainelli 1915, among others). Munier-Chalmas (1891: 29) also reported a "pentacrinid", "*Pentacrinus*" *spileccensis*, from the Spilecco Hill succession (Bolca, Verona province), whose fossiliferous beds are ascribable to the lower Eocene (Papazzoni et al. 2014 and E.F., unpublished data). This taxon, however, is a nomen nudum. During our ongoing investigation on the crinoids from Spilecco we found only small thick isolated columnals having symplexial facets of diplocrinine type, never *Isselicrinus* columnals. "*Pentacrinus*" *spileccensis* probably corresponds to this small isocrinid. This small sized material from Spilecco is likely the same questionably referred to *P. diaboli* by Oppenheim (1902: 281-282), who stated that it was listed by Munier-Chalmas (1891) as *P. spileccensis*.

Geological setting

General setting

The fossils examined come from the surroundings of Cambrigar, a hamlet of Ferrara di Monte Baldo, located in the southern sector of the Monte Baldo range, belonging to the western border of the Lessini Mountains (Southern Alps, Verona province, northeastern Italy) (Fig. 1A). During the early Paleogene, this area was part of the Trento Plateau, a structural high previously characterized by pelagic/hemipelagic sedimentation that was segmented into variously uplifted blocks by local extensional tectonics with associated magmatic activity. Since the early Eocene, various unstable palaeoenvironments developed, including centers of initiation of shallow-water carbonates, finally transforming part of the previous Trento Plateau into the so-called "Lessini Shelf" (e.g., Bosellini 1989; Luciani 1989; Bosellini & Papazzoni 2003). According to Marramà et al. (2021), the Paleogene succession cropping out at Cambrigar belongs to two depositional sequences as defined by Luciani (1989): the lower-middle p.p. Eocene Torbole sequence, that includes the formations of "Calcare di Chiusole" (Chiusole Limestone) and "Calcare di Malcesine" (Malcesine Limestone), and the middle p.p.-upper Eocene p.p. Nago sequence that includes the "Calcare di Nago" (Nago Limestone) and the "Marne di Bolognano" (Bolognano Marls). The succession of Cambrigar testifies to an evolution from a basinal setting (Chiusole Limestone) to shallow-water carbonate deposition (Nago Limestone), followed by a relative deepening recorded by the Bolognano Marls in the late Eocene.

The upper Cambrigar section

Based on fieldwork surveys carried out by two of us (L.G. and C.A.P.), some photographs originally taken by the collector Mr. Antonio Rossi (see below), and testimonies of other private collectors, the study material likely comes from a ca.

Tab. 1 - Material examined belonging to the genus *Isselicrinus* from Cambrigar (Monte Baldo) and San Pancrazio (Berici Hills). MGP-PD: catalogue number of the Section of Geology and Palaeontology of the MNH of the University of Padua, Plc: pluricolumnal, Col: isolated columnal, Sf: stalk fragment (>20 columnals).

MGP-PD	Provenance	Species	Specimen	Material	Figure	Remarks
1307R	Cambrigar	*I. baldoensis*	Rock sample	1 Sf	Fig. 7B	Holotype
1308R	Cambrigar	*I. baldoensis*	Rock sample	1 Sf	Fig. 7A	Paratype 1
1309Ra, b	Cambrigar	*I. baldoensis*	Rock sample	2 Sf	Fig. 5 (1-2)	Paratypes 2a, b
1310Ra-c	Cambrigar	*I. baldoensis*	Isolated Plc	3 Plc	Fig. 4	Paratypes 3a-c
1312R	Cambrigar	*I. baldoensis*	Isolated Plc	1 Plc	Fig. 8C	Paratype 4
1324R	Cambrigar	*I. baldoensis*	Isolated Plc	1 Plc	Fig. 8D	Paratype 5
1313R	Cambrigar	*I. baldoensis*	Isolated Plc	1 Plc	Fig. 8A-B	Paratype 6
1316R	Cambrigar	*I. baldoensis*	Isolated Plc	1 Plc	Fig. 2A	Paratype 7
1317R	Cambrigar	*I. baldoensis*	Isolated Plc	1 Plc	Fig. 2B	Paratype 8
1318R* 1320-22R	Cambrigar	*I. baldoensis*	Isolated Plc	14 Plc	Not figured	Other Paratypes *1318Rb,e,g
1309Rc	Cambrigar	*I. diaboli*	Rock sample	1 Sf	Fig. 5 (3)	
1305Ra, b	Cambrigar	*I. diaboli*	Rock sample	1 Sf+1 Plc	Fig. 6	
1314R	Cambrigar	*I. diaboli*	Isolated Plc	1 Plc	Fig. 13A-B	
1315Ra-b	Cambrigar	*I. diaboli*	Isolated Plc	2 Plc	Fig. 13C	2 Plc attached
1311R	Cambrigar	*I. diaboli*	Isolated Plc	1 Plc	Fig. 13D	
1306R	Cambrigar	*I. diaboli*	Rock sample	1Plc	Fig. 2C	
1318-19R* 1323R	Cambrigar	*I. diaboli*	Isolated Plc	14 Plc+1 Col	Not figured	*1318Ra, c,d,f,h,i
1057	San Pancrazio	*I. diaboli*	Isolated Plc	8 Plc	Not figured	
6347	San Pancrazio	*I. diaboli*	Isolated Plc-Col	18 Plc	Not figured	
7829a	San Pancrazio	*I. diaboli*	Isolated Plc	1 Plc	Fig. 12B	
7829b	San Pancrazio	*I. diaboli*	Isolated Plc-Col	136 Plc+6 Col	Not figured	
18341	San Pancrazio	*I. diaboli*	Isolated Plc	44 Plc	Not figured	
18342	San Pancrazio	*I. diaboli*	Isolated Plc-Col	54 Plc-2 Col	Not figured	
23437a	San Pancrazio	*I. diaboli*	Isolated Plc	1 Plc	Fig. 12A	
23437b	San Pancrazio	*I. diaboli*	Isolated Plc	1 Plc	Fig. 12C-D	Neotype
23437c	San Pancrazio	*I. diaboli*	Isolated Plc	1 Plc	Fig. 12E-F	
23437d	San Pancrazio	*I. diaboli*	Isolated Plc	1 Plc	Fig. 12G	
23437e	San Pancrazio	*I. diaboli*	Isolated Plc	9 Plc	Not figured	

20 m-thick section (herein labelled "upper Cambrigar section") cropping out along a road cut and located ca. 1.5 km north of Ferrara di Monte Baldo (Fig. 1B-C). The lower half of the section, mostly consisting of marly glauconitic calcarenites with interbedded larger foraminiferal calcirudites, yielded, among others, crabs, isocrinid crinoids, plant remains and mollusks (Fig. 1C). The fossiliferous calcarenites are grayish, yellowish when weathered. Isocrinid remains are particularly abundant in the basal 2.5 meters of the section (Fig. 1C) and frequently occur perpendicular to the stratification. Based on macro and microlithological features, the lower half of the section likely represents the transition from Calcare di Chiusole to Calcare di Malcesine and was deposited on a slope setting with redeposition of shallow-water biota transported downslope (Marramà et al. 2021). The upper half of the section, mainly represented by larger foraminiferal calcirudites, is likely referable to the Nago Limestone (Fig. 1C). The "upper Cambrigar section" is located about 125 m north of the nearby "lower Cambrigar section" previously described by Marramà et al. (2021).

A detailed reconstruction and stratigraphic study of the entire lower-middle Eocene succession at Cambrigar is still underway, but it is complicated by rapid, small-scale lateral facies changes, besides the presence of vegetation cover, especially on basal beds.

MATERIAL AND METHODS

Crinoids

The crinoid material from Cambrigar consists of isolated stalk fragments shorter than one noditaxis and 6 rock samples of indurated sediment including 11 stalk fragments collected circa 1980 by the late Mr. Antonio Rossi. The findings are all housed in the Section of Geology and Palaeontology of the Museum of Nature and Humankind (MNH) of the University of Padua (MGP-PD) (Tab. 1). Among a total of 40 pluricolumnals, 5 display a number of columnals greater than 20. We verified the classical attribution to *Isselicrinus diaboli* of these large isocrinid stalk fragments by comparing them to well-preserved material of this species from the type-locality (San Pancrazio, near Mossano, Berici Hills) which belongs to the historical MGP-PD collection (Tab. 1).

In isocrinids, the quantitative columnal characters can vary markedly along the same stalk and from one individual to another (David et al. 2006). Biometric data are important to understand these variations and their origin. New columnals mainly appear just below the aboral cup at the base of the crown. As the aboral cup grows, the next columnals produced present the greatest diameter of the proximal stalk (Dp). Along a given stalk and beyond the proxistele, columnal height (H), diameter (D) and thickness (H/D) increase. As the height increases

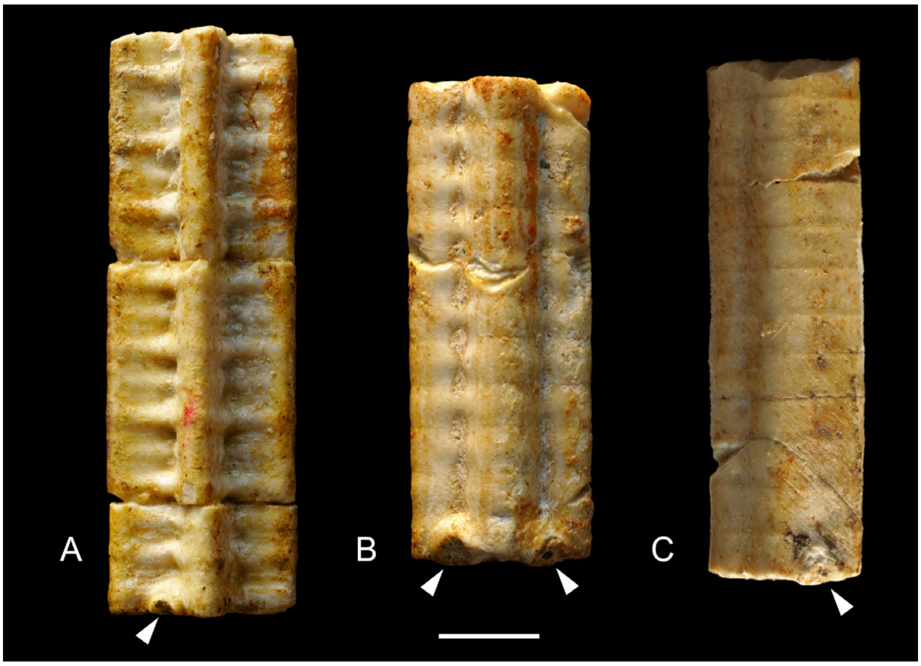


Fig. 2 - The three main features of *Isselicrinus* stalk fragments from Cambrigar related to their place along the stalk. Each fragment is the distal part of a noditaxis ended by a nodal with cirrus sockets (arrow heads); A-B) *Isselicrinus baldoensis* n. sp.; A: proximal stalk, paratype MGP-PD 1316R; B: distal middle stalk, paratype MGP-PD 1317R; C) *I. diaboli*, distalmost stalk, MGP-PD 1306R. Scale bar equals 5 mm.

faster than the diameter, the columnals from the mid and distal stalk are thicker in juveniles than in older specimens. Columnal diameter (D) is used as a growth index of individuals. In the material examined here, no fragment belonging to the proximalmost stalk just below the aboral cup has been identified.

Morphological characters vary along the stalk, too. In the proximal stalk, columnals are usually stellated with deep interarticular pores, and thinner and thicker columnals alternate (Fig. 2A). Distally, they tend to have a more pentagonal cross section, with only a slight variation in columnal thickness and diameter, and interarticular pores are lost (Fig. 2B-C). Based on all these parameters, a biometric and morphological analysis has been carried out in order to properly distinguish and describe the isocrinid taxa studied here. This allowed to hypothesize the location of the fragments along the stalk and to identify the main morphological modifications during the stalk growth with reference to similar extant species (see, for example, the same method used in Roux & Philippe 2021). However, the totality of the ossicles collected in a fossil assemblage (herein 309 and 207 columnals for Cambrigar and San Pancrazio respectively) often represents only a small number of individuals living in a place, given that extant species with the same columnal diameter have an individual stalk made up of 300 to 500 columnals. Therefore, the samples are usually insufficient for a complete statistical analysis. This problem is exacerbated when dealing with material housed in historical collections, since the collecting methods remain unknown.

Usually, in *Isselicrinus* the noditaxes from the mid and distal stalk are longer than in other isocrinids, suggesting that the stalk was substantially longer than that of the largest extant isocrinids (Fujiwara et al. 2005). The latter often reach lengths of 60-80 cm and sometimes up to 1 m (Macurda & Meyer 1974). In comparison, the cumulative length of the fossil stalk fragments analyzed here is less than 45 cm for the Cambrigar material and does not exceed 118 cm for the material from San Pancrazio (see below) and we are only dealing with fragments from different stalks and not with whole individuals. Therefore, the character variation observed in the material must be considered only an approximation of the true species variability.

The number of internodals per mature noditaxis (IN/Ndx) is an important character in taxonomy and for the morphofunctional interpretation of the stalk related to the ecology of the organism (David et al. 2006). In the absence of complete noditaxis, the average IN/Ndx has been estimated by counting the number of nodals relative to the total number of internodals. However, in the case of *Isselicrinus* with a great IN/Ndx (usually >30), the chance of having one nodal within a sample requires a high number of columnals. The reliability of this average number has been tested by comparing it with the maximum number of internod-

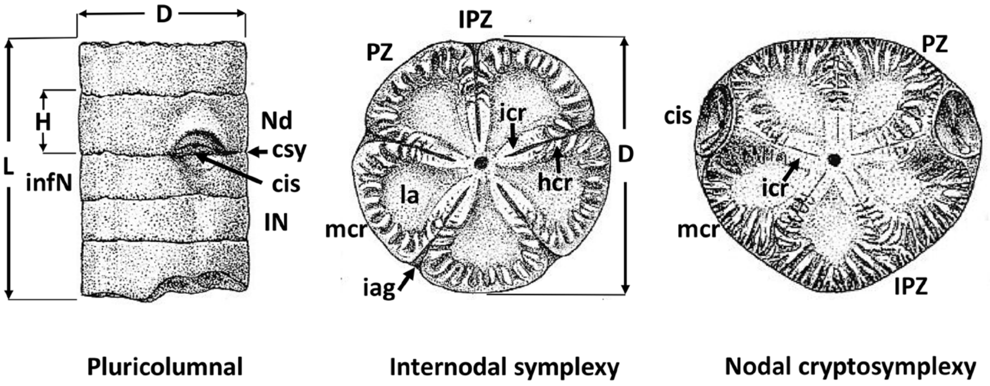


Fig. 3 - Morphological terms and quantitative parameters in *Isselicrinus* stalk. Articular facets and side view of pluricolumnal. For cryptosymplexy, view of distal nodal facet. D: diameter, H: columnal height, L: pluricolumnal length, infN: infranodal, IN: internodal, Nd: nodal, IPZ: interpetaloid zone (radial axe), PZ: petaloid zone (interradial axe), cis: cirrus socket, csy: cryptosymplexy, iag: interpetaloid groove forming interarticular pore on external surface of proximal stalk, hcr: herring bone crenulation, icr: inner crenularium, mcr: marginal crenulation, la: ligament areola. Articular facets of *I. subbasaltiformis* from Rasmussen (1972), modified.

als observed in an incomplete noditaxis. The large number of columnals required was available in the case of the collection from San Pancrazio. At Cambrigar, the exceptional length of the preserved stalk fragments allows a reliable assessment of IN/Ndx despite a smaller total number of columnals.

SEM observations of crinoids were performed at the electron microscopy platform from the Muséum National d'Histoire Naturelle (MNHN) using a Jeol-840A SEM operating at 15 kV. The ossicles were previously ultrasonically cleaned and coated with a colloidal platinum solution.

For general morphological terms see Roux et al. (2002) and Hess (2011), for ossicle articulations see the glossary revised by Améziane et al. (2021). The morphological terms and parameters measured are shown in Fig. 3.

Calcareous nannofossils

As the precise stratigraphic position of the material studied is unknown, one of us (E.F.) analyzed the calcareous nannofossils contained in the matrix of *Isselicrinus* pluricolumnals where it was preserved. For Cambrigar, the samples MGP-PD 1305-1310R collected by A. Rossi were used. For San Pancrazio, we recovered two hand specimens with isocrinids still embedded in their sedimentary matrix (MGP-PD 7827 and 7828) and coming from the historical collection of Roberto De Visiani (1800-1878) housed in the MNH. All samples have been prepared from unprocessed material as smear slides and examined using a light microscope at 1250X magnification to investigate their calcareous nannofossil content. To highlight biostratigraphically useful taxa two kinds of counts were performed: (1) the semi-quantitative counting in a prefixed area of about 8–7 mm^2 (roughly equivalent to three vertical traverses; modified after Gardin & Monechi 1998) of specimens of taxa that are rare but useful for the biostratigraphy; and (2) the quantitative counting of index species within a prefixed number of taxonomically related forms (i.e., *Sphenolithus*; Rio et al. 1990) where the number of the selected taxon was statistically significant (at least 25-50 specimens).

Larger foraminifera

The entire upper Cambrigar section has been biostratigraphically framed based on larger foraminiferal content. The study (performed by C.A.P.) is based on 20 samples mainly coming from the calciruditic samples and indicated in the log (see Fig. 1C). The determination of the taxa retains some degree of uncertainty because it relies on random thin sections. The biozonation adopted follows that of the Shallow Benthic Zones (SB) of Serra-Kiel et al. (1998).

Abbreviations. Abbreviations used for tables and some descriptions: MGP-PD: Section of Geology and Palaeontology of the Museum of Nature and Humankind (MNH) of the University of Padua, HPB "*Harpactocarcinus punctulatus* and *Pentacrinus diaboli* beds", Co: columnal, Cr: crenulae, Cr/PZ: maximum number of marginal crenulae per petaloid zone, D: diameter, Dp: proximalmost stalk diameter, Dm: maximum columnal diameter, H: columnal height, Hm: mean columnal height, H/D: columnal thickness, icr: inner crenularium, infN: infranodal, IN: internodal, IN/Nd: ratio number of internodals to number of nodals, IN/Ndx: number of internodals per noditaxis, IPZ: interpetaloid zone, L: pluricolumnal length, Nb Col: number of columnals, Nb IN: number of internodals, Nb Nd: number of nodals, Nb Plc: number of pluricolumnals, Nd: nodal, Ndx: noditaxis, NPlc: number of pluricolumnals, Plc: pluricolumnal, PZ: petaloid zone.

Results

Biostratigraphic frame of the upper Cambrigar section

According to the larger foraminiferal content, the section can be subdivided into a lower-middle part, where the assemblages indicate the Lutetian SB 14-15 zones (with several specimens of *Nummulites alponensis*) and the Lutetian/Bartonian SB 16-17 zones (with *Nummulites millecaput*), as in the lower Cambrigar section described by Marramà et al. (2021), and an upper part belonging to SB 18 (upper Bartonian-lower Priabonian) because of the presence of *Nummulites maximus*, *N. biedai*, and *N. biarritzensis* (Fig. 1C). The position of the Bartonian/Priabonian boundary is, according to the recently established GSSP of the Priabonian (Agnini et al. 2021), within the SB 18 zone. Indeed, in the lowermost part of the upper Cambrigar section, a single sample corresponding to the first calciruditic interval (Fig. 1C) indicates the upper Ypresian SB 11 zone because of the presence of *Nummulites partschi*, *N. nitidus* and *Alveolina rugosa* (a fragment) but such assignment is problematic because the assemblage could be made up of reworked material.

Biostratigraphic assignment of *Isselicrinus* from San Pancrazio and Cambrigar

The two samples associated with rocky matrix from San Pancrazio (MGP-PD 7827 and 7828) are characterized by a common to abundant and well diversified calcareous nannofossil assemblage in a moderate to good state of preservation. The most common taxa are Noelaerhabdaceae (*Cyclicargolithus floridanus, Dictyococcites* and *Reticulofenestra*), *Sphenolithus*, and *Coccolithus pelagicus*. Rare to few are *Umbilicosphaera protoannulus* (large morphotype), and the genera *Pontosphaera* and *Helicosphaera*. Among the genus *Sphenolithus*, the species *S. furcatolithoides*, *S. spiniger* and *S. strigosus* occur in both samples. Specifically, Sample 7827 is characterized by 18% of *Sphenolithus spiniger*, 6% of *S. furcatolithoides* and 4% of *S. strigosus* while Sample 7828 is comprised of 11% of *S. spiniger*, 2% of *S. furcatolithoides,* 2% of *S. strigosus* and 3% of *Sphenolithus radians*. It is worth pointing out the absence of the marker species *Chiasmolithus gigas* in both samples and the presence of a single specimen of *Reticulofenestra umbilicus* in sample 7828, absent in sample 7827. The calcareous nannofossil data suggest that the Berici samples can be attributed to Zone CNE12 of Agnini et al. (2014) due to the absence of *C. gigas* and common *R. umbilicus* even if a note of caution is needed for sample 7828 due to the presence of exceedingly rare *R. umbilicus*. In addition, according to Cappelli et al. (2021) the presence of *Sphenolithus furcatolithoides*, *S. strigosus* and the absence of *S. cuniculus* (*Furcatolithus cuniculus* sensu Howe 2021) allows to firmly constrain the samples to upper part of CNE12 Zone, corresponding to the mid-upper portion of the Lutetian.

The analyzed sample set from Cambrigar (specimens MGP-PD 1305-1310R) is inhomogeneous. Calcareous nannofossil content of samples 1305 and 1310 is not sufficient for a biostratigraphic constrain. Samples 1306 and 1308 have a few/rare calcareous nannofossils and the preservation state of the assemblage is moderate/poor. The most common taxa are the Noelaerhabdaceae (*Cyclicargolithus floridanus, Dictyococcites* and *Reticulofenestra*) followed by *C. pelagicus* and *Ericsonia* (few/rare). The presence of rare *S. spiniger* in both samples allows assigning them to upper CNE8-basal CNE15 zones (Lutetian-lower Bartonian), corresponding to the total range of *S. spiniger*. In sample 1306 the number of specimens of the genus *Sphenolithus* is not statistically significant, whereas in sample R4 sphenoliths are more common. However, the state of preservation does not allow to further constrain the biozone. Samples 1307 and 1309 are more suitable for biostratigraphic analyses. The calcareous nannofossil assemblage is rich, well preserved and diversified. The Noelaerhabdaceae (*Cyclicargolithus floridanus, Dictyococcites* and *Reticulofenestra*) dominate the assemblage. *Coccolithus pelagicus* and sphenoliths are well represented whereas *Chiasmolithus* is few/rare and *Helicosphaera* is very rare. Within the genus *Sphenolithus* the concurrent presence of *S. furcatolithoides* (1307: 4%; 1309: 2%) and *Sphenolithus cuniculus* (1307: 4%; 1309: 6%) allows to ascribe both samples to the upper part of CNE11 - lower part of CNE12 corresponding to the Lutetian. These latter data are consistent with a provenance of the specimens from the interval spanning the Lutetian larger foraminifera SB 14/15 zones in the upper Cambrigar section (Fig. 1C) as supported by the correlation of Eocene calcareous nannofossil and larger foraminiferal zones presented in the integrated scheme of Speijer et al. (2020: 1106-1107).

Taphonomical observations

A detailed taphonomic analysis is hampered by the fact that the material studied is represented by museum samples. However, some results appear from a few observations in situ and the study of the available material.

In the basal 2.5 meters of the upper Cambrigar section, *Isselicrinus* remains are relatively abundant and a few beds show stalk fragments perpendicular to the stratification indicating that distalmost stalks were buried in life position. In the rock samples collected by A. Rossi, which probably come from the higher part of the section, the stalk fragments do not have a preferred orientation within the sediment, some being perpendicular to each other (Figs. 4-6). Their length is highly variable from 22.4 mm (MGP-PD 1309Rb) to 87.9 mm (MGP-PD 1308R). Sometimes the outer surface of the stalk is smoothed with fine longitudinal striations (Fig. 6B) suggesting friction with the surrounding sediment like reported by Rasmussen (1961) on other *Isselicrinus* pluricolumnals. Fragments ending with an articulation that could allow autotomy (cryptosymplexy) are rare and only observed in *Isselicrinus diaboli*. Most fractures are irregular, very peculiar, and independent of articulations. Some stalks are partially broken with both elements still attached and imbricated into each other (Fig. 6A, C) with parts of the involved columnals missing. Some fractures are irregularly limited by partial shearing fractures oblique to the articulations (Figs. 5C, 6C) showing that the rupture was influenced by rhombohedral cleavage planes related to the monocrystalline character of the columnal stereom. Intact articular facets are rare and poorly preserved at the scale of the stereom. It should also be noted that the stalk fragments are straight, never curved, even the longest.

In the material from San Pancrazio, pluricolumnals are fragments of noditaxes always terminated by an articular facet. Among the 264 pluricolumnals observed, 22 nodals and 10 infranodals were always found at one end of the pluricolumnals, indicating that cryptosymplexies and symplexies participated in the splitting of the stalk. Most isolated columnals and pluricolumnals have <10 ossicles with a maximum of 11. Most commonly, pluricolumnals present 2-5 ossicles (45%). Skeletal elements are usually well-preserved allowing precise observation of the symplexial and cryptosymplexial stereom.

In San Pancrazio, *I. diaboli* shows 10% of star-shaped facets with wide opened pores (proximal stalk). About 12% of the stalk segments show alternation of columnals with various thickness (transition from the proximal to the distal part of the proximal stalk). Pluricolumnals of regularly pentagonal shape with discrete traces of interarticular pores amount to 45% (mid stalk). Pluricolumnals with the most peramorphic characters, independently from diameter size, represented by rounded pentagonal to subcircular facets without conspicuous pores amount to only 13% (distal and oldest stalk). Contrastingly, at Cambrigar, the stalk fragments of *I. diaboli* display more frequently distal peramorphic characters, some of them reaching a larger size, and younger specimens are not available whereas they are observed in *I. baldoensis* n. sp. pluricolumnals.

Systematic palaeontology

Order **Isocrinida** Sieverts-Doreck, 1952

Remarks. We use here the classification of Isocrinida revised by Améziane et al. (2023) which takes into account both the latest results of molecular phylogeny on extant taxa and the analysis of derived morphological characters.

Family Balanocrinidae Roux, 1981
Subfamily Isselicrininae Klikushin, 1977

Remarks. Stalk with nodals bearing 1 to 3 slender cirri alternating along the stalk (alternicirration), cirri always markedly downward, cirrus socket usually small and located on the distal nodal border, maximum number of internodals per noditaxis always >20. Bather (1917) first identified among isocrinids a group of "alternicirrate *Balanocrinus*" which now corresponds to the subfamily Isselicrininae sensu Améziane et al. (2023).

Included genera. *Praeisselicrinus* Klikushin, 1977; *Isselicrinus* Rovereto, 1914; *Panglaocrinus* Améziane, Eléaume & Roux, 2023. Upper Cretaceous (Maastrichtian) - Recent.

Fig. 4 - *Isselicrinus baldoensis* n. sp., rock sample MGP-PD 1310R from Cambrigar with three pluricolumnals; A) morphotype B, paratype MGP-PD 1310Ra (middle stalk). B-C) morphotype A; B: paratype MGP-PD 1310Rb (middle stalk); C: paratype MGP-PD 1310Rc (distal part of proximal stalk). Scale bar equals 10 mm.

Genus *Isselicrinus* Rovereto, 1914

Type species: *Isselicrinus insculptus* Rovereto, 1914.

Remarks. Main derived characters of the stalk are: (1) columnals thick and cylindrical, (2) symplexies with numerous marginal crenellae, outer crenularium of the interpetaloid zones with herringbone crenellation, petaloid zones subtriangular, (3) cryptosymplexies with the interpetaloid zone of the nodal facet forming a coarse ridge when prolonged by a cirrus socket (Améziane et al. 2023).

Occurrence. Worldwide distribution from Upper Cretaceous to Miocene: Europe, Middle East, northern Africa, southern Greenland, northeastern America, Caribbean, southwestern America, Antarctica, Indonesia, western Pacific border from Japan to New Zealand.

Isselicrinus baldoensis n. sp.

Figs. 2A-B, 4, 5 (fragments 1-2), 7, 8

Holotype: MGP-PD 1307R, a mid-stalk fragment (Fig. 7B) from Cambrigar.

Paratypes: 25 stalk fragments from Cambrigar (see Tab. 1 for catalogue numbers).

Etymology: From Monte Baldo, northeastern Italy.

Type locality: Cambrigar near Ferrara di Monte Baldo, Verona province, northeastern Italy.

Diagnosis: Stalk deeply star-shaped proximally, becoming more slightly rounded in the mesistele and subpentagonal in the distalmost noditaxes; interarticular pores large and deep remaining more discrete but often present in the distal mid stalk; rounded ridge at mid columnal height particularly marked between two interarticular pores; maximum diameter up to 10.3 mm proximally, usually 8.5-9.5 mm in the middle and distal stalk; maximum columnal thickness 0.32 in juveniles, 0.24-0.28 in middle and distal stalk; mean number of internodals per noditaxis 32, maximum number of successive internodals observed in an incomplete noditaxis 33; symplexies with up to 20 marginal crenellae per petaloid zone, smooth inner crenularium and lanceolate ligament areolas usually narrow; well-preserved cryptosymplexy unknown.

Description. The biometric and morphological study allowed to recognize two morphotypes, respectively A and B. The stalk of morphotype A (Figs. 2A, 4B-C, 5 fragment 1, supplementary material: Tab. 2) displays a deeply stellated cross section, marked interarticular pores, ribs at mid columnal height, and with relatively small columnal thickness. Only the largest specimens (D> 8.0 mm) present this morphotype. The three fragments with an average columnal thickness of 0.17 to 0.19 and large, deep articular pores (Figs. 4C, 7) indicate a more proximal part of the stalk than the other four, whose columnals are significantly thicker (0.23 to 0.25) (Fig. 4B). Juvenile characters such as the marked interarticular pores and the highly star-shaped columnals are maintained in the more distal and larger diameter fragments, even if they tend to disappear in the most distal columnals observed (Fig. 5B2). The seven pluricolumnal fragments represent a total length of 261.54 mm with 123 internodals + 3 nodals giving an IN/Ndx ratio of 41. Morphotype B (Figs. 2B, 4A, 5 fragment 2, supplementary material: Tab. 3) is stellated in section, with angles moderately rounded. Interarticular pores and ribs are more or less developed but always less pronounced than in morphotype A. Columnal size distribution is very wide, stretching from large specimens (D up to 9.9 mm) to smaller ones (D down to 3.4 mm) presenting juvenile characters (supplementary material: Tab. 3). Distribution of H/D values is wider than

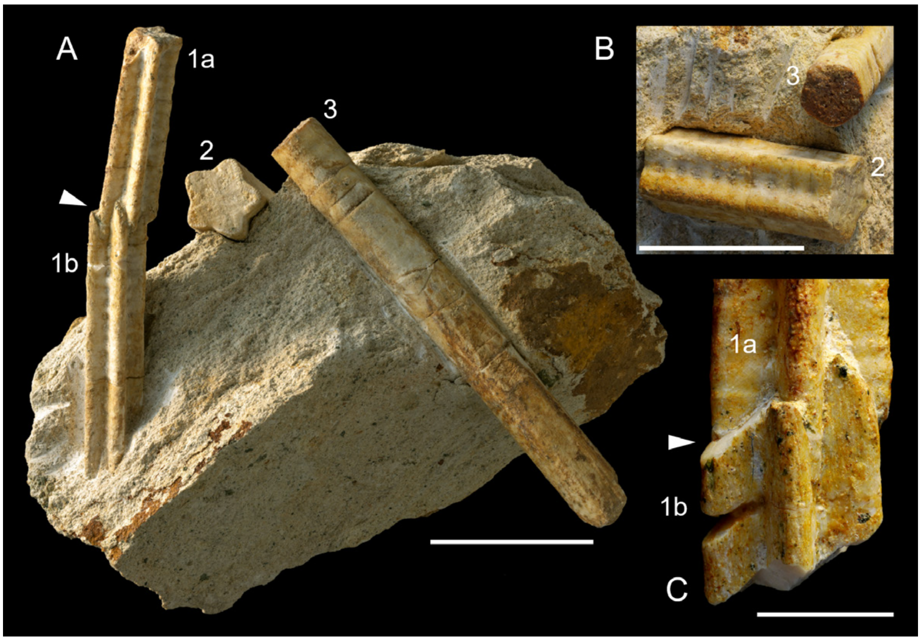


Fig. 5 - Rock sample MGP-PD 1309R from Cambrigar; A) general view. B-C) views after rotation angle of ~90° from A; C: isolated broken part of fragment 1 showing crashed fracture (arrow); 1-2, *Isselicrinus baldoensis* n. sp.: 1, stalk fragment, paratype MGP-PD 1309Ra (proximal stalk, morphotype B); 2, stalk fragment, paratype MGP-PD 1309Rb (middle/distal stalk, morphotype A); 3, *I. diaboli*, stalk fragment MGP-PD 1309Rc (distal stalk). Scale bars equal 2 cm in A and B, 5 mm in C.

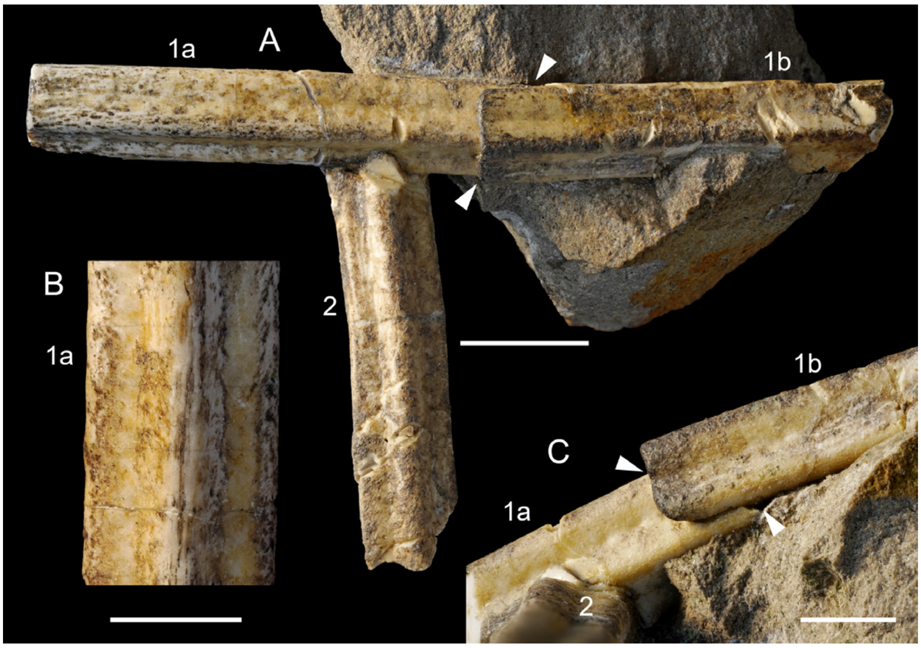


Fig. 6 - Rock sample MGP-PD 1305R from Cambrigar with middle stalk fragments of *Isselicrinus diaboli*; A) general view. B) close up on proximal part (1a) of stalk segment 1; C) after rotation angle of ~90° from A, close up on crashed fracture (arrow heads) at mid length of stalk fragment 1; 1, stalk fragment MGP-PD 1305Ra, 2, stalk fragment MGP-PD 1305Rb. Scale bar equals 10 mm in A, 5 mm in B and C.

in morphotype A. In juveniles (D<7.0 mm), H/D is down to 0.22 proximally and reaches 0.35 in the mid stalk. For the largest pluricolumnals (D>9.0 mm), the thickness is greater (0.26-0.28) and probably indicates a more distal location than in morphotype A (up to 0.25). The 16 fragments correspond to a total length of 348.41 mm with 175 internodals and 7 nodals giving a mean IN/Ndx of 25.

Symplexies display up to 20 crenellae per petaloid zone and no marked grooves on the interpetaloid zones, except sometimes only a discrete axial groove (Fig. 8). Ligament areolas are narrow, lanceolate to slightly lozenge shaped. The inner crenularium remains without crenellae. Cryptosymplexies presents smooth facets and moderate symmorphies.

Remarks. Morphotypes A and B display closely related characters and are interpreted as being referable to different parts of the stalk of the same species (Fig. 9). Morphotype A corresponds to more proximal stalk fragments reaching the largest diameters (D> 8.0 mm). Morphotype B appears to represent a more distal part of the stalk. The values of the IN/Ndx ratio are to be considered an estimate, because most specimens are included in rock samples with at least one unobservable lateral face and the risk of not having identified one nodal is high. In the case of morphotype A the IN/Ndx value of 41 could be overestimated, given that with

Fig. 7 - *Isselicrinus baldoensis* n. sp., two stalk fragments of morphotype A from Cambrigar; A) proximal fragment with conspicuous interarticular pores, paratype MGP-PD 1308R. B) proximal middle stalk fragment, holotype MGP-PD 1307R. Scale bar equals 20 mm.

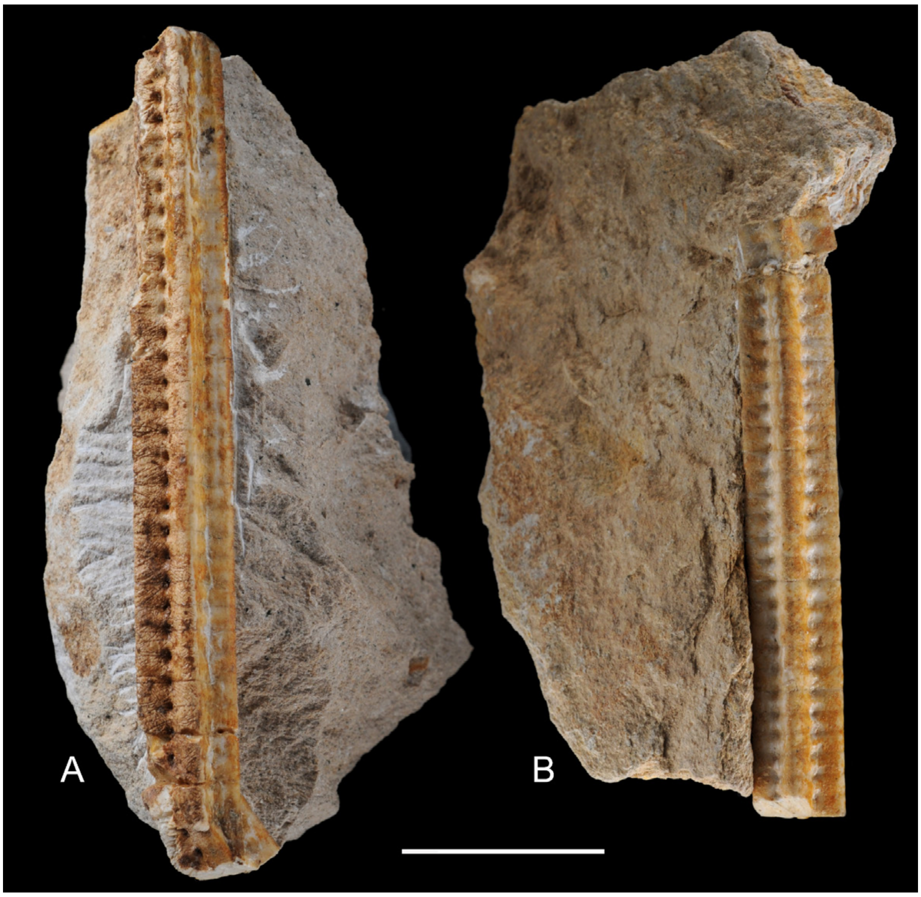
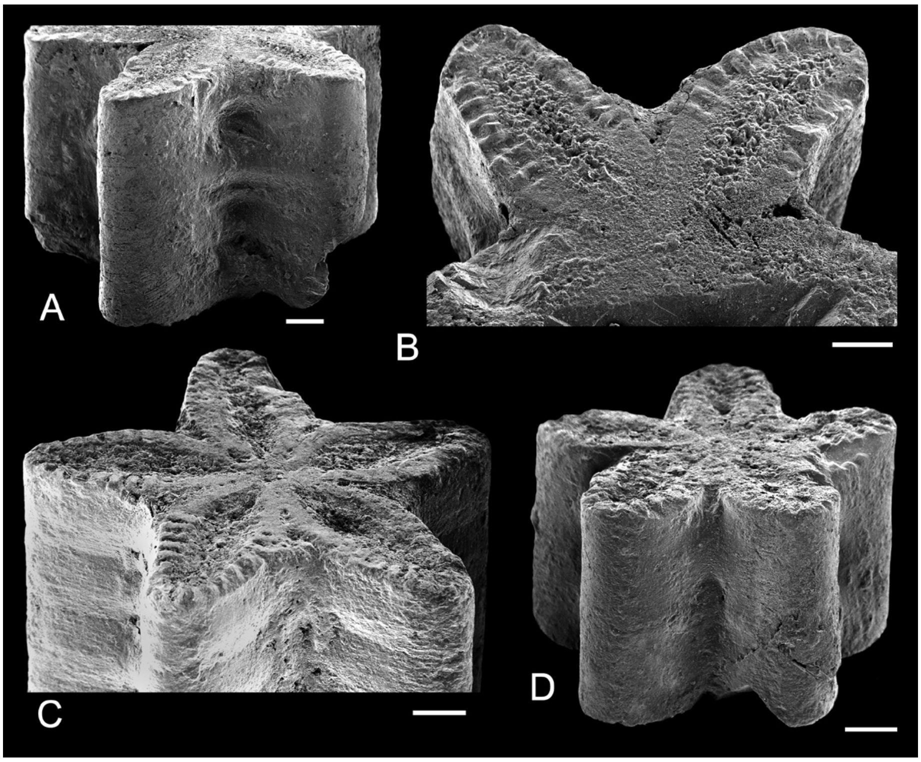


Fig. 8 - Columnal symplexies in *Isselicrinus baldoensis* n. sp. from Cambrigar; A-B) proximal pluricolumnal, paratype MGP-PD 1313R; A: side oblique view; B: articular facet. C) distal pluricolumnal, paratype MGP-PD 1312R, side oblique view. D) middle stalk pluricolumnal, paratype MGP-PD 1324R, side oblique view. Scale bars equal 1 mm.



one additional nodal the ratio IN/Ndx drops to 31; thus, the real value is probably between 31 and 41. The value of 25 for morphotype B is substantially underestimated because the longest stalk fragment, MGP-PD 1309Ra, includes an incomplete proximal noditaxis with 30 successive internodals. Considering morphotypes A and B together, the total number of columnals is 298 including 10 nodals, giv-

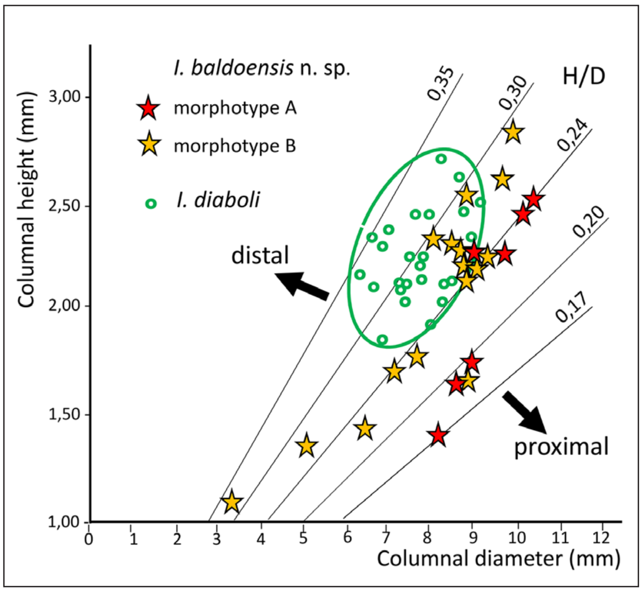


Fig. 9 - Columnal height and diameter values of *Isselicrinus* from Cambrigar plotted in a bivariate graph. Each point corresponds to the mean value in stalk fragments and pluricolumnals. See text for explanation.

ing a mean IN/Nd of 32 with up to 33 successive internodals observed in morphotype A. Within the genus *Isselicrinus*, the columnals of the new species have the most marked isocrinin morphotype (cfr. Roux et al. 2006). It would be useful to complete the description of the joints from columnals with better preserved facets than those of the type series.

Isselicrinus baldoensis n. sp. differs from *I. diaboli* in cumulating pedomorphic columnal characters maintained throughout its stalk. The bivariate analysis (Fig. 9) and the frequency of diameter and thickness values (Fig. 10) confirm the existence of two distinct entities: (1) the pedomorphic *I. baldoensis* in which juvenile (proximal) characters are maintained during growth (strongly star-shaped, irregular thickness, marked interarticular pores), (2) the peramorphic *I. diaboli* in which derived characters dominate (pentagonal to subcircular section, filled interarticular pores, little difference in thickness between successive columnals, increase of thickness from proximal to distal). *I. diaboli* also differs in having a substantially greater mean IN/Ndx of 42 (see below). Comparison of columnal main dimensional characters of the two species in the material from Cambrigar is shown in Tab. 4 of the supplementary material. The stalk of *I. baldoensis* n. sp. differs from previously described *Isselicrinus* species by retaining characters that are usually only proximal along most of its length.

Occurrence. Ferrara di Monte Baldo, Verona province, northeastern Italy. Middle Eocene (Lutetian).

Isselicrinus diaboli (Bayan, 1870)

Figs. 2C, 5 (fragment 3), 6, 12, 13

1870 *Pentacrinus diaboli* Bayan, pp. 453, 485-486.
1908 *Pentacrinus diaboli* - Fabiani, p. 109, pl. 1, fig. 8a-d.
?1917 *Balanocrinus diaboli* - Bather, p. 405.
?1982 *Isselicrinus diaboli* - Klikushin, p. 304.

Type material: Bayan (1870: 476) noted that all the new species described in his paper, including *P. diaboli*, were preserved in the collections of the École des Mines in Paris (ENSMP), which are now housed in the University Claude Bernard in Lyon (UCBL). Unfortunately, the specimens were not found at UCBL and should be considered lost (E. Robert, pers. comm.). Fabiani (1908, fig. 8) figured four pluricolumnals from the type locality San Pancrazio, near Mossano (sample MGP-PD 23437). One of them (fig. 8a) is the specimen of our Fig. 12C-D (MGP-PD 23437b) and we designate it as the neotype of the species.

Material examined: 24 stalk fragments from Cambrigar, 108 columnals and pluricolumnals from San Pancrazio (see Tab. 1 for catalogue numbers).

Type locality: San Pancrazio near Mossano (Berici Hills), Vicenza province, northeastern Italy.

Emended diagnosis: Stalk rarely star-shaped, usually pentagonal, rounded pentagonal to subcircular distally, smooth external surface. Deep interarticular pores up to the proximal part of the mid stalk, disappearing or just discrete traces remaining distally in the mid and distal stalk; no ridge at mid columnal height; maximum distal columnal diameter 8.0 to 9.1 mm; maximum columnal thickness 0.35 to 0.42; mean number of internodals per noditaxis 42 to 58; symplexies with 8 to 12 regular marginal crenellae per petaloid zone, herringbone crenellations in the interpetaloid zone, axial interpetaloid groove becoming discrete in the mid stalk, either five or only three inner crenularia of the mid stalk symplexies with two deep parallel grooves framing the discrete axial groove; proximal cryptosymplexies with marked symmorphy and 16 small marginal crenellae per petaloid zone becoming distally a smooth surface without crenularium.

Description. The stalk shows a cross section moderately stellated to pentagonal with rounded angles. It presents discrete interarticular pores restricted to a few proximal stalk fragments, and no ridge at mid columnal height. The variation of columnal characters is mainly related to their increasing size and the place along the stalk has been estimated in specimens from Cambrigar and San Pancrazio respectively (Fig. 11, supplementary material: Tabs. 5-7). In San Pancrazio, only 10% of columnals are star-shaped with widely open interarticular pores suggesting that the proxistele is relatively short. In the mid stalk, columnal thickness tends to decrease from 0.42 to 0.26 as columnal diameter grows. The samples examined do not include small specimens presenting juvenile characters. The 238 columnals

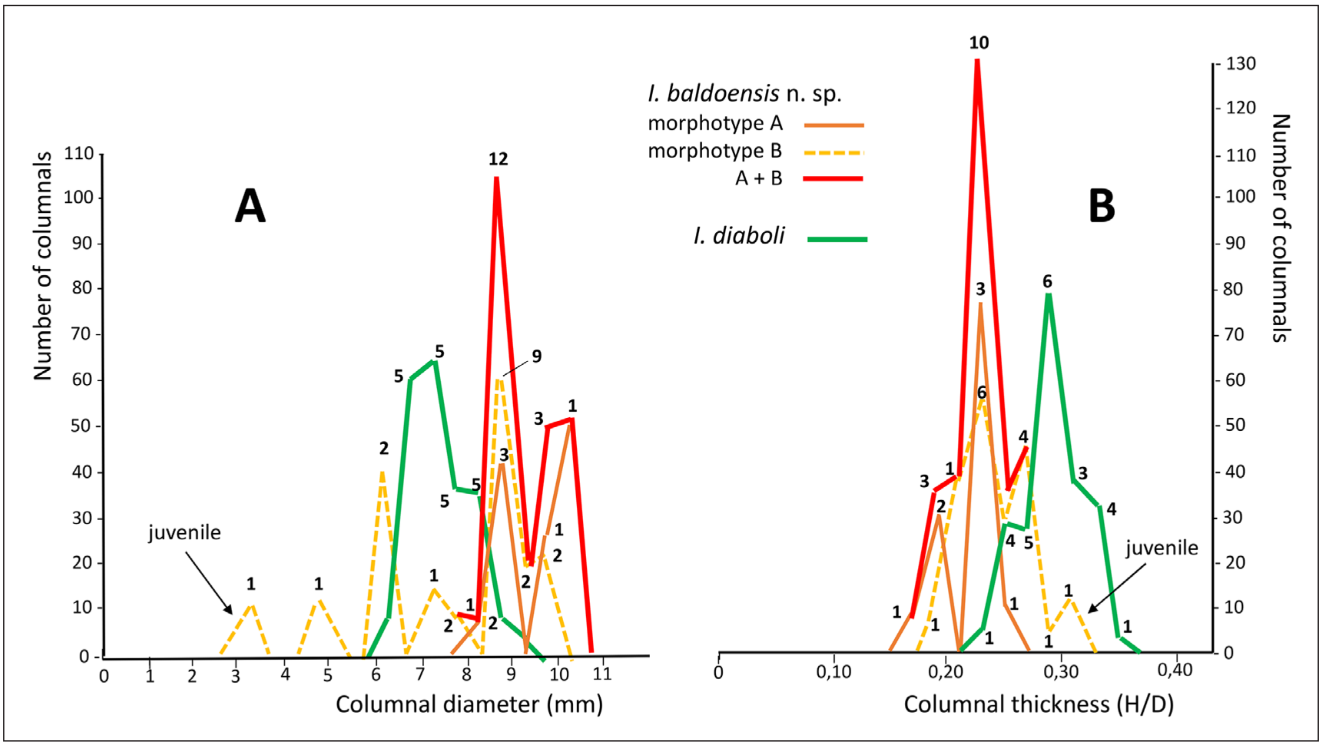


Fig. 10 - Frequency distribution of diameter (A) and thickness (B) in *Isselicrinus* columnals from Cambrigar. Small numbers: number of stalk fragments and pluricolumnals taken in account. See text for explanation.

and pluricolumnals correspond to a total length of 2210 mm, 1275 internodals and 22 nodals giving a mean IN/Ndx of 58. Columnal thickness reaches 0.35 in distalmost rounded pentagonal columnals without pores (Fig. 5B3) and is never under 0.24 in proximal stellated segments. The long fragment MGP-PD 1309Rc (Fig. 5A3) illustrates the distal stalk features of a medium sized specimen with a smooth external surface, rounded pentagonal cross section, and without significant variation in columnal height.

The fragment MGP-PD 1318Ra, which belongs to a likely large sized specimen, displays the same features but with a significant smaller columnal thickness of 0.28 (0.32 in MGP-PD 1309Rc). The rock sample MGP-PD 1305R includes two stalk fragments, one being perpendicular to the other (Fig. 6A). From proximal to distal, the longest stalk fragment, MGP-PD 1305Ra, becomes less stellate with a slight increase of columnal diameter and thickness. In total, the 23 stalk fragments correspond to a length of 439.57 mm with 208 internodals and 5 nodals giving a mean IN/Ndx of 42. This value is rather congruent with the stalk fragment MGP-PD 1305Ra which is an incomplete noditaxis with 30 successive internodals including one infranodal at its proximal end. The specimens of *I. diaboli* from Cambrigar fall within the range of variation of *I. diaboli* from San Pancrazio (Fig. 11), with a similar high mean IN/Ndx (42 and 48-58 respectively).

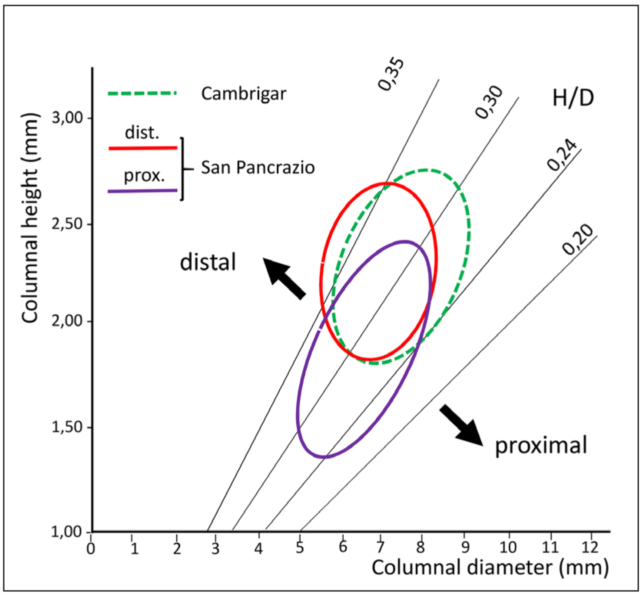


Fig. 11 - Columnal height and diameter values of *Isselicrinus diaboli* from San Pancrazio plotted in a bivariate graph and compared to results from Cambrigar columnals of the same species. Envelopes of points corresponding to the mean value in stalk fragments and pluricolumnals. See text for explanation.

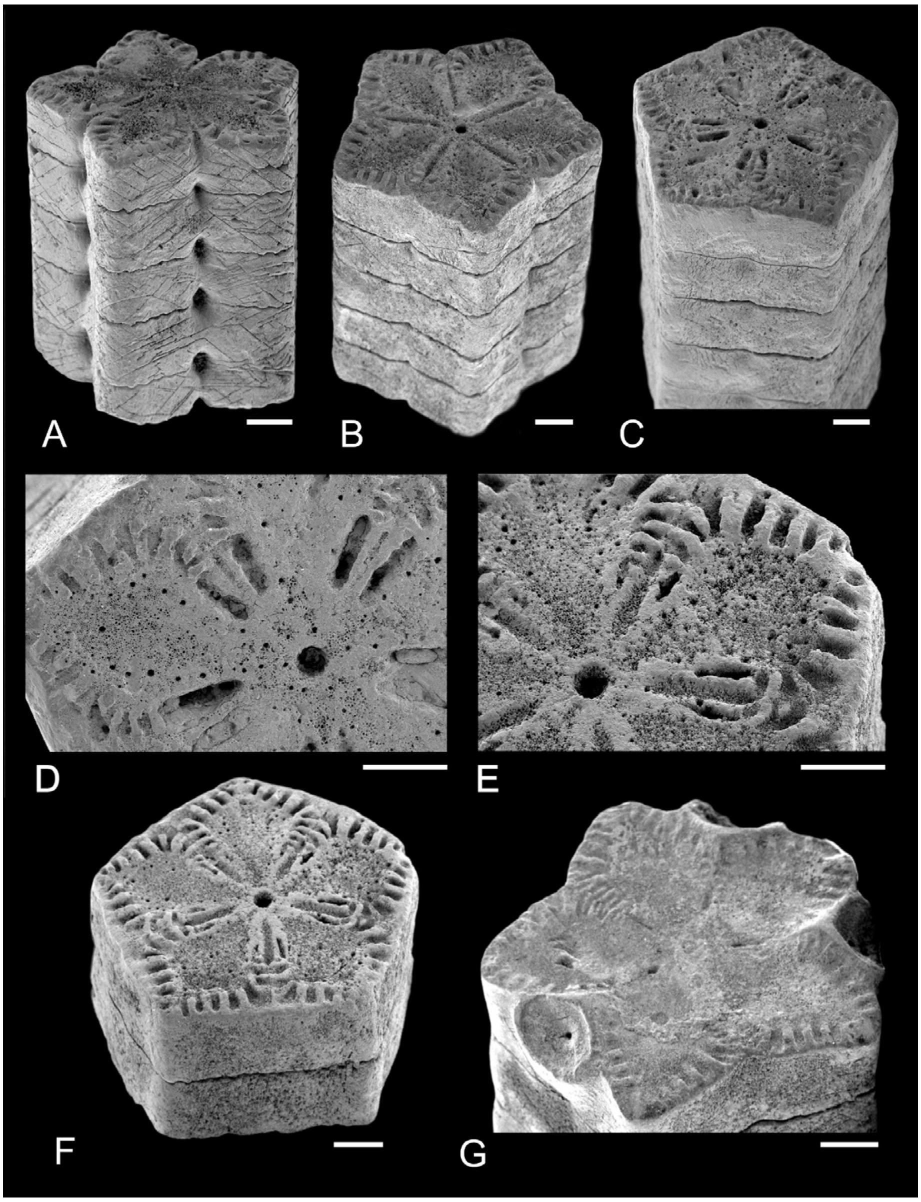
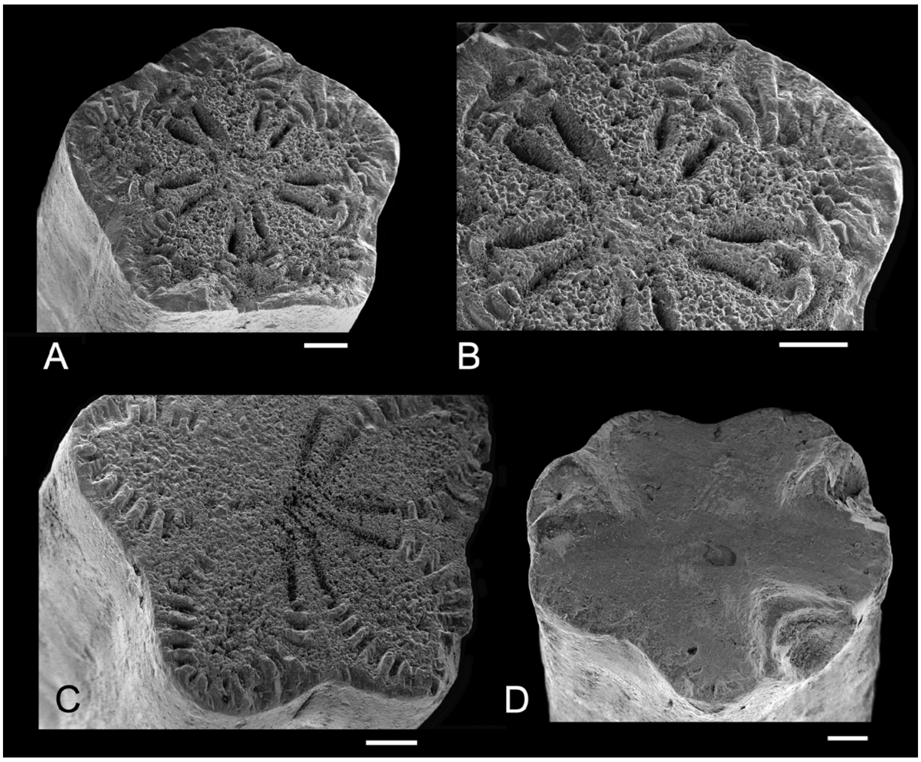


Fig. 12 - Pluricolumnals of *Isselicrinus diaboli* from San Pancrazio. A) distal part of proximal stalk, MGP-PD 23437a. B) pluricolumnal from mid stalk, MGP-PD 7929. C-F) distal stalk with internodals with symplexies; C-D: the neotype herein designated MGP-PD 23437b; E-F: pluricolumnal of two internodals, MGP-PD 23437c; E: close up of a facet showing numerous large meshes among the areola's galleried stereom. G) distal cryptosymplexial facet of a nodal with three cirrus sockets from proximal middle stalk, MGP-PD 23437d. Scale bars equal 1 mm.

The symplexies (Figs. 12A-F, 13A-C) display the usual pattern found in the genus *Isselicrinus* with regular marginal crenellae (8 to 12 per petaloid zone), rarely herring bone crenulations in the interpetaloid zone, and wide lozenge-shaped ligament areas including some larger meshes within their galleried stereom (Fig. 12E). The well-developed interpetaloid axial groove in the proximal symplexies is sometimes maintained in the articulations of the mid stalk (Fig. 12B, E) and is more discrete and restricted to the inner crenularium in the more distal joints (Fig. 12C, 13A). In the latter, two deep parallel grooves develop that frame the axial groove (Figs. 12D, F, 13A-C). The either five or only three interpetaloid areas display this feature. The most proximal cryptosymplexies show a marked symmorphy, with the distal nodal facet very concave and bordered by a marginal crenularium (up to 16 small crenellae per petaloid zone) (Fig. 12G). The interpetaloid zones form coarse ridges, those corresponding to a cirral insertion being particularly prominent. These characters tend to fade in the more distal cryptosymplexies with smooth facets in which the marginal crenularium disappears (Fig. 13D).

Remarks. The original description of Bayan (1870) is very short, poorly detailed and without figure. Therefore, numerous columnals or pluricolumnals from lower to upper Eocene deposits were subsequently attributed to *I. diaboli* without a sound taxonomic base (Biese & Sieverts-Doreck 1939). All these previous attributions need a thorough revision. Consequently,

Fig. 13 - Columnal articulations in *Isselicrinus diaboli* from Cambrigar; A-C) internodal symplexies; A-B: pluricolumnal MGP-PD 1314R; C: pluricolumnal MGP-PD 1315R. D) cryptosymplexy, distal nodal facet of pluricolumnal MGP-PD 1311R. Scale bars equal 1 mm.



the list of synonymies must be restricted to the unique reference with figures of a few specimens from the type locality (Fabiani 1908, pl. 1, fig. 8a-d) belonging to the sample MGP-PD 23437, and to the references corresponding to change in the generic attribution. The articulations of *Isselicrinus diaboli* columnals documented here for the first time show a derived character previously undescribed in the genus *Isselicrinus* and other isocrinid genera: two deep parallel grooves bordering the inner crenularium of the stalk symplexies. Symplexies with two parallel deep grooves bordering the inner crenularium have only been observed in a few columnals from the Bartonian of southwestern France but whose other characters differ from *I. diaboli* (Roux et al. 2006, fig. 3b; M.R. unpublished data).

Klikushin (1982; 1992) identified a few columnals of lower Eocene *Isselicrinus* from Armenia as *I. diaboli* and gave SEM views of their symplexy and cryptosymplexy. Unfortunately, they show characters differing strongly from those described here on specimens from the type locality. *Isselicrinus subbasaltiformis* (Miller, 1821) is the only species of *Isselicrinus* known from stalk and crown (Bather 1917; Rasmussen 1972; Roux 1977). Its type-stratum in the boreal province is the lower Ypresian London Clay. The mature columnals with a smooth external surface are smaller than in *I. diaboli* with a maximum diameter of 7.0 mm and a height up to 2.5 mm but with a similar thickness (0.33 to 0.40). Their shape is more frequently subcircular. The two species share a smooth external surface and the same general pattern of articular facets, except a more conspicuous interpetaloid axial furrow in the middle to distal stalk and the absence of the two parallel deep grooves bordering the inner crenularium in *I. subbasaltiformis* (Fig. 3). The latter species also differs in having substantially shorter noditaxes with up to 29 internodals. *Isselicrinus didactylus* (d'Archiac, 1846) is the third Eocene species known from numerous stalk fragments from the "Marnes à Pentacrines" horizon at Biarritz (southwestern France), dated to the Bartonian-Priabonian transition. It differs from the preceding species in having variable ornamentation consisting of tubercles or a wrinkle at mid-height (Bather 1917). Usually, the diameter of the subcircular columnals reaches 9.5 mm and their thickness (H/D) 0.27 to 0.30. Symplexies are very similar to those of *I. subbasaltiformis*. In the present state of knowledge, no studies have been carried out in sufficient detail to identify robust characters that would enable us to distinguish the different *Isselicrinus* species.

DISCUSSION

Stratigraphic distribution of *Isselicrinus* in the Veneto region

The calcareous nannofossil assemblage associated to pluricolumnals indicate that specimens of *Isselicrinus* from Cambrigar and the type locality of *Isselicrinus diaboli* have about the same Lutetian age, confirming the previous age assignment of Marramà et al. (2021) for the isocrinids coming from the lower half of the "lower Cambrigar" section. Beds with *Harpactocarcinus punctulatus* and "*Pentacrinus" diaboli* (HPB) cropping out in Veneto region are likely heterochronous and/or they span a much larger stratigraphical interval than previously expected. The possible Ypresian occurrence of isocrinids in the region needs to be verified through careful bed by bed study of the basal portion of the Cambrigar section and detection and reappraisal of other classical historical sites, such as San Pancrazio and Albettone Hill. The HPB are to be clearly distinguished from the much older fossiliferous Spilecco beds of Bolca, containing a different crinoidal fauna and referred to the lower part of the Ypresian (calcareous nannofossil Zone NP10 of Martini 1971; see Papazzoni et al. 2014 and E.F., unpublished data).

Taphonomy

The observations of broken stalks made on Cambrigar specimens are similar to those made by Donovan et al. (2019, fig. 5d-g) on *Isselicrinus* from the Paleogene of the Americas. They suggest a very rapid, even catastrophic burial within a mass flow. The columnal joints of the living individuals were held in compression by the powerful paraxial ligaments that ensure the cohesion of the stalk and its rigidity. It is these ligaments that prevent the separation of two fragments at the level of a fracture (Figs. 5A-C; 6C).

Frequently, fossilized *Isselicrinus* stalk fragments are found perpendicular to the stratification indicating a rapid burial of the erect part of the stalk during the individual's lifetime and thus a high rate of sedimentation (Roux & Plaziat 1978; Fujiwara et al. 2005; Mulumian & Olivero 2005). At Cambrigar, such distalmost stalk fragments preserved in living position were only observed in the lower part of the section. In the upper part of the section, this may have been the case for *I. diaboli* before the mud flows were triggered, because only fragments of the distal part of the stalk were found. The mud flows have disturbed the vertical position breaking long stalk fragments into several smaller fragments, while the proximal part and the crown were sheared off and separated from the distal stalk at the water/sediment interface dragging them further away. A similar explanation for *I. baldoensis* is difficult to envisage since different parts of the stalk are present within mud flows. It is unlikely that during the animal's lifetime, its stalk was buried in a vertical position up to its most proximal part. Nevertheless, samples MGP-PD 1310R (Fig. 4) and MGP-PD 1309Rb (Fig. 5B2) show relatively short segments of *I. baldoensis* limited on both sides by symplexies, which suggests some beginning of post-mortem fragmentation (maybe related to distal stalk autotomy) before the fast burial event. Such hypotheses should be tested by further detailed field investigations.

In San Pancrazio, the good preservation of the skeletal elements and the frequency of isolated short pluricolumnals suggest a stay on the sea floor with ligament decay followed by a rapid burial ensured by a high sedimentation rate or/and by bioturbation. The latter could also have contributed to the dissociation at the level of symplexies as soon as the ligaments disappeared. Thus, the mode of burial in San Pancrazio (post-mortem dissociation of columnals and pluricolumnals and progressive burial) was very different from that in Cambrigar (catastrophic burial of living individuals within a mud flow/grain flow).

Palaeoecology

During the Eocene, stalked crinoids of the genus *Isselicrinus* were most often associated with terrigenous sediments (dark grey or blue marls of the lower Ypresian, Bartonian and Priabonian) in a context of high sedimentation rate (Roux & Plaziat 1978). At Cambrigar, we did not observe any bundles of distal parts of *Isselicrinus* stalks, which would have suggested an anchoring relay strategy adapted to muddy sea floor with a high sedimentation rate, as described by Fujiwara et al. (2005) in Cenozoic environments from Japan. The great length of the noditaxes and most probably of the erected stalk part of *Isselicrinus* including numerous noditaxes allowed both to compensate for rapid sedimentation and to rise up the crown as high as possible above the bottom to reach laminar water currents fast enough to ensure efficient filtration. According to Roux et al. (2006), a shorter *Isselicrinus* stalk with a star-shaped cross section (isocrinid ecophenotype) would be adapted to a more irregular, sometimes turbulent current near the seafloor, while a longer stalk pentagonal to circular in cross section (balanocrinid ecophenotype) would allow for a higher elevation of the crown in the sea water column to filter a steadier and moderately faster laminar current. A model of niche differentiation as observed by David et al. (2006) in Diplocrininae in the Bahamas could explain the co-occurrence of the two species of *Isselicrinus* in the same environment at Cambrigar: *I. diaboli* might have filtered food supply higher up in the water column than *I. baldoensis* n. sp. At this site, the presence of juvenile stages of *I. baldoensis* n. sp. (Figs. 9 and 10) indicates that the population was likely thriving before its catastrophic burial. This is not the case for *I. diaboli*, which is mainly represented by distal stalk parts with diameter >6 mm, and from which juveniles are absent.

In San Pancrazio, *I. diaboli* shows a wider size distribution with columnal diameter from 5.2 to 7.7 mm, the maximum size being smaller than in Cambrigar (Fig. 11). The whole sample includes only 13% of distal columnals with the most peramorphic characters indicating the complete development of ontogenic trajectory. This can be interpreted as the characters of a young, developing population, and also as the consequence of slower growth due to a deeper, less food-rich environment.

A cluster of five large individuals of *Cenocrinus asterius* (Linnaeus, 1767), the largest extant isocrinid in the Caribbean, was observed in situ from a submersible for twenty years (Messing et al. 2007). It probably takes nearly ten years for it to reach its maximum size. Thus, the longevity of this species is at least thirty years. The large size reached by the two *Isselicrinus* species at Cambrigar requires a living environment rich in food particles, with moderate and steadier water currents for several decades. On this timescale, it suggests an environment sheltered from the major hydrological disturbances caused by storm waves (Roux 1987). With reference to the relationship found by Roux et al. (2006, fig. 4) between the depth of the environment, the diameter of the *Isselicrinus* columnals and their thickness, the ecological niche of the two Cambrigar species would be located at a depth of about 250-350 m on a steep slope. However, since the taphonomic signatures suggest a burial caused by gravity sedimentation, the depositional environment was possibly deeper. The smaller diameter and longer noditaxes of *I. diaboli* specimens from San Pancrazio suggest an environment with less food supply and current velocity on a moderate slope at a depth of about 400 m or more.

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References

Agnini C., Backman J., Boscolo-Galazzo F., Condon D.J., Fornaciari E., Galeotti S., Giusberti L., Grandesso P., Lanci L., Luciani V., Monechi S., Muttoni G., Pälike H., Pampaloni M.L., Papazzoni C.A., Pearson P.N., Pignatti J., Premoli Silva I., Raffi I., Rio D., Rook L., Sahy D., Spofforth D.J.A., Stefani C. & Wade B.S. (2021) - Proposal for the Global Boundary Stratotype Section and Point (GSSP) for the Priabonian Stage (Eocene) at the Alano section (Italy). *Episodes,* 44(2): 151-173.

Agnini C., Fornaciari E., Raffi I., Catanzariti R., Pälike H., Backman J. & Rio D. (2014) - Biozonation and biochronology of Paleogene calcareous nannofossils from low and middle latitudes. *Newsletters on Stratigraphy*, 47(2): 131-181.

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

Améziane N., Eléaume M. & Roux M. (2023) - Classification of Isocrinida (Echinodermata, Crinoidea) with the description of *Panglaocrinus isseliformis* n. gen., n. sp., a new extant isocrinid from western Pacific. *Zoological Journal of the Linnean Society*, Advance articles, zlad101: 1-19.

Bather F.A. (1917) - *Balanocrinus* of the London Clay. *Annals and Magazine of Natural History*, series 8, 120: 385-407.

Bayan F. (1870) - Sur les terrains tertiaires de la Vénétie. *Bulletin de la Société géologique de France*, série 2, 27: 444-486.

Beschin C. & De Checchi A. (2020) - Nuova specie di

Tumidocarcinidae (Crustacea, Decapoda, Xanthoidea) nell'Eocene del Monte Baldo (Verona, Italia nordorientale). *Studi e Ricerche - Associazione Amici del Museo - Museo Civico "G. Zannato" Montecchio Maggiore (Vicenza)*, 27: 5-10.

Beschin C., De Angeli A. & Checchi A. (2011) - *Baldoplax bonizzatoi* gen. nov., sp. nov., (Crustacea, Decapoda, Euryplacidae) dell'Eocene di Ferrara di Monte Baldo (Verona, Italia settentrionale). *Studi e Ricerche - Associazione Amici del Museo - Museo Civico "G. Zannato" Montecchio Maggiore (Vicenza)*, 18: 5-10.

Biese W. & Sieverts-Doreck H. (1939) - Crinoidea caenozoica. In: Quenstedt W. (Ed.) - Fossilium Catalogus, I: Animalia, 80. W. Junk, 's-Gravenhage, 155 p.

Bosellini A. (1989) - Controls on carbonate platform and basin development. In: Crevello P.D., Wilson J.L., Sarg J.F & Read J.F. (Eds.) - Dynamics of Tethyan carbonate platforms, S.E.P.M., Special Publication, 44: 3-13.

Bosellini F.R. & Papazzoni C.A. (2003) - Palaeoecological significance of coral-incrusting foraminifera associations. A case-study from the Upper Eocene of northern Italy. *Acta Palaeontologica Polonica*, 48(2): 279-292.

Cappelli C., Bown P.R., de Riu M. & Agnini, C. (2021) - The evolution of Eocene (Ypresian/Lutetian) sphenoliths: Biostratigraphic implications and paleoceanographic significance from North Atlantic site IODP U1410. *Newsletters on Stratigraphy*, 54(4): 405-431.

Dainelli G. (1915) - L'Eocene Friulano. Monografia geologica e paleontologica. Le Memorie Geografiche, Firenze, 721 pp.

D'Archiac A. (1846) - Description des fossiles recueillis par M. Thorent dans les couches à Nummulites des environs de Bayonne. *Mémoires de la Société géologique de France*, 4(2)2, 189-217.

David J., Roux M., Messing C.G. & Améziane N. (2006) - Revision of the pentacrinid stalked crinoids of the genus *Endoxocrinus* (Echinodermata, Crinoidea), with a study of environmental control of characters and its consequences for taxonomy. *Zootaxa*, 1156(1): 1-50.

De Zigno A. (1861) - Cenni sulla costituzione geologica dei Monti Euganei. *Rivista periodica dei lavori della I. R. Academia di Scienze, Lettere ed Arti in Padova*, 9: 93-108.

De Zigno A. (1879) - Annotazioni paleontologiche. Nuove aggiunte alla fauna eocena del Veneto. *Memorie del Reale Istituto veneto di Scienze, Lettere ed Arti*, 21: 775-789.

Donovan S.K, Nielsen S. N., Velez-Juarbe J. & Portell R.W. (2019) - The isocrinine crinoid *Isselicrinus* Rovereto from the Paleogene of the Americas. *Swiss Journal of Palaeontology*, 138: 317-324.

Fabiani R. (1905) - Studio geo-paleontologico del Colli Berici (nota preventiva). *Atti del Reale Istituto veneto di Scienze, Lettere ed Arti*, 64: 1797-1839.

Fabiani R. (1908) - Paleontologia dei Colli Berici. *Memorie della Società Italiana delle Scienze (detta dei XL)*, III, 15: 45-250.

Fabiani, R. (1915) - Il Paleogene del Veneto. *Memorie dell'Istituto geologico della Regia Università di Padova*, 3: 1-336.

Fabiani R. (1922) - Il Terziario del Trentino. *Memorie dell'Istituto geologico della Regia Università di Padova*, 6: 1-60.

Fujiwara S., Oji T., Tanaka Y. & Kondo Y. (2005) - Relay strategy and adaptation to a muddy environment in *Isselicrinus* (Isselicrinidae: Crinoidea). *Palaios*, 20(3): 241-248.

Garassino A., De Angeli A. & Pasini G. (2009) - In situ hermit crab (Crustacea, Anomura, Paguroidea) from the Early Eocene (Ypresian) of NE Italy. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 150: 229-238.

Gardin S. & Monechi S. (1998) - Palaeoecological change in middle to low latitude calcareous nannoplankton at the Cretaceous/Tertiary boundary. *Bulletin de la Société géologique de France*, 169(5): 709-723.

Hess H. (2011) - Isocrinida. In: H. Hess, C.G. Messing & W.I. Ausich (Eds.) - Treatise on Invertebrate Paleontology, Part T, Echinodermata 2 Revised, Crinoidea, 3, pp. 42-69, University of Kansas Press, Lawrence.

Howe R. (2021) - Ultrastructure and taxonomy of the family Sphenolithaceae. *Journal of Nannoplankton Research,* 39(1): 29-75.

Klikushin V.G. (1977) - Sea lilies of the genus *Isselicrinus*. *Paleontologicheskiy Zhurnal*, 1: 87-95 [in Russian].

Klikushin V.G. (1982) - Taxonomic survey of fossil isocrinids with a list of the species found in the USSR. *Geobios*, 15(3): 299-325.

Klikushin V.G. (1992) - Fossil pentacrinid crinoids and their occurrence in the USSR. Leningrad Palaeontological Laboratory, Sankt-Peterburg, 358 p. [in Russian].

Linnaeus C. (1767) - Systema Naturae. 12th ed., 1, Part 2: 533-1327. Laurentius Salvius, Holmiae, Stockholm.

Luciani V. (1989) - Stratigrafia sequenziale del Terziario nella catena del Monte Baldo (Province di Verona e Trento). *Memorie di Scienze Geologiche*, 41: 263-351.

Macurda D.B. & Meyer D.L. (1974) - Feeding posture of modern stalked crinoids. *Nature*, 247: 394-396.

Marramà G., Giusberti L., Papazzoni C.A. & Carnevale G. (2021) - An Eocene soldierfish (Teleostei: Holocentridae) from Monte Baldo (NE Italy). *Bollettino della Società Paleontologica Italiana*, 60(2): 135-147.

Martini E. (1971) - Standard Tertiary and Quaternary calcareous nannoplankton zonation. In: Farinacci, A. (Ed.) - Proceedings 2nd International Conference Planktonic Microfossils Roma, Rome (Edizioni Tecnoscienza), 2: 739-785.

Messing C.G., David J., Roux M., Améziane N.& Baumiller T.K. (2007) - In situ stalk growth rates in tropical western Atlantic sea lilies (Echinodermata: Crinoidea). *Journal of Experimental Marine Biology and Ecology*, 353: 211-220.

Miller J.S. (1821) - A natural history of crinoidea or lily-shaped animals with observations on the genera *Asteria*, *Euryale*, *Comatula* and *Marsupites*. C. Frost, Bristol, 150 p.

Mulumian N. & Olivero E.B. (2005) - Shallow-water late middle Eocene crinoids from Tierra del Fuego: a new southern record of a retrograde community structure. *Scientia Marina*, 69, Suppl. 2: 349-353.

Munier-Chalmas E. (1891) - Étude du Tithonique, du Crétacé et du Tertiaire du Vicentin. Thèses Faculté des Sciences de Paris pour obtenir le grade de Docteur en Sciences naturelles, Paris, Série A, n. 150, 184 pp., Paris.

Nicolis E. (1882) - Note illustrative alla carta geologica della provincia di Verona. Stabilimento tipografico di G. Franchini, Verona, 142 pp.

Oppenheim P. (1902) - Revision der tertiären Echiniden Venetiens und des Trentino, unter Mittheilung neuer Formen. *Zeitschrift der Deutschen geologische Gesellsc*haft, 54: 159-283.

Papazzoni C.A., Giusberti L. & Trevisani E. (2014) - The Spilecco site. In: Papazzoni C.A, Giusberti L., Carnevale G., Roghi G., Bassi D. & Zorzin R. (Eds.) - The Bolca *Fossil-Lagerstätten*: A window into the Eocene World. *Rendiconti della Società Paleontologica Italiana*, 4: 105-110.

Rasmussen H.W. (1972) - Lower Tertiary Crinoidea, Asteroidea and Ophiuridea from northern Europe and Greenland. *Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter*, 19(7): 1-83.

Rio D., Raffi I. & Villa G. (1990) - Pliocene-Pleistocene calcareous nannofossil distribution patterns in the western Mediterranean. In: Kastens K.A., Mascle J., et al. (Eds.) - Proceedings of the Ocean Drilling Program, Scientific Results, 107: 513-533. Ocean Drilling Program, College Station.

Roux M. (1977) - The stalk-joints of recent Isocrinidae (Crinoidea). *Bulletin of the British Museum (Natural History), Zoology*, 3(3): 45-64.

Roux M. (1981) - Echinodermes: crinoïdes Isocrinidae. In: Forest J. (Ed.) - Résultats des Campagnes MUSORTOM I - Philippines (18-28 mars 1976). *Mémoires O.R.S.T.O.M.*, 91: 477-543.

Roux M. (1987) - Evolutionary ecology and biogeography of recent stalked crinoids as a model for the fossil record. In: Jangoux M. & Lawrence J.M. (Eds.) - Echinoderm Studies, Volume 2, 1-53. A.A. Balkema, Rotterdam.

Roux M., Cahuzac B. & Sztrákos, K. (2006) - Les paléoenvironnements éocènes à Crinoïdes pédonculés des marnes de Miretrain (Angoumé, SW de la France): interprétations paléobathymétriques. *Comptes Rendus Géoscience*, 338(4): 262-271.

Roux M., Messing C.G. & Améziane N. (2002) - Artificial keys to the genera of living stalked crinoids (Echinodermata). *Bulletin of Marine Science*, 70(3): 799-830.

Roux M. & Philippe M. (2021) - Early Miocene stalked crinoids (Echinodermata) from the southern Rhodanian basin (southeastern France). Paleoenvironments and taxonomy. *Zootaxa*, 5052(3): 301-331.

Roux M. & Plaziat J.C. (1978) - Inventaire des Crinoïdes et interprétation paléobathymétrique des gisements du Paléogène pyrénéen franco-espagnol. *Bulletin de la Société géologique de France*, 7, 10: 299-308.

Rovereto G. (1914) - Nuovi studi sulla stratigrafia e sulla fauna dell'Oligocene ligure. Oliveri, Genova, 178 pp.

Serra-Kiel J., Hottinger L., Caus E., Drobne K., Ferrandez C., Jauhri A.K., Less G., Pavlovec R., Pignatti J., Samsò J.M., Schaub H., Sirel E., Strougo A., Tambareau Y., Tosquella J. & Zakrevskaya E. (1998) - Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. *Bulletin de la Société géologique de France*, 169(2): 281-299.

Sieverts-Doreck H. (1952) - Articulata. In: Moore R.C., Lalicker C.G. & Fischer A.G. (Eds.) - Invertebrate fossils. McGrawHill, New York, Toronto and London, 614 pp.

Speijer R.P., Pälike H., Hollis C.J., Hooker J.J., & Ogg G.M. (2020) - The Paleogene Period. In: Gradstein F.M., Ogg J.G., Schmitz, M.D. & Ogg G.M. (Eds.) - The Geologic Time Scale 2020: 1087-1140. Elsevier, Oxford.