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REGULAR RESEARCH ARTICLE

Stalked crinoids from Gan (Late Ypresian, southwestern France): exceptional stereom preservation, paleoecology and taxonomic affinities

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Abstract

Exceptionally well-preserved ossicles of xenomorphic stalked crinoids (Echinodermata) were found into the Late Ypresian clay of the Tuilerie de Gan (Pyrénées-Atlantiques, southwestern France). Three kinds of columnal articulation correspond to three different genera, including the new genus *Eocenocrinus*. These columnals are attributed to *Paraconocrinus romanensis*, *Democrinus londinensis* and *Eocenocrinus hessi* n. gen., n. sp. Associated benthic fauna as well as columnal characters related to water depth confirm an increasing depth to an epibathyal environment as previously suggested by mollusk and foraminifer associations. *Paraconocrinus romanensis* associated with *Democrinus londinensis* mark the maximum water depth, which did not exceed 300 m. Distal columnal series with proximal roots of *P. romanensis* and *D. londinensis* were collected with their ossicles connected, indicating that these species lived on a muddy bottom. *E. hessi* n. gen., n. sp. is suspected to have been attached on hard substrate. Without diagenetic crystallizing, the crinoid stereom and its micro-biocorrosion appear as in extant specimens. We attribute to *Eocenocrinus* n. gen. large columnals previously described from northeastern Italy and recognize two species: *E. bayani* n. gen., n. sp. (Middle Lutetian) and *E. didymus* (Priabonian). *E. hessi* n. gen., n. sp. may represent the oldest known species in the family Phrynocrinidae.

Keywords Crinoidea · Echinodermata · Eocene · Paleoenvironment · New taxa

Introduction

Aboral cups and columnals of stalked crinoids from the Marnes de Gan Formation at Bosdarros near Gan (Pyrénées-Atlantiques, southwestern France) (Fig. 1) were first described briefly and figured by d'Archiac (1850) and Rouault (1850) and attributed to *Bourgueticrinus thorenti* d'Archiac, 1846. Roux and Plaziat (1978) listed stalked crinoids from the Pyrenean Paleogene but only referred to the occurrence of Thanetian columnals collected in the vicinity of Gan. Merle (1985, 1986) identified several beds containing crinoid ossicles in the section known as Tuilerie de Gan. Most of the specimens were isolated columnals, except for two distal stalk segments with proximal articulated roots. These columnals belong to xenomorphic stalks in which proxistele, mesistele and dististele have contrasted external morphologies. They were traditionally attributed to the genus *Conocrinus* (Rasmussen 1978; Hess 2011). They display a twisted arrangement: elliptical articular facets with deep eight-shaped ligament fossae and the greater facet diameter axis on successive facets rotated by as much as 90° (Fig. 2a). Such a mode of articulation is called ligamentary synarthry and is frequently observed in crinoids with a xenomorphic stalk from Upper Cretaceous to Recent (Hess 2011).

In Gan, fossilization within clay allows exceptional preservation of the calcite network (stereom) that constitutes crinoid ossicles (Macurda et al. 1978) and facilitates

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Fig. 1 Location of Gan (Pyrénées-Atlantiques) in southwestern France

comparison with extant taxa, discussion of taxonomic affinities and interpretation of paleoenvironment.

The genus *Conocrinus* was placed either in the family Bathycrinidae (Rasmussen 1978) or in Bourgueticrinidae (Hess 2011). Recent molecular phylogenies (Rouse et al. 2013; Hemery et al. 2013) revealed that extant crinoids with a xenomorphic stalk have a polyphyletic origin and frequent phenotypic convergences. Therefore, the classification of fossil and extant species which was mainly based on external morphological characters must be thoroughly revised using more robust characters, changes throughout ontogeny and congruencies with molecular data (Roux et al. 2013). Such a revision was recently made for *Conocrinus* and taxa with close affinities, which were placed within the family Rhizocrinidae (Roux et al. 2018). They constitute a lineage clearly distinct from Bourgueticrinidae and Bathycrinidae. These authors subdivided *Conocrinus* (sensu lato) into three genera: *Conocrinus* (sensu stricto), *Paraconocrinus* and *Pseudoconocrinus*. Complementary descriptions of many extant and fossil taxa are required, especially for fossils only known from dissociated ossicles. Therefore, fossil articular facets with well-preserved stereom are particularly useful because they allow detailed comparison with extant taxa. Whereas Rasmussen (1972, pl. 1, fig. 9) provide the only figure of a Cenozoic fossil crinoid with a xenomorphic stalk with the ossicles of its proximal stalk, cup and proximal arms partly articulated, here we describe the first discovery in Cenozoic beds of distal stalk segments with their proximal roots.

Large columnals from the Eocene of northern Italy, housed in the collection of the Muséum national d'Histoire naturelle (MNHN) in Paris, have close affinities with one of the columnal types found at Gan. We include this Italian

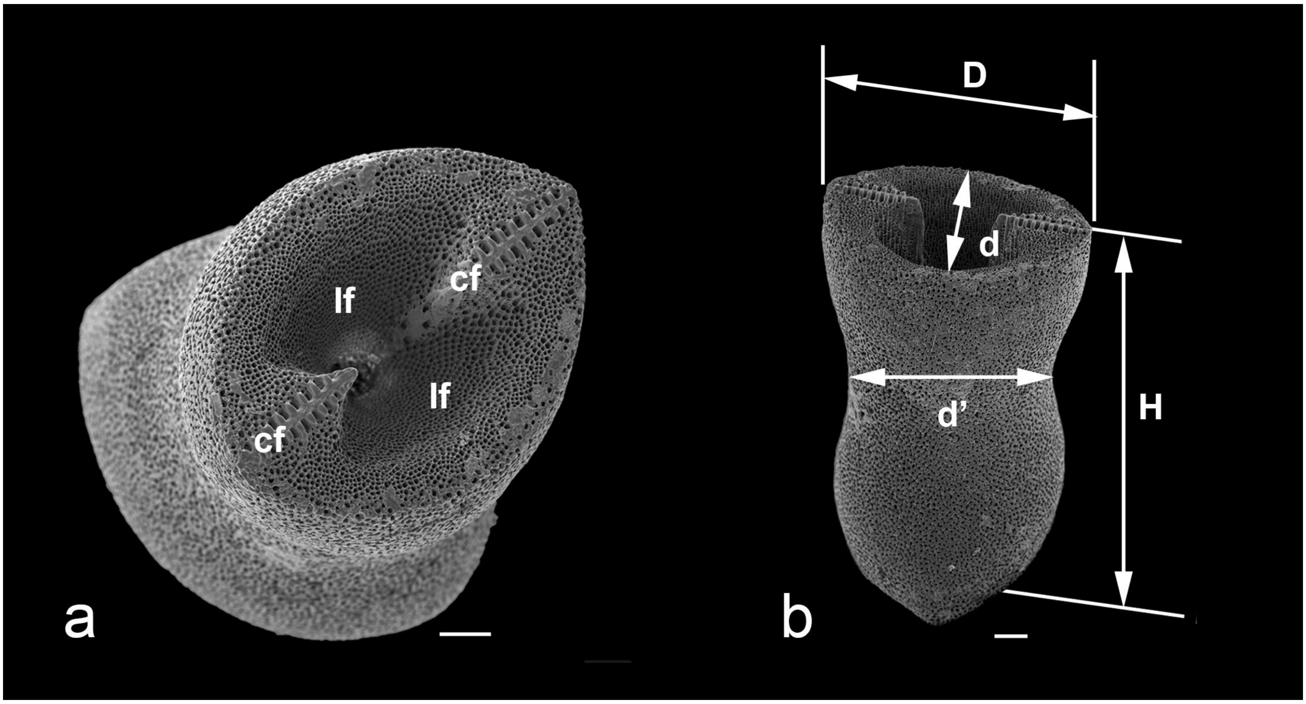

Fig. 2 Morphology of *Conocrinus*-type columnal (**a**) and quantitative characters measured (**b**). *cf* fulcral ridge, *lf* 8-shaped ligament fossae, *D* greatest facet diameter, *d* smallest facet diameter, *d*′ diameter at mid-height, *H* ossicle height. Scale bar: 100 μm

material in our study, because it gives important complementary data on morphology and paleoecology, which justify the creation of a new genus and contribute to a better interpretation of paleoenvironments.

Geological, stratigraphical and environmental setting of the Tuilerie de Gan section

During the Early Eocene, the Gan area was inside the northern Pyrenean foreland basin. The Marnes de Gan Formation was deposited between two main tectonic events: the first during Late Ilerdian (end of Early Ypresian) and the second at the Ypresian-Lutetian boundary (Gély and Sztrákos 2000). Sedimentation began with a transgressive glauconitic layer dated base of upper part of NP12. Frequently reworked microfauna suggests an unstable environment before the NP13 zone. In the vicinity of Gan, maximum subsidence allowed several hundred meters of terrigenous sediments dated to P7–8 and NP12–13 to accumulate (Steurbaut and Sztrákos 2002; Nolf et al. 2002). Associations of benthic foraminifera suggest an increase to epibathyal depths followed by a regressive trend which reached a shallow water environment (infralittoral) at the top of Marnes de Gan Formation.

The old quarry known as the Tuilerie de Gan consists of clay beds about 50 m thick. The sandy component increases in the upper part of the section. It is a famous site known for its highly diverse molluscan fauna (Cossmann and O'Gorman 1923). Currently, only the lowest part is accessible, the top being buried under vegetation. Merle (1985, 1986) distinguished six layers from base to top:

- Bed 1: 6.60 m of blue-gray clay characterized by splintered fragments and without macrofossils.
- Bed 2: 0.60 m of blue-gray silty clay with abundant *Nummulites* and macrofossils.
- Bed 3: 1.70 m of blue-gray clay, poor in macrofossils.
- Bed 4: 1.00 m of blue-gray silty clay with *Nummulites* and abundant macrofossils.
- Bed 5: 0.40 m of beige to reddish indurated sandy clay with *Nummulites* and abundant macrofossils.
- Bed 6: 5.90 m of blue-gray clay characterized by splintered fragments and with sparse macrofossils, at the lowermost base.

The crinoids here analyzed were collected in beds 2–6. The distal stalk segments and roots with articulated ossicles came from 10 cm of Orthophragmine-rich clay at base of bed 6. The section starts within NP12, and NP13 was identified beginning at bed 4 (Nolf et al. 2002).

Merle (1985, 1986) studied paleoecological changes throughout this section by analyzing benthic mollusk assemblages and characterizing them based on the Perès and Picard (1964) method. The transition between circalittoral and epibathyal (upper part of continental slope) is usually located at a depth circa 150 m (Perès 1976). It was not possible to characterize any assemblage from beds 1 and 6 because of the scarcity of fossils. From base to top:

- Bed 2: an assemblage dominated by *Sigmesalia duvali* (Rouault, 1850) (Turritellidae) and *Hemiconus rouaulti* (d'Archiac, 1850) (Conidae) was defined. It is notable for the abundance of carnivores and the scarcity of phytophagous taxa (Merle 1984, 1985). Suspension feeders are mainly represented by *S. duvali* and the bivalve *Corbula* (*Varicorbula*) *archiaci* (Rouault, 1850) (Corbulidae). In this bed, columnals of crinoids are common. The mollusk assemblage suggests a depositional environment at a depth below the euphotic zone.
- Bed 3: this bed is characterized by the disappearance of sessile epifauna, which correlates with the loss of silts and *Nummulites*. An assemblage dominated by *C.* (*V.*) *archiaci* and *Conomitra hordeola* (Deshayes, 1865) (Volutomitridae) was defined. These two infauna species may be regarded as opportunists. This assemblage appears to be a remnant of the *S. duvali* and *H. rouaulti* assemblage and resembles a circalittoral soft mud facies (Merle 1985).
- Bed 4: an assemblage dominated by *S. duvali* and *Thericium* (sensu lato) *pratti* (Rouault, 1850) (Cerithiidae). Its composition is similar to that of the bed 2 assemblage, based on the reappearance of crinoid ossicles that disappeared in bed 3. However, it is characterized by a significant increase in number of phytophagous species *T.* (*s.l.*) *pratti*, suggesting a depth closer to the euphotic zone.
- Bed 5: an assemblage dominated by *Lunulites puntatus* Leymerie, 1846 (bryozoan) and "*Serpula*" *subgranulosa* Rouault, 1850 (Polychaeta, annelid) in this indurated sandy clay. The sessile organisms, such as the bivalves *Dimya*, *Plicatula* and the crinoids do not seem to have been affected by this lithological change. On the other hand, the disappearance of phytophagous *T.* (*s.l.*) *pratti* suggests a deeper depositional environment.
- Bed 6: this bed was first analyzed by one of us (DM) in 1990s, not by Merle (1985, 1986). Macrofossils were found just above the indurated bed 5. The macrofaunal assemblage contains scattered forms including *Sindiluta prevosti* (Rouault, 1850) (= *Volutilithes ogormani* Cossmann and O'Gorman, 1923; gastropod, Volutidae), *C.* (*V.*) *archiaci* and *Lunulites punctatus* which are associated with some articulated crinoid stalk ossicles.

Both benthic mollusk assemblages suggest a relatively deep environment of outer shelf to further offshore (circalittoral to epibathyal zones). Such assemblages are closely related to benthic communities with *Hinia* and *Cadulus* described by Baldi (1973) and correspond to muddy bottom characterized by a lack of algae and weak currents (Merle 2000) at a depth of more than 120 m (Merle 1985). Dolin and Ledon (2002) and Lozouet (2004) proposed the same interpretation and suggested that macrofauna of the Tuilerie de Gan inhabited epibathyal depths. By contrast, Nolf et al. (2002) deduced a depth shallower than 50 m from fish otolith assemblages.

Geological and stratigraphical setting of northeastern Italian sites with crinoids closely related to the Gan fauna

The area cited in the current study is located NE of Verona (Lessini mounts, Southern Alps). During Eocene times, the Lessini carbonate shelf developed with a variety of biogenic sedimentary facies which were analyzed by Nebelsick et al. (2005). Tectonic activity and magmatism acted during sedimentation (Rasser and Harzhauser 2008; Papazzoni, Bassi et al. 2014; Papazzoni, Carnevale et al. 2014). Fabiani (1915) gave a useful revision of Eocene stratigraphy in northeastern Italy. Bayan (1870) first detailed Eocene stratigraphy between Monte Spilleco and Monte Postale. He pointed out that "grands *Bourgueticrinus*" occured in a reddish calcareous bed with *Conoclypeus conoideus* just above alveolinid-rich beds at Val della Gichelina. Other sites where such *Bourgueticrinus* were cited are Val di Ciuppio, Croce grande and Pozza. Guichelina and Ciuppio are the two sites mentioned as the origin of large columnals housed in MNHN collection. Munier-Chalmas (1891) attributed calcareous beds with alveolinids, nummulitids and *Conoclypeus conoideus* to Middle Eocene. Currently, they are known as San Giovanni Ilarione horizon belonging to Middle Lutetian, SBZ14–NP15 zones (see Agnini et al. 2011, tabl. 1. A mesopelagic ichthyofauna interbedded with allochthonous sediments from the outer platform was recently discovered (Giusberti et al. 2014). That first suggests a possible epibathyal slope.

Materials and methods

The fossil material here described is housed in the paleontological collection of the Muséum national d'Histoire naturelle (MNHN) in Paris, and referenced MNHN.F. Specimens are listed in Table 1. All the dissociated columnals used to describe the new species *Eocenocrinus hessi* and *E. bayani* belonged to different individuals. Consequently, we catalogued them as syntypes, without distinction of a holotype.

A few columnals and root ossicles were extracted after washing of sediment from Gan bed 6. Most of ossicles were slightly cleaned using ultrasound. For scanning electron microscopy (SEM), ossicles were washed in distilled water, air dried, mounted on stubs, and coated with colloidal gold. They were examined in a JEOL-840A operated at 15 kV in the MNHN platform of electronic microscopy.

Thin slides of the bioclastic limestone fragment from d'Orbigny's collection (no. 9017) were made by D. Delor and analyzed by V. Barbin (both University of Reims): benthic foraminifer content suggests a Middle Eocene age (Middle to Late Lutetian).

Specimens of *Democrinus* sp. (Fig. 12) collected off Madeira, cruise of N/O Jean Charcot, station 49, 18/07/1966, 32°27′N–16°32′W, depth 450–500 m, are housed in the MNHN zoological collection (catalogue number: MNHN-IE-2016-562) and were used to illustrate mode of attachment of extant bourgueticrinids.

For stalked crinoid morphological terminology see Roux et al. (2002) and Hess (2011); for stereom see Macurda et al. (1978).

Taxonomy

Preliminary remark Pragmatically, we use the distinction between Bourgueticrinidae and Phrynocrinidae sensu Hess (2011). As the classification of extant crinoids with a xenomorphic stalk is not clearly established at the order and family levels (see discussion in Messing 2016), the taxonomic attributions of the fossil columnals here described are inevitably provisional, waiting more material, especially well preserved aboral cups and brachials. Synonymies are restricted to main references that include illustration.

Family Rhizocrinidae Jaekel, 1894

Genus *Paraconocrinus* Roux, Eléaume and Améziane, 2018

Paraconocrinus romanensis (Roux and Plaziat 1978)
Figures 3a–c, 4a, 5b, f–g, 6a, b, 8, 9, 10

Synonymy Bourgueticrinus thorenti sensu Rouault, 1850 [non d'Archiac, 1846]: 437, pl. A, figs. 13–14; *Conocrinus romanensis* Roux and Plaziat 1978: 304, fig. 4.

Material examined Syntypes A (MNHN.F.A69327, Roux and Plaziat 1978, Fig. 4), two aboral cups and two columnals from San Roman (Santander Province, Spain); Syntypes B (MNHN.F.A69328, not figured), three aboral cups and 56 columnals from same location; MNHN.F.A69329, two aboral cups from Bosdarros near Gan; Specimen A (MNHN.F.A69330, Fig. 4a), one distal stalk with its proximal roots from Gan bed 6; Specimen B

Table 1 Fossils examined in this study and housed in the MNHN paleontological collection

Catalogue number	Species	Age	Occurrence	Remarks
MNHN.F.A69327	*Paraconocrinus romanensis*	Late Ypresian	SP—San Roman	Syntypes A, 2 cups + 2 columnals (Roux and Plaziat 1978, Fig. 4)
MNHN.F.A69328	*Paraconocrinus romanensis*	Late Ypresian	SP—San Roman	Syntypes B, 3 cups + 56 columnals (not figured)
MNHN.F.A69329	*Paraconocrinus romanensis*	Late Ypresian	FR—Bosdarros	2 aboral cups
MNHN.F.A69330	*Paraconocrinus romanensis*	Late Ypresian	FR—Gan bed 6	Sp. A, 1 dististele + rhizoids (Fig. 4a)
MNHN.F.A69331	*Paraconocrinus romanensis*	Late Ypresian	FR—Gan bed 6	Sp. B, 1 isolated columnal (Fig. 3a, b)
MNHN.F.A69332	*Paraconocrinus romanensis*	Late Ypresian	FR—Gan bed 6	Sp. C, 2 isolated columnals (not figured)
MNHN.F.A69333	*Paraconocrinus romanensis*	Late Ypresian	FR—Gan bed 4	Sp. D, 1 isolated columnal (Fig. 3c)
MNHN.F.A69334	*Paraconocrinus romanensis*	Late Ypresian	FR—Gan bed 6	Sp. E, 3 rhizoid ossicles (Fig. 5a, f, g) detached from Sp. A
MNHN.F.A69335	*Paraconocrinus romanensis*	Late Ypresian	FR—Gan beds 2–4	Sp. F, 3 isolated columnals (not figured)
MNHN.F.A69336	*Democrinus londinensis*	Late Ypresian	FR—Gan bed 6	Sp. A, 1 dististele + rhizoids (Figs. 3h, i, 4c)
MNHN.F.A69337	*Democrinus londinensis*	Late Ypresian	FR—Gan bed 6	Sp. B, isolated columnal (Fig. 3d–g)
MNHN.F.A69338	*Democrinus londinensis*	Late Ypresian	FR—Gan bed 6	Sp. C, proximal isolated root (Fig. 4b)
MNHN.F.A69339	*Paraconocrinus/Democrinus*	Late Ypresian	FR—Gan bed 6	6 isolated rhizoid ossicles (Fig. 5b, e)
MNHN.F.A69340	*Paraconocrinus/Democrinus*	Late Ypresian	FR—Gan bed 6	29 isolated rhizoid ossicles (not figured)
MNHN.F.A69341	*Eocenocrinus hessi*	Late Ypresian	FR—Gan beds 2–4	Syntype A, 1 isolated columnal (Fig. 6a–d)
MNHN.F.A69342	*Eocenocrinus hessi*	Late Ypresian	FR—Gan beds 2–4	Syntype B, 1 isolated columnal (Figs. 6e, f, 11e, f)
MNHN.F.A69343	*Eocenocrinus hessi*	Late Ypresian	FR—Gan beds 2–4	Syntypes C, 27 isolated columnals (not figured)
MNHN.F.A69344	*Eocenocrinus bayani*	Middle Lutetian	I—Vicentin[a]	Syntype A, bioclastic limestone with 1 columnal (Fig. 7e)
MNHN.F.A69345	*Eocenocrinus bayani*	Middle Lutetian	I—Guichelina[a]	Syntypes B, 4 isolated columnals (not figured)
MNHN.F.A69346	*Eocenocrinus bayani*	Middle Lutetian	I—Guichelina[a]	Syntypes C, 1 isolated columnal (Fig. 6g, h)
MNHN.F.A69347	*Eocenocrinus bayani*	Middle Lutetian	I—Guichelina[a]	Syntypes D, 4 isolated columnals (Fig. 7f–i)
MNHN.F.A69348	*Eocenocrinus bayani*	Middle Lutetian	I—Guichelina[a]	Syntype E, 1 isolated columnal, not figured)
MNHN.F.A69349	*Eocenocrinus bayani*	Middle Lutetian	I—Ciuppio	Syntype F, 3 columnal pairs, Fig. 7a–c
MNHN.F.A69350	*Eocenocrinus bayani*	Middle Lutetian	I—Ciuppio	Syntype G, 1 isolated columnal, Fig. 7d
MNHN.F.A69351	*Eocenocrinus bayani*	Middle Lutetian	I—Ciuppio	Syntype H, 7 isolated columnals, not figured

FR SW France, *I* NE Italy, *SP* N Spain

[a] d'Orbigny's collection no. 9017

(MNHN.F.A69331, Fig. 3a, b), 1 isolated columnal from the same bed and location; Specimens C (MNHN.F.A69332, not figured), 2 isolated columnals from the same bed and location; Specimen D (MNHN.F.A69333, Fig. 3c), one isolated columnal from bed 4, same location; Specimen E (MNHN.F.A69334, Fig. 5a, f, g), 3 rhizoid ossicles detached from Specimen A; Specimen F (MNHN.F.A69335, not figured), 3 isolated columnals from bed 2–4, same location.

Description Usually, each distal columnal with a single conspicuous root socket prolonging the greatest diameter of one articular facet, a few cases with two sockets of the same size (one adjacent to each facet). Maximum size: H 3.5 mm, D 3.75 mm, d 2.75 mm, d' 3.5 mm. H/D 0.72–0.95 and D/d 1.36–1.66 in dististele. H/D up to 1.22 and D/d about 1.50 in two mesistele columnals. Distal columnals variously inflated at mid-height. Articular facet with eight-shaped ligament fossae larger than in the two other species from Gan, width 1/2 d (Fig. 3a). Fulcral ridge forming a conspicuous relief between the two adjacent slightly depressed areas with conspicuous parallel borders, its axis filled in with massive calcite and bordered on each side by 20–25 small regularly arranged crenulae (Fig. 3b). Dististele from bed 6 consisting of eight columnals articulated over a length of 20 mm (Fig. 3a), columnal shape very variable (Fig. 10). Two roots branched on one side and a third on the other side. Main root beginning with a short ossicle ($H = 0.7$ mm, $D = 1.0$ mm) followed by a long axillary (2.5 mm) with an isometric branching. On one branch, a second highly anisometric division occurring at 2.3 mm, the other branch remaining undivided over 7.9 mm with three observable ossicles. Root ossicles articulated by synostoses. Largest root ossicles having

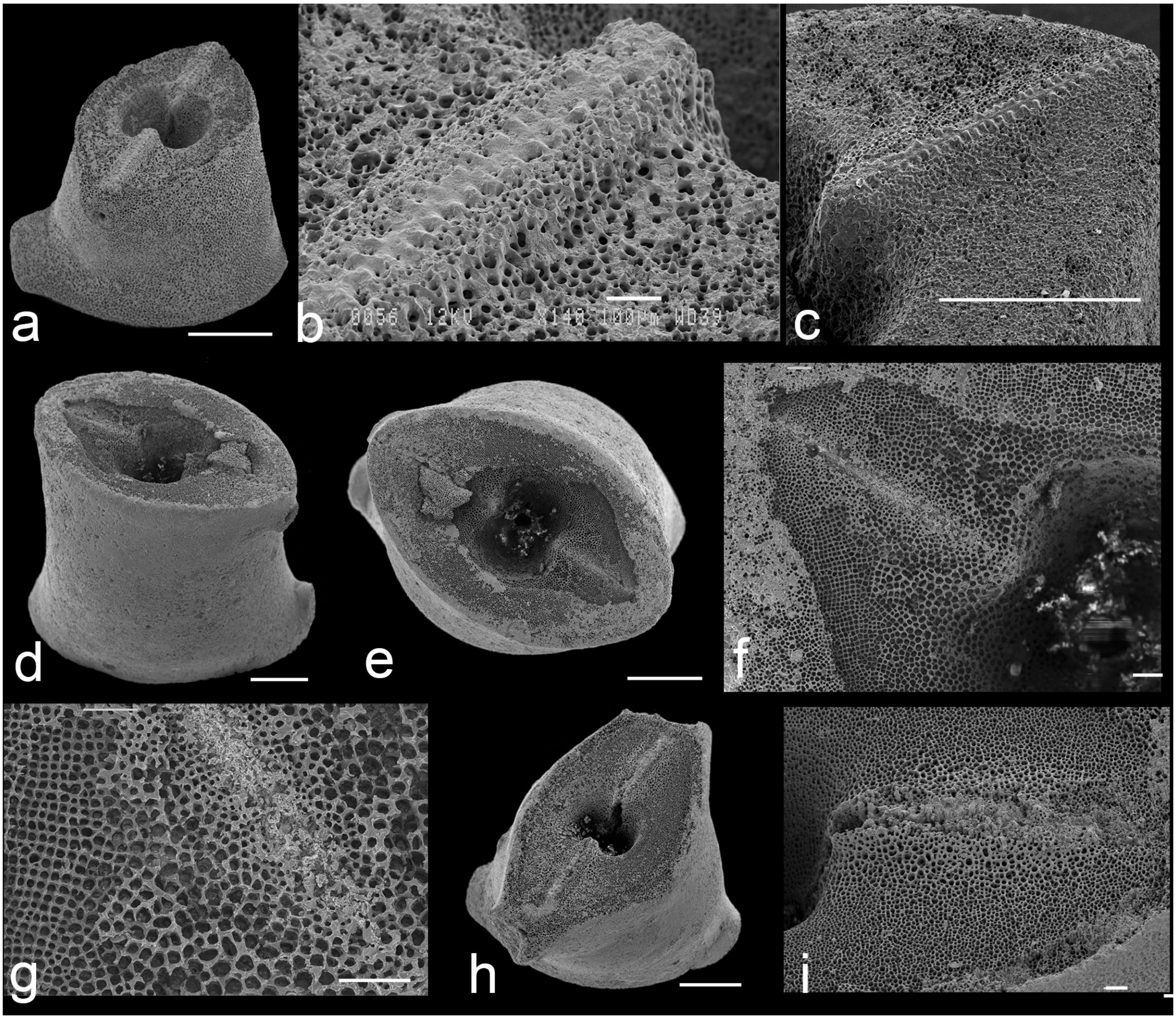

Fig. 3 Columnals of Rhizocrinidae from Tuilerie de Gan (Late Ypresian). **a–c** *Paraconocrinus romanensis* (Roux & Plaziat, 1978), **a**, **b** columnal from dististele segment in bed 6 (spm B, MNHN.F.A69331, **b** close up of the well-preserved fulcral ridge, **c** articular facet of isolated distal columnal from bed 4 with surface covered by micrite (spm D, MNHN.F.A69333), **d–i** *Democrinus londinensis* (Forbes, 1852) from bed 6, **d–g** isolated proximal columnal of dististele with anchylosed articulation (spm B, MNHN.F.A69337), **d**, **e** general view showing the flat anchylosed facet partly broken, **f**, **g** previous functional synarthry preserved under the flat anchylosed surface, **g** close up of the well-preserved stereom of fulcral ridge and adjacent ligament depression, **h**, **i** distal-most columnal of the preserved dististele segment, i: well-preserved facet stereom (spm A, MNHN.F.A69336). Scale bars: **a**, **c**, **d**, **e**, **h** = 1 mm; **b**, **f**, **g**, **i** = 100 µm

articular facet with a slight depression around the axial canal (Fig. 5a, f, g).

Remarks No significant correlation between shape (*H*/*D* and *D*/*d*) and size (*d*′) could be documented because the shape of successive columnals in the distal segment varied substantially, and the sample size was too small (Figs. 8, 9). Mesistele and dististele columnals in the type-series of *P. romanensis* from Upper Ypresian of Spain (Roux and Plaziat 1978) are very similar of those from Gan. They share the same fulcral ridge characters with mesistele columnals of *P. handiaensis* Roux, 1978a, from the Bartonian at the base of the Biarritz Eocene section (Roux 1978b, pl. 2 fig. 5). However, distal columnals of *P. handiaensis* differ in having a hollowed fulcral ridge axis as observed in the extant species *C. cabiochi* Roux, 1976, from the Bay of Biscay (Roux 1977a, pl. 4 fig. 3). The type-series of *P. romanensis* includes five aboral cups. The two cups (MNHN.F.A69329), unfortunately in poor preservation, and those figured with associated columnals

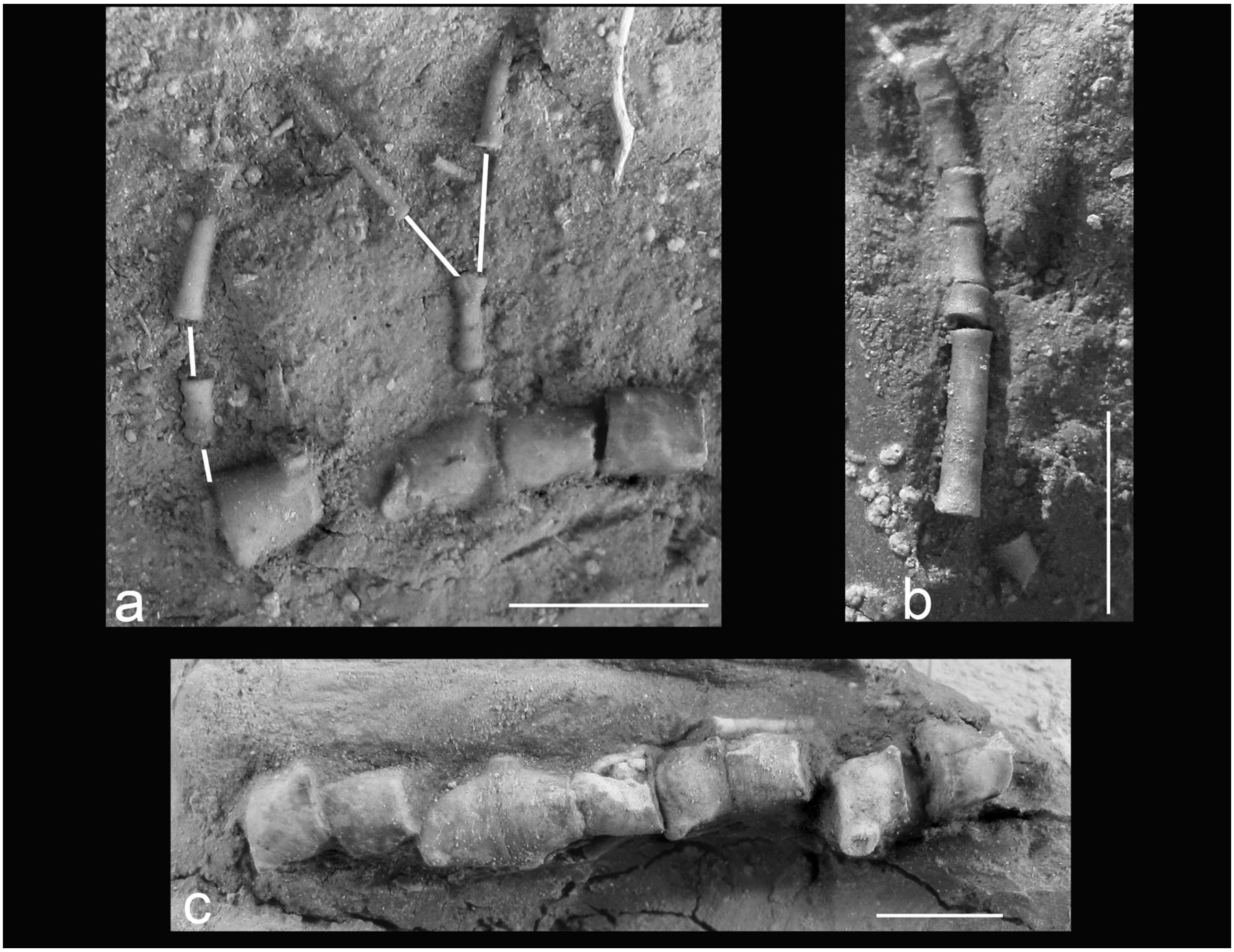

Fig. 4 Segments of dististele and root with ossicles in connection from "Tuilerie de Gan" bed 6 (Late Ypresian). **a** *Paraconocrinus romanensis* (Roux and Plaziat 1978) (spm A, MNHN.FA69330), **b**, **c** *Democrinus londinensis* (Forbes, 1852), **b** proximal segment of root (distal end at top) (spm C, MNHN.F.A69338), **c** dististele segment partly slipped and dislocated (arrow head: proximal part of root) (spm A, MNHN.F.A69336). Scale bar: 5 mm

by Rouault (1850, pl. A, figs. 13, 14), both from Bosdarros near Gan, could belong to the same species.

Occurrence Upper Ypresian of Bosdarros and Gan (SW France) and San Roman (Santander, Spain), Ypresian/Lutetian boundary of Sierra de Cadi (Lerida, Spain).

Genus *Democrinus* Perrier, 1883

Democrinus londinensis (Forbes, 1852)

Figures 3d–i, 4b, c, 8, 9, 10

Synonymy Bourgueticrinus londinensis Forbes, 1852: 36, fig. 4; *Democrinus londinensis* Rasmussen, 1972: 31–33, pl. 1 fig. 9; Roux, 1978b: 226–227, fig. 13, pl. 2 figs. 6–11.

Material from Gan, bed 6 Specimen A (MNHN.F.A69336, Fig. 4c), one distal stalk with a few proximal root ossicles, including one columnal detached for SEM study (Fig. 3h, i); specimen B (MNHN.F.A69337, Fig. 3d–g), one isolated distal columnal; specimen C (MNHN.F.A69338, Fig. 4b), one isolated root fragment. Root ossicles collected by sediment washing and attributable to either *C. romanensis* or *D. londinensis* (see Remarks): (MNHN.F.A69339, Fig. 5b–e), six ossicles; (MNHN.F.A69340, not figured), 29 ossicles.

Description Each distal columnal with one or several root sockets, sometimes of various size, developed from the outer ends of fulcral ridge, inflation at mid-height variable. Isolated columnal with an ankylosed facet (Fig. 3d): H 4.2 mm, D 4.15 mm, d 2.3 mm, d' 3.4 mm, H/D 1.01, D/d 1.43. Columnals in the distal stalk segment (Fig. 3c): H 2.9–3.05 mm, D 4.1–4.25 mm, d 2.6–2.7 mm, d' 3.0–3.15 mm, H/D 0.68–0.74 and D/d 1.56–1.62. Articular

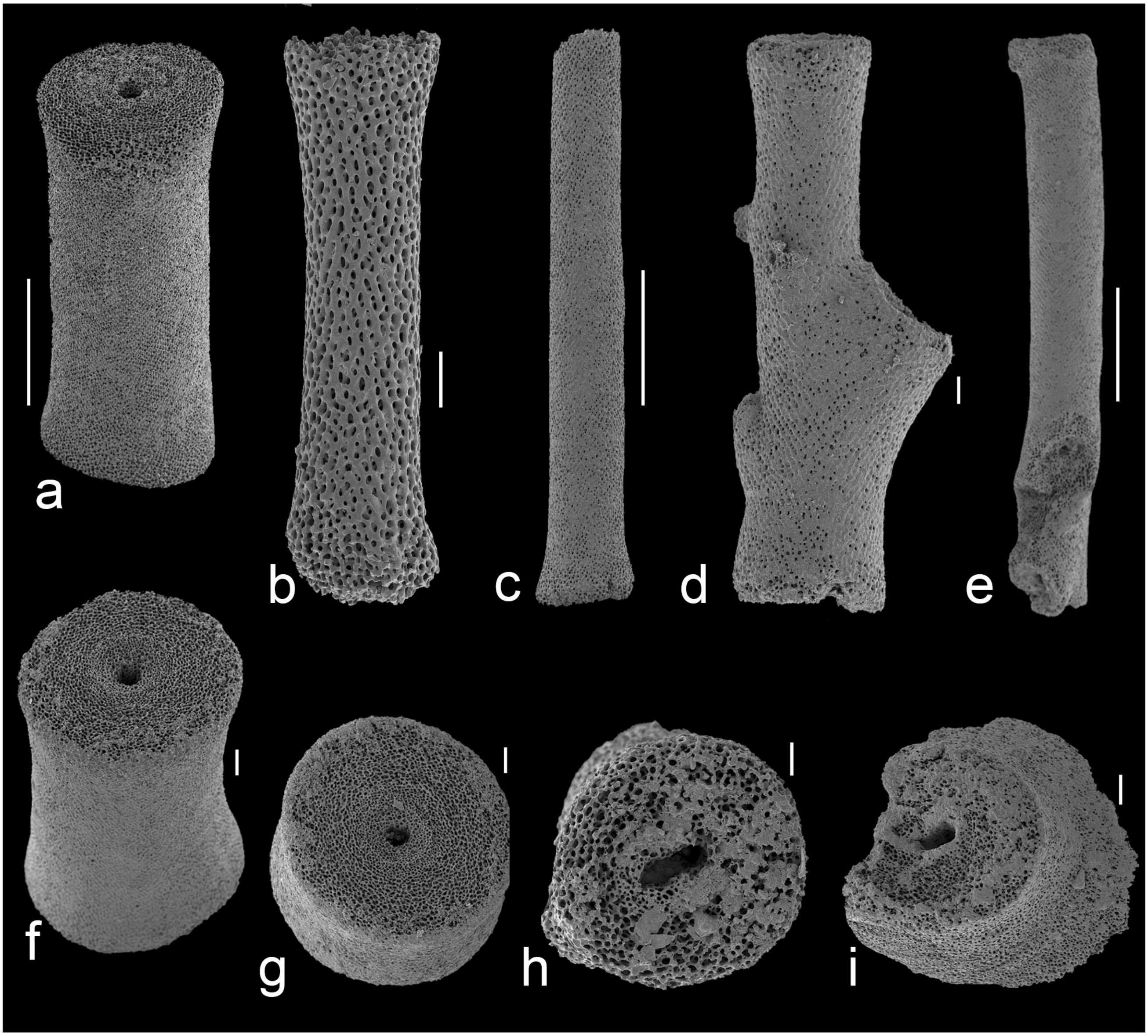

Fig. 5 Root ossicles from "Tuilerie de Gan" bed 6 (Late Ypresian). **a**, **f**, **g** Ossicles detached from proximal roots of *Paraconocrinus romanensis* (Roux and Plaziat 1978) (spm E, MNHN.F.A69334), **b**–**e** and **h**–**i** isolated ossicles of *Paraconocrinus* or *Democrinus* from sediment washing (MNHN.F.A69339). Scale bar: **a**, **c**, **e** = 1 mm; **b**, **d**, **f**–**i** = 100 µm

facet with 8-shaped ligament fossae of width usually 1/3 *d*, other parts of ligament area significantly more depressed than in *C. romanensis* (Fig. 3h). Fulcral ridge axis without massive calcite and lateral crenulae, filled in with irregular stereom except for a conspicuous hollowed area near the ligament fossae, lateral ridge borders progressively depressed and marked by stereom of larger meshes (Fig. 3f–i). Isolated columnal (probably from proximal diststele of another specimen) displaying articulation anchylosis with development of a thin layer of synostosial stereom on outer facet (Fig. 3d, e), previous functional synarthry (well-preserved under this layer) with ligament fossea width about 1/2 *d* (Fig. 3e–g). Diststele from bed 6 with 11 articulated columnals together 44 mm long. Several articulations partly slipped or slightly dislocated, and two columnals tilted (Fig. 4c). Proximal root ossicles subparallel to the stalk and dislocated. A single root segment 12 mm long, of seven articulated ossicles of variable length (Fig. 4b), found 30 mm away from the columnals. The proximal-most ossicle the longest (4.3 mm) with maximum diameter of 1.1 mm. Distal end of the four distal ossicles bearing one socket of 0.5 mm in diameter indicating highly anisometric branching. One small branch ossicle still connected to the sixth main root ossicle.

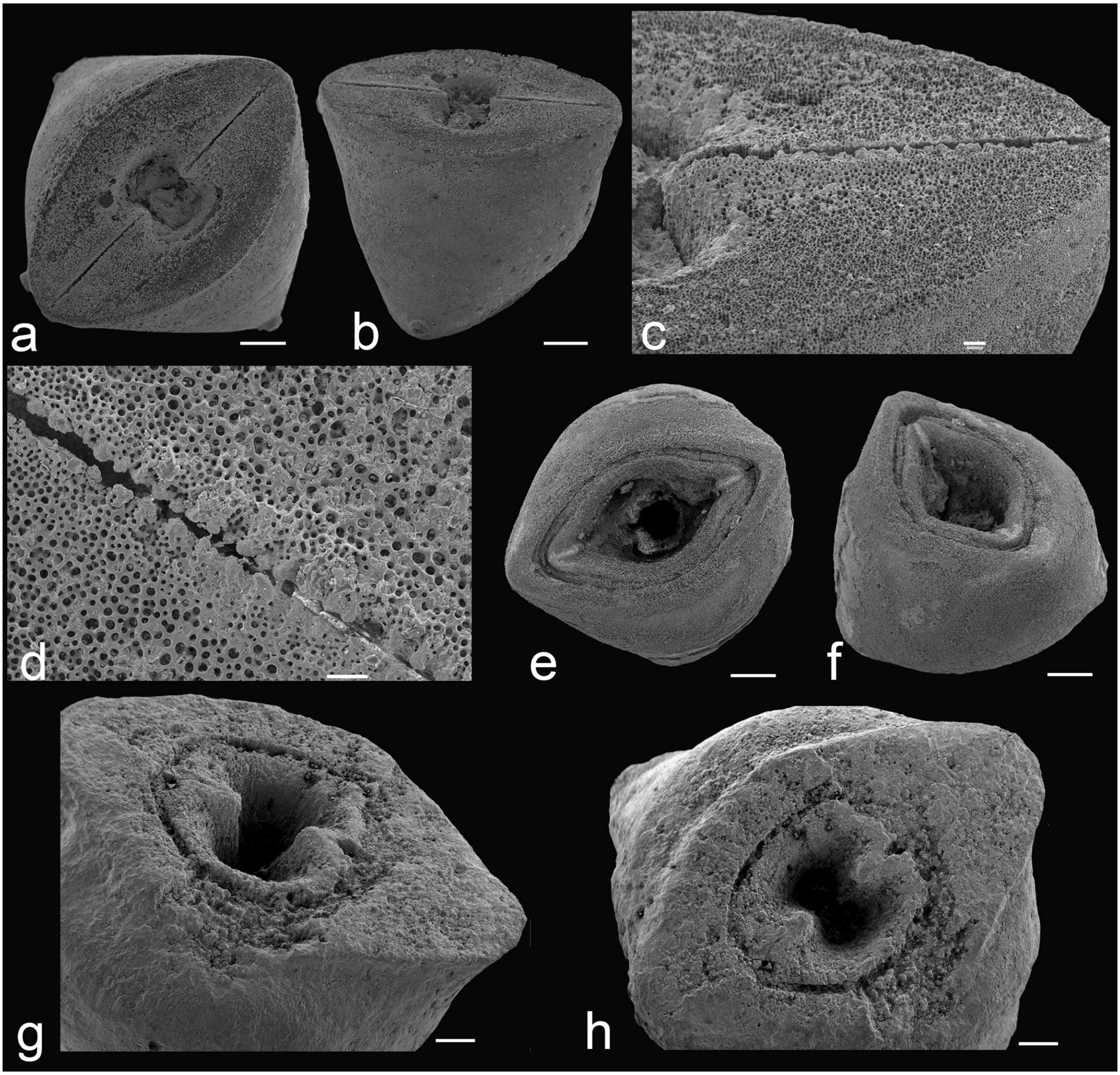

Fig. 6 Columnals of *Eocenocrinus* n. gen. **a**–**f** *E. hessi* n gen., n. sp. from "Tuilerie de Gan" beds 2–4 (Late Ypresian), **a**–**d** (syntype A, MNHN.F.A69341): columnal of distal mesistele with flat synarthry, **d** close up on fulcral ridge with rudimentary crenularium, **e**, **f** (syntype B, MNHN.F.A69342): biocorroded distal columnal with anchylosed articulations, **g**, **h** *E. bayani* n. gen., n. sp. (syntypes C, MNHN.F.A69346) from Val della Gichelina, northeastern Italy (Middle Lutetian), distal columnal with cryptosynarthry (early anchylosed articulation). Scale bars: **a**, **b**, **e**, **f**, **g**, **h** = 1 mm, **c**, **d** = 100 µm

Remarks The Natural History Museum and Geological Survey in London house numerous columnals of *D. londinensis* from the London Clay (Early Ypresian, NP11–12) (Aldiss 2014). Their maximum size is lower than in those from Gan: $H < 3.5$ mm and $D < 3$ mm (Roux 1978b, fig. 13). Articular facets in distal mesistele and dististele (Roux 1978b, pl. 2 figs. 6–8) and anchylosed articulations in distal mesistele (M.R. unpublished SEM views) share exactly the same characters with those from Gan. In both sites, the stereom is exceptionally preserved. All root ossicles collected by sediment washing (Fig. 5b–e, h, i) and the root fragment found near the stalk segment (Fig. 4b) suggest that both *D. londinensis* and *P. romanensis* share the same dendritic root pattern. The longest root ossicle is 4.7 mm long, 1.2 mm across its greatest diameter, and has three branch sockets at its distal end (Fig. 5e). One isolated distal-most root ossicle displays a small incrusting disk which was probably attached on a

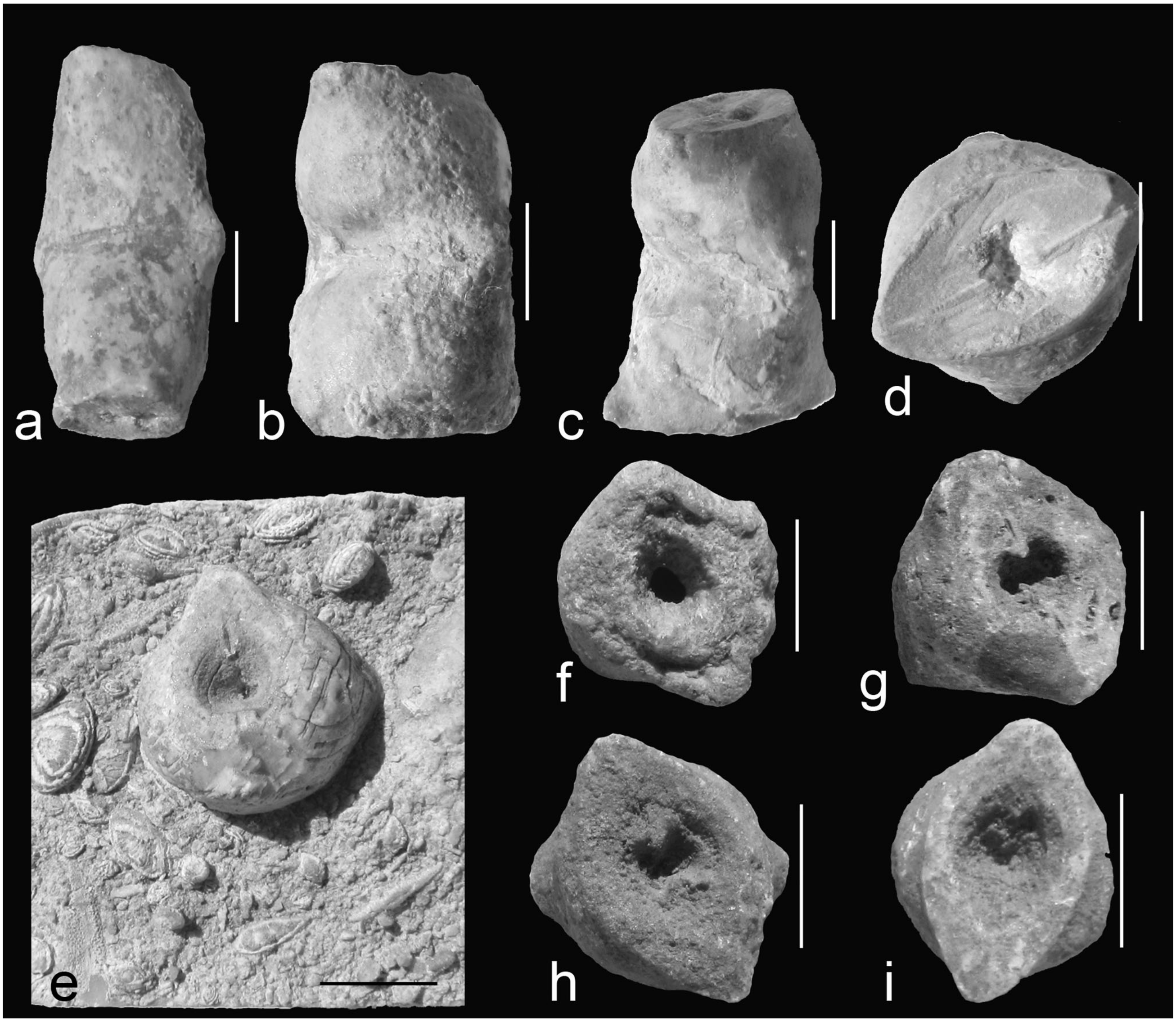

Fig. 7 Columnals of *E. bayani* n. gen., n. sp. from northeastern Italy (Middle Lutetian). **a**–**d** [syntypes F, MNHN.F.A69349 (**a**–**c**) and syntype G, MNHN.F.A69350 (**d**)]: distal mesistele columnals from Val di Ciuppio, **a**–**c** side views of columnal pairs, **d** synarthry of isolated columnal, **e**–**i** [syntype A, MNHN.F.A69344 (**e**) and syntypes C, MNHN.F.A69347 (**f**–**i**)] isolated columnals from dististele with anchylosed articulations, detailed location unknown (d'Orbigny's collection), **e** columnal with early anchylosed articulation embedded in limestone including large benthic foraminifera, **f** columnal highly biocorroded (compare to Fig. 6e, f), **g**–**i** columnals with early to late anchylosed articulations, respectively. Scale bar: 5 mm

shell fragment (Fig. 5i). In contrast, columnal shape in the dististele of *D. londinensis* preserved at Gan is less variable than in *P. romanensis* (Fig. 10).

Occurrence Early Ypresian (London Clay, G.B.), Late Ypresian of Tuilerie de Gan (SW France).

Family Phrynocrinidae A.H. Clark, 1907

Genus *Eocenocrinus* n. gen.

Type species of the genus Eocenocrinus hessi n. gen. n. sp.

Diagnosis Crinoid with its distal xenomorphic stalk (distal mesistele and dististele) having frequent successive articulations anchylosed (cryptosynarthries). Anchyloses developed at various ontogenic stages with flat outer ring on columnal facets (secondary synostoses). Fulcral ridge in distal columnals with hollow axis bordered by small rudimentary crenulae. Usually, columnals without root socket or with rudimentary ones. Possibly stalked attachment to hard substrate by encrusting disk or roots.

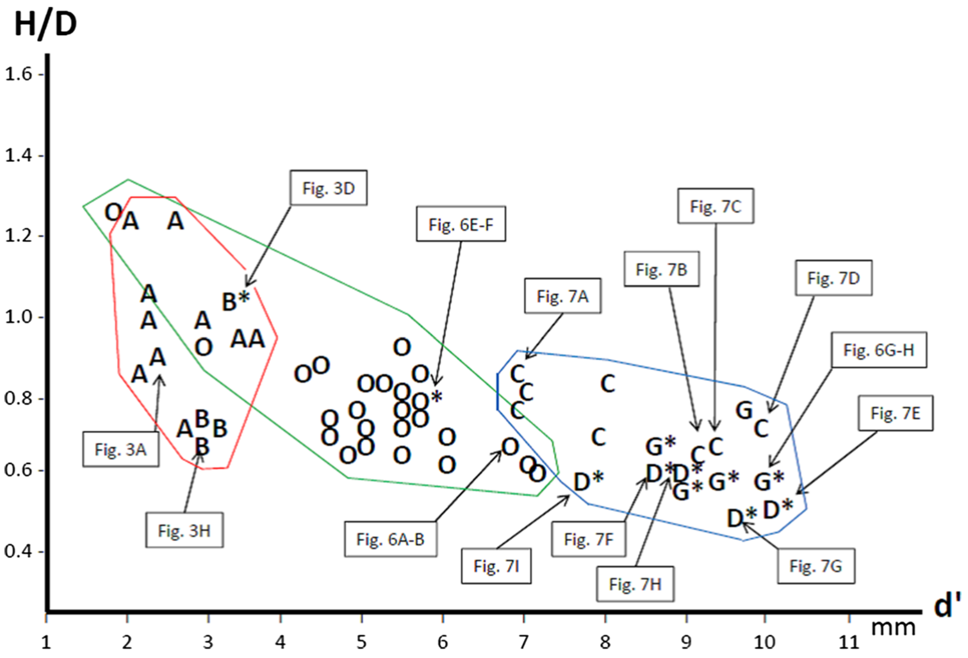

Fig. 8 Biometrical graph of columnals from Tuilerie de Gan (Late Ypresian) and northeastern Italy (Middle Lutetian) with H/D plotted against d' (growth index). From Tuilerie de Gan—A: *Paraconocrinus romanensis* (Roux & Plaziat, 1978), B: *Democrinus londinensis* (Forbes, 1852) (A and B surrounded by red line), O: *Eocenocrinus hessi* n. gen., n. sp. (surrounded by green line). From northeastern Italy, Middle Lutetian—C, D and G: *Eocenocrinus bayani* n. gen., n. sp. (surrounded by blue line), C: Val di Ciuppio, D: d'Orbigny's collection, G: Val della Gichelina. Asterisk: anchylosed articulation (color figure online)

Included species Eocenocrinus hessi n. gen. n. sp., *E. bayani* n. gen. n. sp., *E. didymus* (Schauroth, 1855).

Remarks In extant crinoids with a xenomorphic stalk, rigidity or low flexibility of the distal stalk is associated with attachment to a hard substrate. Frequent cryptosynarthries, sometimes with several successive anchylosed articulations, are especially known in the genus *Porphyrocrinus* (Phrynocrinidae). In this genus, the outer ring of a

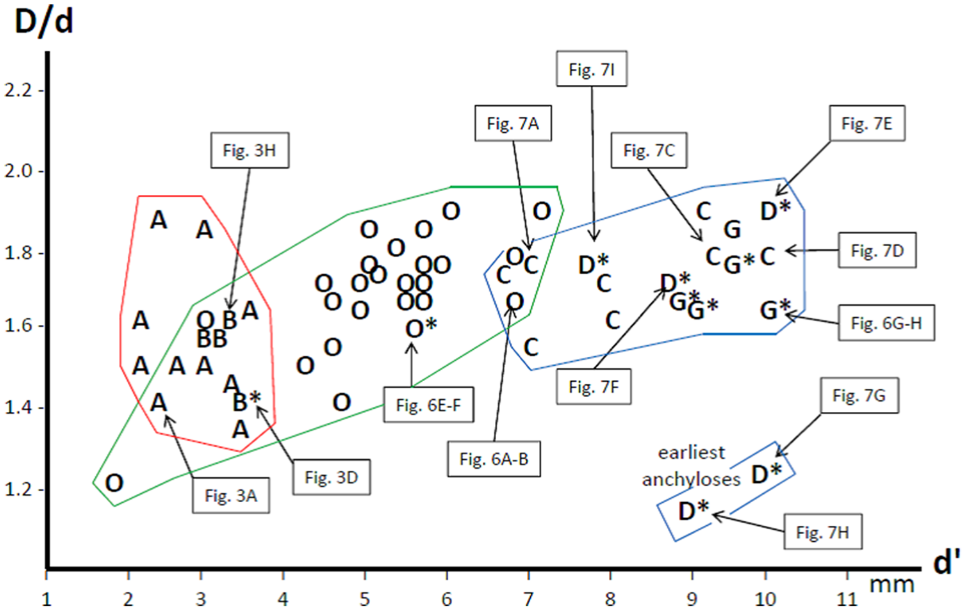

Fig. 9 Biometrical graph of columnals from Tuilerie de Gan (Late Ypresian) and northeastern Italy (Middle Lutetian) with D/d plotted against d' (growth index). See Fig. 8 for caption

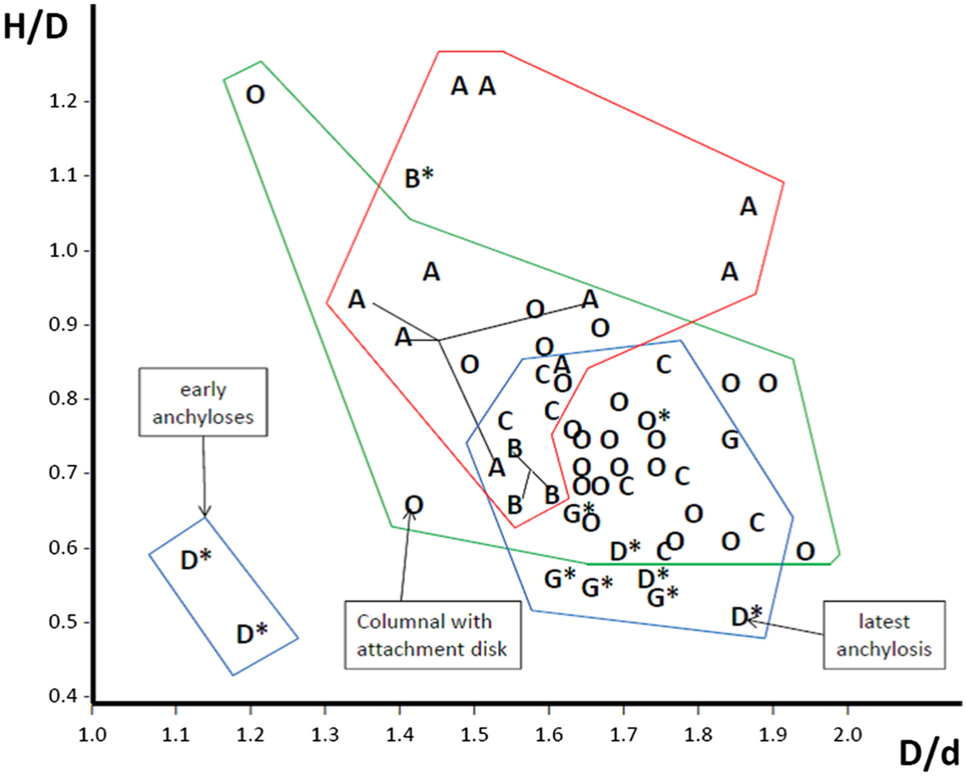

Fig. 10 Biometrical graph of columnals from Tuilerie de Gan (Late Ypresian) and northeastern Italy (Middle Lutetian) with H/D plotted against D/d. See Fig. 8 for caption. Columnals A and B displaced from distal stalk segments of Fig. 4 are joined by thin lines

cryptosynarthrial facet is a secondary syzygy with a conspicuous crenularium (A.M. Clark 1973; Roux 1977a; Messing 2016). Moreover, phrynocrinid stalk synarthries have the fulcral ridge completely surrounded by a deep ligamentary area, which is a highly derived character (Donovan and Pawson 1994; Messing 2016). *Eocenocrinus* differs in combining several plesiomorphies in its mesistele: a flat synarthrial facet, fulcral ridge with rudimentary crenularium, and deep areola restricted to an 8-shaped ligament pit. It could represent the Eocene ancestor of extant Phrynocrinidae, preceding development of derived characters in the stalk such as large deep synarthrial ligament fossae, which first appear in the Late Eocene species *E. didymus*. The single previously known fossil phrynocrinid, *Porphyrocrinus fossilis* Roux and Montenat, 1977, from Late Miocene of Spain, bears distal columnals with the ligament depression as deep and as large as in extant representatives of the genus.

Occurrence Late Ypresian (SW France), Middle Lutetian to Priabonian (northeastern Italy).

Eocenocrinus hessi n. gen., n. sp.

Figures 6a–f, 8, 9, 10

Etymology Dedicated to Hans Hess who published numerous fine and significant studies on post-Paleozoic crinoids.

Type material Syntype A (MNHN.F.A69341, Fig. 6a–d), 1 isolated columnal; syntype B (MNHN.F.A69342, Figs. 6e–f, 11e–f), 1 isolated columnal; syntypes C (MNHN.F.A69343, not figured), 29 columnals, all from beds 2 and 4 of Tuilerie de Gan.

Diagnosis As in description

Description Each columnal with fulcral ridges at opposite ends oriented 90° from each other, no conspicuous root socket (Fig. 6a). Small spines or rudimentary root sockets prolonging the greatest facet diameter. A single columnal, unfortunately poorly preserved, with distal half resembling an attachment disk, including a conspicuous root socket. Maximum size: *H* 5.75 mm, *D* 9.5 mm, *d* 5.1 mm; *d′* 7.25 mm. Usually *H*/*D* 0.60–0.91 and *D*/*d* 1.50–1.92. Smallest columnal (proximal mesistele): *H* 2.6 mm, *D* 2.1 mm, *d* 1.7 mm, *d′* 1.85 mm, *H*/*D* 1.24, *D*/*d* 1.21. Figures 8 and 9 document change in columnal shape (decrease in *H*/*D* and increase in *D*/*d*) related to size and growth from proximal to distal stalk, with the smallest, most proximal at left in both figures. Articular facet

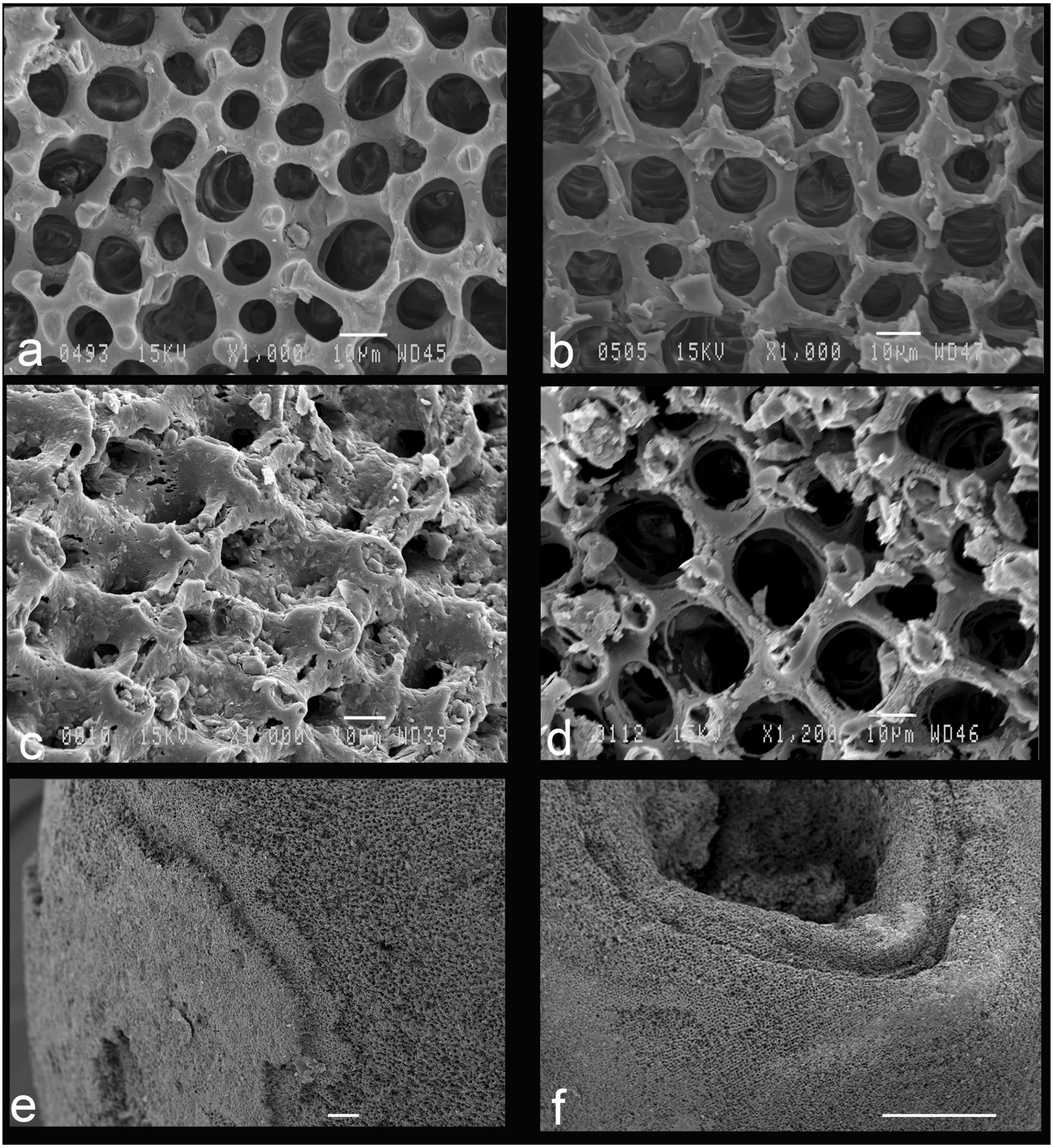

Fig. 11 Stereom biocorrosion in columnals from Tuilerie de Gan bed 6 (Late Ypresian). **a** *Eocenocrinus hessi* n. gen., n. sp. (syntype A, MNHN.F.A69341, same specimen as in the Fig. 6a, b), stereom without biocorrosion, facet surface of columnals articulated when collected, washed under ultrasound; **b** *Democrinus londinensis* (Forbes, 1852) (specimen B, MNHN.F.A69337, same specimen as in Fig. 3d–g) isolated columnal, galleried stereom in ligament area, thin biocorroded layer removed by washing under ultrasound (arrows: broken or altered stereom indicating lower boundary of biocorrosion, stereom preserved as in A below this surface); **c** *Paraconocrinus romanensis* (Roux and Plaziat 1978) (specimen E, MNHN.F.A69334, same specimen as in Fig. 5a), biocorroded stereom partly coated by micrite, external columnal surface in contact with clay, soft washing without ultrasound; d: *Paraconocrinus romanensis* (specimen B, MNHN.F.A69328, same specimen as in Fig. 3a, b) close up on biocorroded stereom (arrow: window showing hollow framework); **e**, **f** *Eocenocrinus hessi* (syntype B, MNHN.F.A69342, same specimen as in Fig. 6e, f), highly biocorroded columnal (same ossicule in Fig. 6e, f); **e** flaky appearance of eroded external surface; **f** external surface with all angles smoothed. Scale bars: **a**–**d** = 10 µm, **e**, **f** = 1 mm

relatively flat (Fig. 6b, c) with eight-shaped ligament fossae width usually $< 1/2$ *d*, sometimes as little as 1/3 *d*. Hollow fulcral ridge axis bordered on each side by rudimentary small crenulae (Fig. 6d). A single columnal without spine or root socket (probably from distal mesistele) and with both facets exhibiting the ankylosed articulation characteristic of late ontogeny (Fig. 6e, f): flat outer ring surrounding the previous functional synarthry with partly altered or resorbed stereom at center.

Remarks The characters visible in the well-preserved synarthries of *E. hessi* n. gen, n. sp. were previously unknown in either fossil or extant xenomorphic stalks. The columnal with its two facets indicating anchylosed articulations documents a series of three successive columnals fused during late ontogeny within the distal mesistele. Such relatively flat synarthries suggest low flexibility in the distal stalk (at least in distal mesistele). However, a differentiated dististele could be formed by a few distal-most columnals, which were absent in our material from Gan (see Discussion below). Rudimentary root sockets or small spiny expansions cannot contribute to permanent stalk attachment to the substrate. The single columnal, presumably from a distal-most stalk, displays both an attachment disk and a conspicuous socket, possibly corresponding to encrusting roots.

Occurrence Late Ypresian of Tuilerie de Gan (SW France)

Eocenocrinus bayani n. gen., n. sp.

Figures 6g, h, 7, 8, 9, 10

Etymology Dedicated to Ferdinand Bayan (1845–1874) who first mentioned this "grand *Bourgueticrinus*" in his description of the Eocene section in Val della Guichelina.

Synonymy Bourgueticrinus sp. Bayan, 1870: 459 and 461; *Conocrinus didymus* Pasotti, 1929, pl. 1, figs. 4, 18 and 21.

Type material Syntype A (MNHN.F.A69344, collection d'Orbigny no. 9017, Fig. 7e), one large columnal from Vicentin; syntypes B (MNHN.F.A69345, MNHN collection d'Orbigny no. 9017 not figured), four isolated columnals from Val della Gichelina; syntypes C (MNHN.F.A69346, Fig. 6g, h), one columnal from Val della Gichelina near Malo, NE Italy; syntype D (MNHN.F.A69347, Fig. 7f–i), four columnals from the same location; syntype E (MNHN.F.A69348, not figured), one columnal from the same location; syntype F (MNHN.F.A69349, Fig. 7a–c), three connected columnal pairs from Val di Ciuppio; syntype G (MNHN.F.A69350, Fig. 7d), one isolated columnals from the same location; syntype H (MNHN.F.A69351, not figured), seven isolated columnals from the same location. All from northeastern Italy.

Diagnosis As in description.

Description Large columnals without root sockets, most with articular facets poorly preserved. Distal mesistele columnals from Ciuppio with moderate inflation at mid-height: *H* 6.5–8.4 mm, *D* 8.4–12.0 mm, *d* 5.2–6.7 mm, *d′* 6.9–10.05 mm, *H*/*D* 0.63–0.86, *D*/*d* 1.61–1.89. Main characters of articular facets as in *E. hessi*. Most other dististele columnals strongly inflated and joined by cryptosynarthries: *H* 5.45–8.6 mm, *D* 10.1–12.6 mm, *d* 5.8–7.8 mm, *d′* 7.75–10.0 mm, *H*/*D* 0.49–0.75, *D*/*d* 1.13–1.87. Several cryptosynarthries are anchylosed articulations characterized by an interior, early ontogenetic stage synarthry with conspicuous 8-shaped ligament pit ("*Conocrinus* stage" sensu Roux 1977) surrounded by a flat outer ring (Figs. 6g, h, 7e, g, h).

Remarks Columnal biometry shows the same ontogenetic trends in *E. hessi* and in *E. bayani*, the later having larger distal columnals with frequent cryptosynarthries (Figs. 8, 9). The graph of *H*/*D* versus *D*/*d* (Fig. 10) illustrates the main variations in columnal shape independent of growth. The substantial overlap in values, confirms that the two species are closely related. Of the three columnals figured by Pasotti (1929: pl. 1) and attributed to *Conocrinus didymus* (Schauroth, 1855), two from San Giovanni Ilarione are articulated (Pasotti 1929: pl. 1, fig. 4) and strongly resemble MNHN columnals from Ciuppio. In the third columnal from Val della Gichelina, one facet is a functional synarthry with a markedly depressed areola (Pasotti 1929: pl. 1, fig. 18), and the other is an early anchylosed articulation (Pasotti 1929: pl. 1, fig. 21). Undoubtedly, these three columnals belong to *E. bayani* n. sp. Columnals belonging to different stalk segments were found in different localities: from dististeles at Val della Gichelina and from mesisteles at Val di Ciuppio and San Giovanni Ilarione.

Occurrence Middle Lutetian of northeastern Italy (Val di Ciuppio, Croce grande, Val della Gichelina, San Giovanni Ilarione, Pozza).

Eocenocrinus didymus (Schauroth, 1855)

Synonymy ?Bourgueticrinus ellipticus Schauroth, 1855: 546–547, pl. 3 fig. 10; Schauroth, 1865: 188, pl. 8 fig. 4; *?Bourgueticrinus didymus* Schauroth, 1855: 547; *Bourgueticrinus ?didymus* Oppenheim, 1900–1901; 97–98, pl. 18 fig. 4.

Remarks Schauroth (1855, 1865) figured two columnals from the Late Eocene of Priabona with a maximum diameter of 11 mm, no inflation at mid-height, H/D of about 0.5, well developed fulcral ridges, and the whole ligament area markedly depressed. They strongly resemble proximal mesistele columnals of the large extant species

Phrynocrinus nudus or *Porphyrocrinus thalassae*. Oppenheim (1900–1901) figured another columnal from the Late Eocene of Costalunga near Possagno resembling Ciuppio columnals but displaying a more conspicuous fulcral ridge, 8-shaped ligamentary pit small or lacking, and no inflation at mid-height. Schauroth's columnals could belong to the flexible proximal mesistele and Oppenheim's columnal to the more rigid distal mesistele of the same species. However, it cannot be excluded that they belong to two distinct species. Additional material is required for a robust diagnosis of *E. didymus* and to clarify its relationships with the other species of the genus *Eocenocrinus*. *E. bayani* n. gen., n. sp. differs in having columnals more inflated, $H/D > 0.6$, and articular facets usually with 8-shaped ligament fossae. The presence of stalk synarthries with the whole areola completely depressed places *E. didymus* closer to extant phrynocrinids than to *E. hessi* n. sp. However, in *E. didymus*, this character could represent an adaptation to deeper environment.

Occurrence Late Eocene (Priabonian) of northeastern Italy.

Exceptional preservation of stereom and biocorrosion

As in other echinoderms, the crinoid skeleton is a low density Mg calcite network (stereom) with meshes of various sizes and arrangements, each ossicle having the optical characters of a calcite mono-crystal (Macurda et al. 1978). Usually, during early diagenesis, each ossicle recrystallizes into dense syntaxical calcite or is altered by pyrite (Gaspard and Roux 1974; Szczepanik and Sawlowicz 2005). In contrast, in the Gan clay, the original stereom is perfectly preserved (Fig. 11a) and can be observed as in extant specimens, especially the galleried stereom which characterized the ligament areas (Fig. 11b). As clay adhered to the external ossicle surface, biocorrosion developed and fragmented the calcite network into small particles (micrite). Microborings (Fig. 11c, d) are identical to those described on extant ossicles buried in bathyal sediment, which have mainly been attributed to fungal or bacterial activity (Améziane-Cominardi and Roux 1987). The thickness of the biocorroded layer is usually 40–60 µm, except in a single distal columnal of *Eocenocrinus hessi* n. gen., n. sp. (Fig. 6e, f), in which micro-borers penetrated more deeply (> 100 µm) into the ossicle and developed a fragile flaky altered layer (Fig. 11e, f). Therefore, such fragile ossicles are easily rounded off after reworking, washing or mechanical erosion. When two columnals remained tightly connected as in bed 6 or with anchylosed articulation, sediment did not penetrate the inter-articular space, and the facet stereom appears perfectly preserved without biocorrosion (Fig. 6d–i).

Such quality of fossilization was previously only known in some columnals of *Democrinus londinensis* and *Isselicrinus subbasaltiformis* from the London Clay (Roux 1978b, pl. 2, figs. 6–10, and 1977b, fig. 3C, respectively). However, stereom micro-biocorrosion similar to that at Gan was not observed in London Clay, in which thin-grained or framboid pyrite is frequent (M.R., unpublished SEM observations).

Taphonomy and paleoecology

In spite of biocorrosion that made their stereom fragile, most of the isolated columnals from Gan have their articular facets well-preserved, which suggest rapid burial that restricted biocorrosion to a thin layer, followed by no reworking. The exception of the distal columnal of *Eocenocrinus hessi* n. sp. (Figs. 6e, f, 11e, f) indicates that this ossicle was exposed for a longer time to biocorrosion before rapid burial into clay. In this case, articular facet surfaces were partly altered, especially in the central ligament area (Fig. 6e, f).

In the base of bed 6,ististeles and roots with articulated ossicles (Fig. 4) imply that the distal-most stalk and roots of *Paraconocrinus romanensis* and *Democrinus londinensis* were buried within the muddy sediment as in some extant *Democrinus* (Fig. 12b). Such preservation also implies a low rate of bioturbation, which limited dissociation of distal stalks to a few segments of roots and rare isolated columnals. Partly slipped, tilted or slightly dislocated columnals (Fig. 4) can be attributed to compaction of water-rich sediment through geological time. The absence of mesistele ossicles suggests post-mortem displacement above the sediment surface due to sea floor currents, which did not affect the buried distal stalk. In contrast, all columnals are isolated in beds 2–4, and most columnals of *Eocenocrinus hessi* n. sp. belong to mesistele. The exceptions are two distal columnals, which are either poorly preserved and probably reworked (columnal showing both root socket and presumed attachment disk) or were highly biocorroded before burial (Figs. 6e, f, 11e, f). In northern Italy, mesistele and dististele columnals of *Eocenocrinus bayani* n.sp. seem also to occur in different localities (see above). Mesistele columnals exhibit substantially better preservation, frequently with several articulated ossicles, than dististele columnals, which were always isolated and usually highly corroded.

The base of clayed bed 6 overlaps indurated, ferruginous, sandy clay (bed 5) which likely corresponds to a

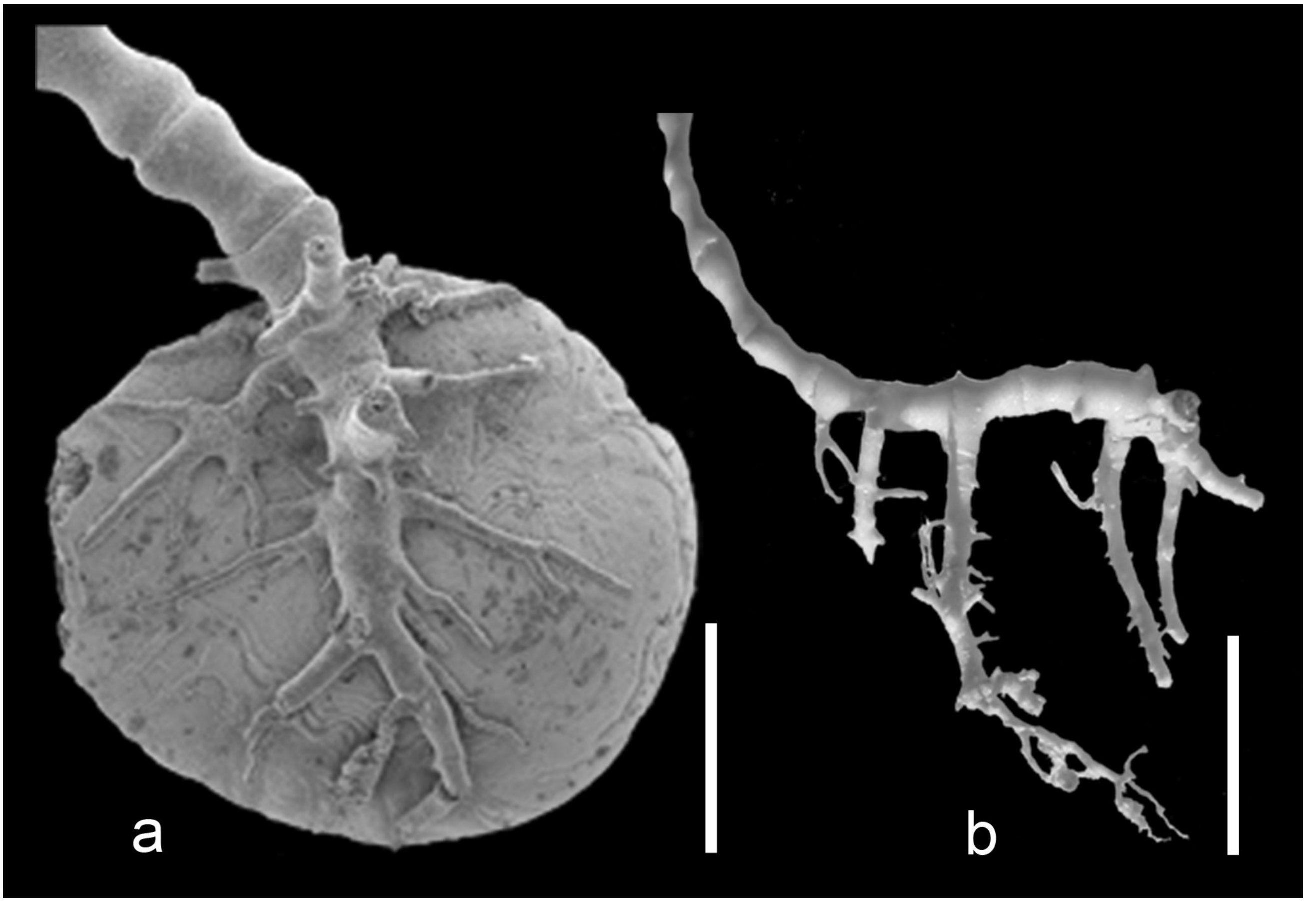

Fig. 12 Contrasting modes of attachment of distal stalk in an extant population of *Democrinus* sp. at a depth of 450–500 m off Madeira (MNHN-IE-2016-562). **a** Juvenile attached to a shell fragment, **b** distal stalk with roots penetrating muddy sediment (distal roots broken). Scale bar: **a** 1 mm, **b** 5 mm

substantial decrease of sedimentation rate that allowed a diverse macrobenthos dominated by suspension feeders to develop (Merle 1985, 1986). Extant stalked crinoids frequently settle in environments with gentle water flow and hard substrates partly covered by sediment (Tunnicliffe et al. 2016). Young bourgueticrinids are usually attached to shell fragments, pebbles or rock slabs by a small encrusting disk such as those observed in bed 6 (Fig. 5i). Jagt et al. (2012) described such small bougueticrinid holdfasts fixed on Late Cretaceous sea urchin skeletons. Larger specimens develop branching roots from distal columnals either encrusting hard substrate (Fig. 12a) or penetrating sediments (Fig. 12b).

All these facts drive interpreting Gan crinoid fauna as inhabiting a paleoenvironment with moderate water flow, in which, despite a primarily muddy sea floor, surrounding hard substrates could be present, especially where *Eocenocrinus* occurs in the lower part of the section (bed 2–4). These hard grounds likely correspond to surfaces swept by water flow rather than bed rock basement. *Paraconocrinus* and *Democrinus* from bed 6 are undoubtedly autochthonous. In the lower part of the section, *Paraconocrinus* columnals are likely subautochthonous, but *Eocenocrinus* columnals are allochthonous, displaced from hard substrates. All dissociated columnals, including the allochthonous mesistele columnals of *Eocenocrinus* species, were rapidly buried and only briefly exposed to biocorrosion. Only their distal-most stalk columnals were exposed to biocorrosion for a longer time with a greater risk that they were partly or completely destroyed by transformation into micrite.

Paleobathymetry

Roux (1987) suggested that the absence of extant stalked crinoids at depths > 100 m is due to their crown posture that implies morphofunctional constraints incompatible with wave turbulence. He reconsidered the traditional paradigm in which stalked crinoids inhabited shallow water environments in the past and were restricted to greater depths mainly as a result of the predatory pressure of bony fish radiation (Meyer and Macurda 1977). Therefore, some extant stalked crinoid characters related to depth may be used to estimate paleodepth of epibathyal environments (see for example Bourseau et al. 1988). The frequent convergence of adaptive characters in distant taxa was confirmed by molecular phylogeny (Roux et al. 2013). During Eocene, in the north Pyrenean foreland basin, both stalked crinoid characters, benthic foraminifera and additional fossil benthic organisms, coupled with sedimentology, revealed a bathymetric zonation in the genus *Isselicrinus* similar to those in extant isocrinids (Roux et al. 2006).

For extant crinoids with a xenomorphic stalk, such as bourgueticrinids, the main columnal character used as a depth index is large and deep ligament depression in synarthries, which restricts the calcite volume allocated to skeleton as the food supply decreases with depth (Roux 1987). This character first appears at a depth of about 200 m, corresponding to the shallowest depth known for the extant species of *Porphyrocrinus* (see Messing 2007). It becomes more frequent at depths > 400 m (Tunnicliffe et al. 2016). Using this criterion, the presence of *Democrinus londinensis* at base of bed 6 documents a paleodepth of at least 200 m. In the London Clay, based on results from *Nautilus* shell studies of Hewitt (1988, 1989), the beds containing *D. londinensis* correspond to depths between 150 and at least 300 m. Such values agree with paleodepth estimations from benthic foraminifera and mollusk associations found at Gan (Steurbaut and Sztrákos 2002; Merle 1985, 1986; Dolin and Ledon 2002; Lozouet 2004). Moreover, the diversity at Gan contrasts with the monospecific fauna of stalked crinoids found in the Lower Ypresian of the eastern part of the Pyrenean foreland basin (Corbières gulf). In Corbières Ilerdian marls, relatively abundant isolated aboral cups and columnals of *Pseudoconocrinus doncieuxi* (Roux, 1978c) and their highly variable morphology (Roux 1978b, c) suggest an opportunistic species living just below the threshold above which stalked crinoids cannot tolerate wave turbulences (see Bourseau et al. 1988) at a depth of about 100 m (Roux and Plaziat 1978). That suggests a deeper environment at Gan than in the Corbières gulf. The increasing depth of the environment to bed 6 at Tuilerie of Gan suggested by Merle (1985, 1986) using mollusk associations is confirmed by depth estimations using crinoids: *E. hessi* living at depth of about 150 m, *D. londinensis* in 200–300 m, and more eurybathic *P. romanensis* in 150–300 m. Within the sedimentary sequence, the lower part of bed 6 overlapping the indurated bed 5 could correspond to the maximum flooding.

In northeastern Italy, *E. bayani* was found in Val della Gichelina within (or associated with) a bioclastic facies of large benthic foraminifers as in the sample from d'Orbigny's collection (Fig. 7e), in which *Alveolina* and *Nummulites* were frequently broken or corroded in contrast with the better preservation of *Assilina*, *Operculina* and *Discocyclina*, the latter usually interpreted as living on an outer platform. Giusberti et al. (2014) described such allochthonous carbonates interbedded within epibathyal sediments including lagerstätte of well-preserved mesopelagic ichthyofauna. Extant large crinoids with a xenomorphic stalk have been observed attached on steep slopes subject to occasional sediment slumping (Tunnicliffe et al. 2016, fig. 21a). Therefore, *E. bayani* and *E. hessi* likely lived at similar depths, but slopes bordering the Lessini carbonate shelf were steeper than at Gan. However, the substantially larger size of *E. bayani* with the more depressed areola on its distal columnals (Pasotti 1929, pl. 1, fig. 18) suggest a slightly deeper environment. Based on its columnals with the deep ligamentary depression extending across the whole facet, *E. didymus* seems to have occurred in the deepest habitat (circa 200 m?) among the known species of *Eocenocrinus* (see above the same criterium used comparing *P. romanensis* and *D. londinensis*). However, more well-preserved ossicles of *E. didymus* and additional studies on associated benthic fauna are needed to confirm such hypothesis and precise the paleodepth.

Conclusion

The crinoid fauna from Ypresian marls of Gan present both affinities with north European London Clay fauna via *Democrinus londinensis* and Tethyan (Alpine Sea) fauna of northern Italy via the new genus *Eocenocrinus*. *Paraconocrinus romanensis* was previously known from Spain (Roux and Plaziat 1978). Based on micropaleontological data and mollusk associations, crinoids document a depositional environment reaching depths of 150–300 m. The Lower Ypresian fauna of Corbières gulf with *Pseudoconocrinus doncieuxi* corresponds to a shallower environment at a depth of about 100 m (Roux and Plaziat 1978). In a deeper and more stable environment, the Gan fauna exhibits a higher taxonomic diversity, with three species belonging to three different genera and two families. Fossilization in clay without thin-grained or framboid pyrite allows exceptionally well-preserved ossicle stereom with microbiocorrosion similar to that observed on extant crinoid ossicles buried at bathyal depths (Améziane-Cominardi and Roux 1987). Dististeles of *P. romanensis* and *D. londinensis* had the same mode of anchorage with dendritic roots penetrating sediment, and are preserved in situ with articulated ossicles in the bed corresponding to maximum depth. However, the characters of synarthries articulating their distal columnals clearly differentiate the two species.

New genus *Eocenocrinus* is suspected to belong to family Phrynocrinidae, and *E. hessi* may be the oldest currently known representative. This species was probably attached to hard bottom. *E. bayani* of Middle Eocene age is undoubtedly closely related to *E. hessi*. *E. didymus* from Upper Eocene near Priabona differs in having stalk synarthries with a large and deep ligamentary depression as in extant phrynocrinids, but is only known from too few columnals. The attribution of *Eocenocrinus* to Phrynocrinidae must be confirmed by discovery of new material including crown ossicles.

Regarding the high quality of stereom preservation and theististeles fossilized with articulated ossicles, it is hoped that future investigations in Tuilerie de Gan will reveal more complete specimens (at least, isolated crown ossicles) of the three species, here described only from columnals. Such material will permit more detailed comparisons with their extant representatives and help fill the great gap in our current knowledge of crinoid evolution between Upper Cretaceous and Recent.

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