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A diverse crinoid fauna (Echinodermata, Crinoidea) from the Lower Eocene of the Gulf of Languedoc (Corbières, Aude, southern France)

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Abstract

Detailed studies of the middle Ilerdian (lower Ypresian) blue marls of the Gulf of Languedoc (Corbières, Aude, France), belonging to the north Pyrenean foreland basin, have revealed a more abundant and diverse crinoid fauna than previously documented from the Lower Eocene. Here we describe five species of stalked crinoids in the family Rhizocrinidae (*Cherbonniericrinus requiensis* **n. sp.**, *?Democrinus elongatus*, *Globulocrinus amphoraformis* **n. gen., n. sp.**, *Pseudoconocrinus doncieuxi* and *P. lavadensis* **n. sp.**), one barnacle-like species in the stalkless family Holopodidae (*Holopus plaziati* **n. sp.**) and a single feather star in the family Conometridae (*Amphorometra atacica*). Several sites have yielded brachials and rhizoids in addition to abundant aboral cups and columnals indicating *in situ* fossilisation of the dissociated skeletal elements. *P. lavadensis* **n. sp.** and *?D. elongatus* have been collected only from outcrops located in the upper part of the middle blue marls, while *P. doncieuxi* predominates, with a wide range of morphological variation, in the lower blue marls. The fossil assemblage at the locality of Réqui near Montlaur differs from the others in the smaller size of most individuals and the presence of *H. plaziati* **n. sp.**, *C. requiensis* **n. sp.**, *G. amphoraformis* **n. gen., n. sp.**, and *P. doncieuxi suboblongus* **n. subsp.** This particular association with high juvenile mortality corresponds to an unstable environment with mixed substrates (muddy and rocky). The crinoid fauna of the Corbières appears to be the most diverse of Early Eocene age known to date. With the fauna of the London Clay, a boreal formation of the same age, it shares the presence of the genera *Democrinus* and *Amphorometra* in an open-sea environment. A comparison with extant faunas allows the depth of deposition at the Ypresian sites in the Gulf of Languedoc to be estimated between from 100 and 140 meters.

Key words: Lower Ypresian, Corbières, Echinodermata, Crinoidea, Conometridae, Holopodidae, Rhizocrinidae, *Amphorometra*, *Cherbonniericrinus*, *Democrinus*, *Globulocrinus* **n. gen.**, *Holopus*, *Pseudoconocrinus*, new taxa.

Running title: Early Eocene crinoids from southern France.

Résumé

Une recherche approfondie dans les marnes bleues de l'Ilerdien moyen (Yprésien inférieur) du Golfe du Languedoc (Corbières, Aude, France) appartenant au bassin d'avant-pays pyrénéen a révélé une faune de crinoïdes plus abondante et diversifiée que celle précédemment connue dans l'Eocène inférieur. Nous décrivons cinq espèces de crinoïdes pédonculés appartenant à la famille des Rhizocrinidae (*Cherbonniericrinus requiensis* **n. sp.**, *?Democrinus elongatus*, *Globulocrinus amphoraformis* **n. gen., n. sp.**, *Pseudoconocrinus doncieuxi*, *P. lavadensis* **n. sp.**), une espèce sans pédoncule de la famille des Holopodidae (*Holopus plaziati* **n. sp.**) et une espèce de comatule de la famille des Conometridae (*Amphorometraatacica*). Plusieurs gisements ont fourni, en plus d'abondantes coupes aborales et columnales, des brachiales et des rhizoïdes indiquant une fossilisation *in situ* des éléments dissociés du squelette. *P. lavadensis* **n. sp.** et *?D. elongatus* n'ont été récoltés que dans les gisements situés dans la partie supérieure des marnes bleues moyenne, tandis que *P. doncieuxi* prédomine avec une grande variation morphologique dans les marnes bleues inférieures. L'assemblage fossile du gisement de Réqui près de Montlaur diffère des autres par des individus généralement de plus petite taille, la présence d'*H. plaziati* **n. sp.**, *C. requiensis* **n. sp.**, *G.*

amphoraformis n. gen., n. sp., et *P. doncieuxi suboblongus* n. subsp. Cette association particulière avec une mortalité juvénile fréquente correspond à un environnement instable avec des fonds mixtes (vaseux et rocheux). La faune crinoïdique des Corbières s'avère être la plus diversifiée connue dans l'Eocène inférieur. Avec les gisements boréaux du même âge de l'Argile de Londres, elle partage la présence des genres *Democrinus* et *Amphorometra* dans un environnement de mer ouverte. Une comparaison avec les faunes actuelles permet d'estimer la profondeur des sites yprésiens du Golfe du Languedoc entre 100 et 140 mètres.

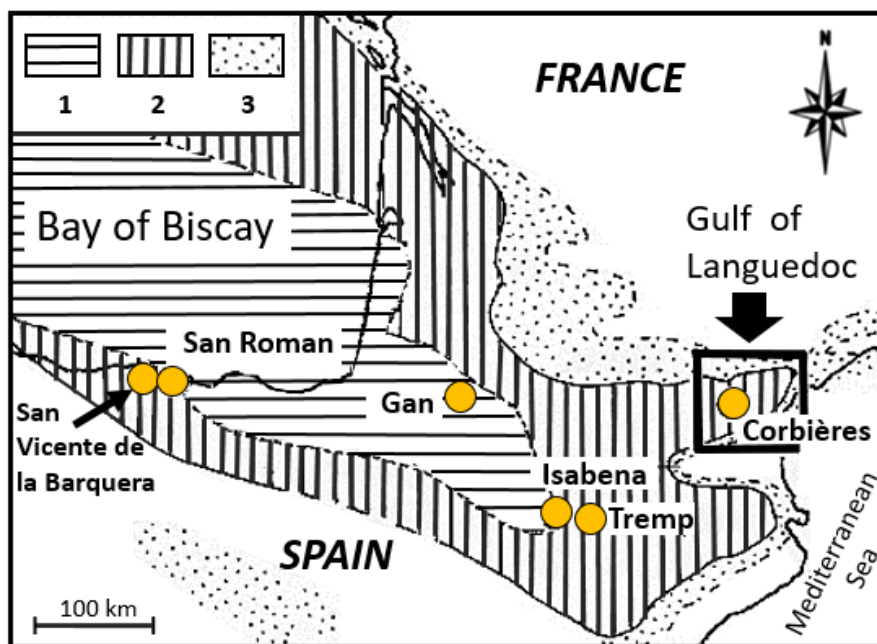


FIGURE 1. Palaeogeography during the maximum marine transgression in the early Ypresian (Ilerdian) across the Pyrenean domain (modified after Roux & Plaziat 1978). Legend: 1 - bathyal marls (depths >150 m); 2 - neritic limestones and marls (depths <150 m); 3 - continental detrital facies. Orange dots indicate localities with crinoid-bearing Ypresian strata.

Introduction

In France, Eocene stalked crinoids are known only in two marine basins in the south (Roux and Plaziat 1978). One of these, the southwestern basin, is related to the history of the Pyrenees and the Bay of Biscay, the other corresponding to the last marine transgressive episode of the Alpine sea, the Nummulitic southeastern basin. Marine deposits along the northern Pyrenean foreland reach their maximum easterly extension in the Corbières during the early Ypresian (= Ilerdian) (Fig. 1) (Plaziat 1984b). Doncieux (1911) identified two species of stalked crinoids that he attributed to the genus *Conocrinus*, i.e., *C. pyriformis* von Münster in Goldfuss, 1826 and *C. thorenti* d'Archiac, and described a single, new species of feather star as *Antedon atacicus*. Only a single centrodorsal of the latter species has ever been illustrated. A study of numerous aboral cups of *Conocrinus*, collected mostly near Fontcouverte (Aude) and of a wide morphological range of variation, seemed to indicate that they belonged to a single opportunistic species, *C. doncieuxi* Roux, 1978a, which was distinct

from both *C. pyriformis* and *C. thorenti*. Following a recent revision of the genus *Conocrinus* (Roux *et al.* 2019), this species is now attributed to the genus *Pseudoconocrinus*, which first appeared during the Danian. New field work conducted by two of us (A.M., D.V.) in the Ilerdian blue marls of the Corbières and particularly in the vicinity of Fontcouverte and Montlaur has yielded a much more diverse crinoid fauna which includes several new species and a new genus in the family Rhizocrinidae and in the stalkless genus *Holopus* (Holopodidae). These taxa are here named and palaeoecological and palaeogeographical implications are discussed.

Material and methods

Genus, species, subspecies	Catalogue number	Locality	Ossicle(s)	Figures	Remarks
<i>Pseudoconocrinus doncieuxi</i>	UCBL-FSL 170248a	Fontcouverte 1	20 AC, 20 C	Roux 1978a	Type series
<i>Pseudoconocrinus doncieuxi</i>	MNHN.F.A69944a	Fontcouverte 2	1 AC	Fig. 6A-C	Coll. Bories
<i>Pseudoconocrinus doncieuxi</i>	MNHN.F.A81993	Fontcouverte 2	1 AC	Fig. 6D-F	Coll. Bories
<i>Pseudoconocrinus doncieuxi</i>	MNHN.F.A69944b	Fontcouverte 2	1 AC	Fig. 6I	Coll. Bories
<i>Pseudoconocrinus doncieuxi</i>	MNHN.F.A81994	Fontcouverte 2	4 Brax	Fig. 6M-T	Coll. Martinez
<i>Pseudoconocrinus doncieuxi</i>	MNHN.F.A81995	Fontcouverte 2	12 IIBr	Fig. 7A-R	Coll. Martinez
<i>Pseudoconocrinus doncieuxi</i>	MNHN.F.A69946	Fontcouverte 2	4 C	Fig. 8O-Q	Coll. Plaziat
<i>Pseudoconocrinus doncieuxi</i>	MNHN.F.A81996	Fontcouverte 3	1 AC	Fig. 6G-H	Coll. Plaziat
<i>Pseudoconocrinus doncieuxi</i>	MNHN.F.A81997	Ribaute	1 IBrax	Fig. 6J-L	Coll. Martinez
<i>P. doncieuxi suboblongus</i>	MNHN.F.A81998	Fontcouverte 3	1 AC	Fig. 8A-C	Holotype
<i>P. doncieuxi suboblongus</i>	MNHN.F.A81999	Lavade	1 AC	Fig. 8D-E	Paratype
<i>P. doncieuxi suboblongus</i>	MNHN.F.A82000	Réqui	1 AC	Fig. 8F	Paratype
<i>Pseudoconocrinus lavadensis</i>	MNHN.F.A82001	Lavade	1 AC	Fig. 10A-B	Holotype
<i>Pseudoconocrinus lavadensis</i>	MNHN.F.A82002	Lavade	6 AC	Fig. 10C-L	Paratypes
<i>Pseudoconocrinus lavadensis</i>	MNHN.F.A82003	Lavade	8 AC	Not figured	Paratypes
<i>Pseudoconocrinus lavadensis</i>	MNHN.F.A82004	Lavade	2 IBrax	Fig. 11A-C	Paratypes
<i>Pseudoconocrinus lavadensis</i>	MNHN.F.A82005	Lavade	4 IBrax, IBr1	Not figured	Paratypes
<i>Pseudoconocrinus lavadensis</i>	MNHN.F.A82006	Lavade	4 Cprox	Fig. 11D-G	Paratypes
<i>Pseudoconocrinus lavadensis</i>	MNHN.F.A82007	Lavade	31 Cprox	Not figured	Paratypes
<i>Pseudoconocrinus lavadensis</i>	MNHN.F.A82008	Lavade	3 C, 3 Rh.	Fig. 11H-O	Paratypes
<i>Pseudoconocrinus lavadensis</i>	MNHN.F.A82009	Lavade	37 C, 7 Rh.	Not figured	Paratypes
? <i>Democrinus elongatus</i>	MNHN.F.A82010	Lavade	1 AC	Fig. 8G-I	Coll. Martinez
<i>Globulocrinus amphoraformis</i>	MNHN.F.A82011	Réqui	1 AC	Fig. 14G	Holotype
<i>Globulocrinus amphoraformis</i>	MNHN.F.A82012	Réqui	9 AC	Fig. 14A-F, H-L	Paratypes
<i>Cherbonnierocrinus requiensis</i>	MNHN.F.A82013	Réqui	1 AC	Fig. 16E-G	Holotype
<i>Cherbonnierocrinus requiensis</i>	MNHN.F.A82014	Réqui	3 AC	Fig. 16A-D	Paratypes
<i>Cherbonnierocrinus requiensis</i>	MNHN.F.A82015	Réqui	1 AC	Not figured	Paratype
<i>C. cherbonnieri</i>	MNHN.IE.2016.748	G. de Gascogne	1 AC	Fig. 16H	Recent
<i>Holopus plaziati</i>	MNHN.F.A82016	Réqui	7 IBrax, 1IIBr	Fig. 17	Syntypes
<i>Amphorometra atacica</i>	UPS BO-347	Fontcouverte 1	1 Cd	Doncieux 1911	Holotype
<i>Amphorometra atacica</i>	MNHN.F.A82017	Le Coucou	2 Cd	Fig. 18A-F	Coll. Martinez
<i>Amphorometra atacica</i>	MNHN.F.A82018	Lavade	1 Cd, 5 Br	Fig. 18G-Q	Coll. Martinez

TABLE 1. Specimens of the type series of species described herein and other specimens illustrated. Fontcouverte 1: site of Les Lanes Sud; Fontcouverte 2: site of ancient Tuilerie (Mourrel de la Borio); site of Fontcouverte 3: site of L'Estagnol. AC: aboral cup; Br: non-axillary brachial; IBr: primibrachial; IIBr: secundibrachial; Brax: axillary brachial; IBrax: axillary IBr; Co: isolated columnals or pluricolumnals (mesistele and dististele); Cd: centrodorsal; Cprox: proxistele columnals; Rh: rhizoid fragment.

The material studied was collected by two of us (A.M., D.V.) and previously by Jean-Claude Plaziat. Part of the Doncieux Collection, including the type series of *Pseudoconocrinus doncieuxi* from southwest of the village of Fontcouverte, is housed in the palaeontological collections of the University Claude Bernard in Lyon (abbreviation: UCBL-FSL). The holotype (a centrodorsal) of *Antedon atacicus* Doncieux, 1911 (= *Amphorometra atacica*, as here interpreted), from southwest of the same village, belongs to the Bories Collection and is housed in the palaeontological holdings of the University Paul Sabatier in Toulouse (abbreviation: UPS). The type series of the new taxa described and specimens illustrated herein are deposited in the palaeontological collections of the Muséum national d'Histoire naturelle (abbreviation: MNHN) in Paris. All catalogue numbers are listed in Table 1. Other specimens examined for the present paper are part of the private collections of two of us (A.M. and D.V.).

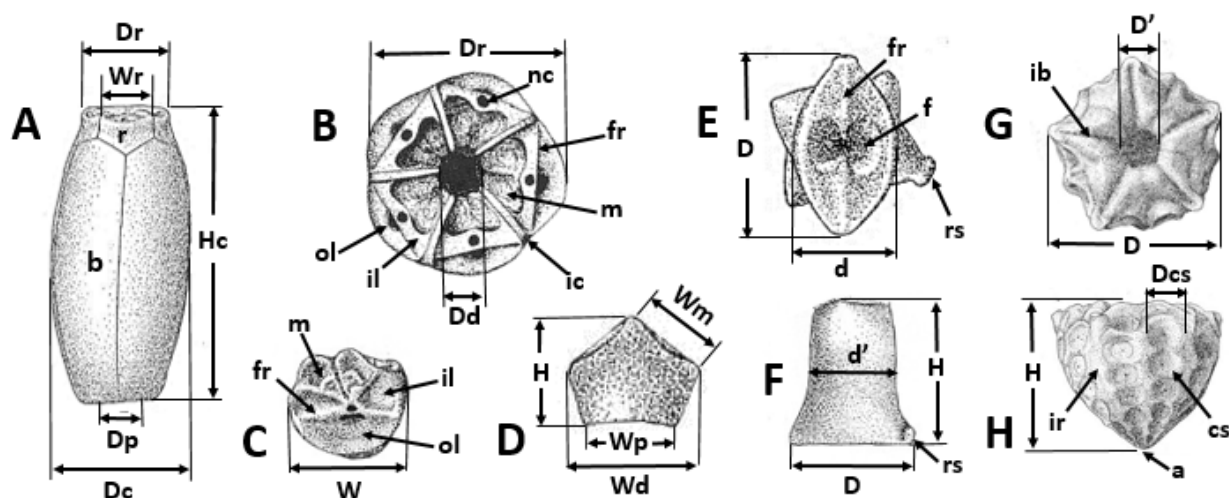


FIGURE 2. Characters and main parameters of aboral cups, brachials and columnals in Rhizocrinidae and the centrodorsal of *Amphorometra*. A-B: aboral cup, A: lateral view (b: basal, r: radial, Dc: maximum diameter, Dp: diameter of stalk insertion = proximalmost stalk diameter, Dr: diameter of distal radial circling, Hc: height), B: distal face of radial circling [Dc: maximum diameter, Dd: diameter of central cavity, fr: fulcral ridge, ic: interradial crest, il: inner (adoral) ligament, m: muscular insertion, nc: neural canal, ol: outer (aboral) ligament, Wr: width of radial]; C: muscular synarthrial facet of non-axillary brachial (W: maximum width parallel to fulcral ridge, other abbreviations as in B); D: external face of axillary brachial (H: height, Wd: distal width, Wm: width of articulation with IIBr1, Wp: proximal width); E-F: distal columnal (f: 8-shaped ligament fossa, fr: fulcral ridge, D: largest facet diameter, d: smallest facet diameter, d': mid-height diameter, H: height, rs: rhizoid socket), E: view from articular facet, F: lateral view; G-H: *Amphorometra* centrodorsal (a: aboral apex, cs: cirrus socket, D: maximum diameter, D': diameter of central cavity, Dcs: diameter of largest cirrus socket, ib: insertion of basal, ir: interradial ridge), G: adoral view, H: lateral view.

In addition to surface-collected specimens at each outcrop, 10 to 20 kg of sediment were screen washed and in sifted to determine the abundance and relative proportions of the different types of ossicles. All samples were cleaned using ultrasounds. Scanning electron microscope (SEM) observations were carried out using a JEOL-840A type microscope at 12-15 kV (Plateau Technique de Microscopie Électronique et de Microanalyses du Muséum national d'Histoire naturelle, Paris) after coating with a colloidal gold or platinum solution. Often partially or totally pyritised and subsequently oxidised by atmospheric alteration, the quality of preservation of echinoderm ossicles is variable. However, the microstructure of some ossicles is preserved (Szczepanik and Sawlowicz 2005; Merle and Roux 2018), and details of articulation facets can be described as if these were Recent specimens.

For morphological terms, reference is made to recent syntheses on extant and fossil crinoids, such as Roux *et al.* (2002, 2019) and Hess and Messing (2011). Figure 2 shows the main qualitative and quantitative characters examined, as well as the main abbreviations used in the text. Other abbreviations are explained in captions of illustrations. In view of the fact that new species are described exclusively on the basis of dissociated ossicles of different individuals, only well-preserved aboral cups can serve as holotypes. In the absence of aboral cups, those ossicles (brachials, columnals, rhizoids) on which the description is based and which are figured herein are designated as syntypes.

Geological, stratigraphical, structural and palaeogeographical setting

From the Bay of Biscay, the easterly extension of the Cenozoic sea reached the present-day cities of Narbonne and Béziers (Bay of Languedoc) during the middle Ilerdian (Fig. 1). This reflects a relative pause in the uplift of the Pyrenees, followed by a major tectonic phase during which a detrital formation (“Molasse de Carcassonne”), which filled the eastern part of the bay in late Ypresian times, formed (Plaziat 1981; Sztrakos *et al.* 1998; Gély and Sztrakos 2000). In the French-Spanish Pyrenean Basin, the Ilerdian Stage has recently been redefined in the stratotypical area near Tremp, south of the Pyrenees, where it corresponds to the early Ypresian (Pujalte *et al.* 2009). The Paleocene–Eocene boundary (just below the Ilerdian) is characterised by a significant drop in $\delta^{13}\text{C}$ values within a range referred to as the carbon isotopic excursion (CIE) or Paleocene-Eocene Thermal Maximum (PETM) (McInerney and Wing 2011). This interval was identified along the southern border of the Bay of Languedoc, south of Coustouge, predating the development of the first marine strata that mark the onset of the Ilerdian transgression (Yans *et al.* 2014).

Martin-Martin *et al.* (2001) subdivided the Ilerdian section into four depositional sequences: (1) 20–25 meters of a transgressive “Calcaire marin basal”, often rich in alveolinid foraminifera and oolites; (2) a set showing important lateral variations with either predominant carbonates locally including the Foraminifera *Solenomeris* bioconstructions (Plaziat and Perrin 1992), or a predominance of silty marls often rich in Gasteropoda of the genus *Turritella* and Brachiopoda of the genus *Terebratulina* (lower blue marls); (3) the middle blue marls, capped by the first detritic beds; (4) the upper blue marls, overlain by sandstones and marls with oysters and Gasteropoda of the genus *Potamides* and the first beds with traces of emersion (Plaziat 1964). The lower and middle blue marls may form a continuous formation that attains a thickness of up to 450 meters in the Montlaur syncline. The crinoids studied herein were collected several tens of meters above the base of the lower blue marls (the *Terebratulina*-rich marls of Plaziat 1984a), except at the locality of Lavade to the west of Fontcouverte and at La Côte, south of Moux; these two are situated in the middle blue marls.

Most of the lower and middle blue marls have classically been considered to be of middle to late Ilerdian age (Plaziat 1984b; Plaziat in Berger *et al.* 1990). The onset of the Ilerdian transgression is placed in biozone NP9 (Yans *et al.* 2014). Pirkenseer *et al.* (2013) noted that, to the south of Pradelles-en-Val, 130 meters of middle blue marls belonged to biozone SBZ8 and the upper part of biozone NP11, with the transition to the SBZ9 and NP12 biozones situated in the upper blue marls. From this, we deduce that the crinoid sites within the lower blue marls, still deposited later than the formation of the *Solenomeris* bioconstructions, correspond to biozone NP10 and the lower part of NP11, and that the younger sites (i.e., Lavade-Fontcouverte and La Côte-Moux) belong to the upper part of NP11. The entire series may reach a thickness of 500 to 550 meters, deposited over a period of ~3 to 5 million years, which implies rapid subsidence at least during transgression and a high sedimentation rate estimated, on average, at ~32 cm/kyr by Pirkenseer *et al.* (2013) during the final stage of infill of the bay. The available space required to accumulate this series finds its origin not

only from a rise in global sea level, in part related to the thermal optimum (PETM), but also from large wave tectonic deformations (Plaziat 1984b; Plaziat and Perrin 1992).

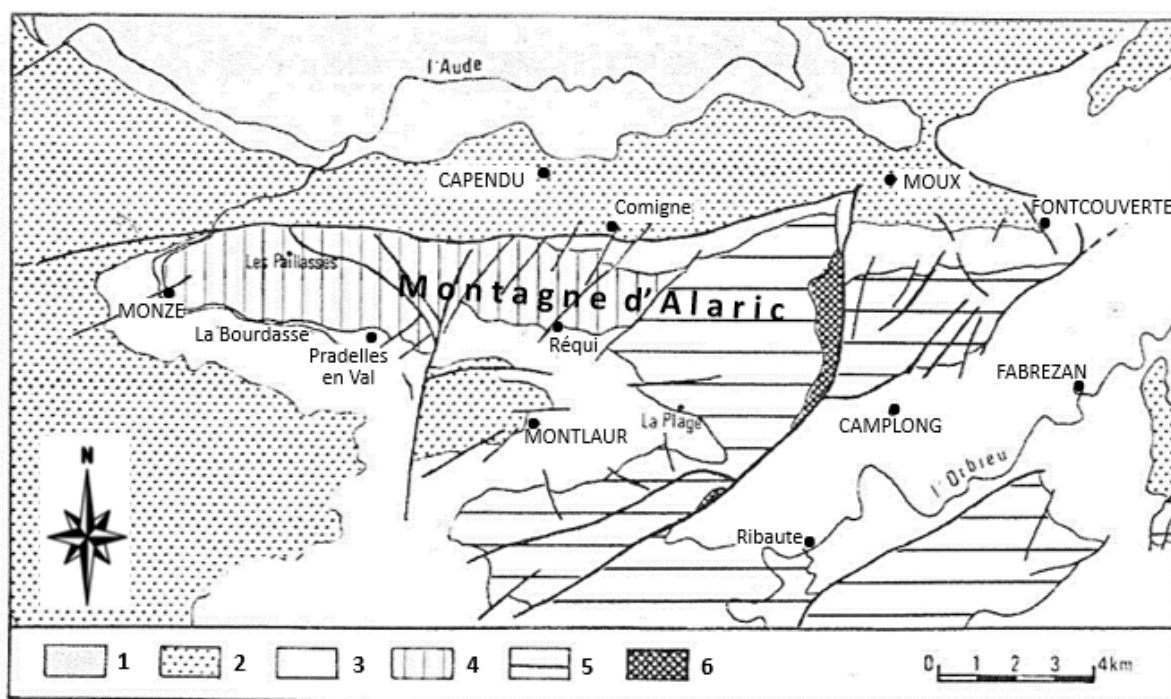


FIGURE 3. Simplified geological and structural map of the study area (modified after Bousquet 1979). Legend: 1: Quaternary (Aude Valley and north of Foncouverte), 2: Carcassonne molasse (late Ypresian to Bartonian), 3: predominantly marly series (middle-late Ilerdian), 4: mixed series with predominantly bioclastic limestones, 5: Late Cretaceous to early Ilerdian (basal marine limestone), 6: Palaeozoic.

The tectonic framework of the study area (Fig. 3) comprises a faulted zone near Lézignan-Corbières, which is globally NE-SW oriented (prolonging or parallel to the Nîmes fault) and an E-W anticline (the Alaric Mountain), which is bordered to the south by the Montlaur syncline. A major submeridian fault exposing the Palaeozoic basement affects the eastern end of the Alaric Mountain. It separates the Fontcouverte-Camplong-Ribaute compartment to the east and south from the Montlaur-Monze compartment to the west. The Montlaur syncline as well as the Alaric Mountain are affected in the east by smaller faults (Plaziat and Perrin 1992: fig. 22) in the area where the Ilerdian marls reach their maximum thickness. Substantial local variations in facies and thickness are interpreted as being related to active synsedimentary tectonics (Bousquet 1979; Martin-Martin *et al.* 2001).

The Gulf of Languedoc is bordered to the north by the carbonate platform of the Minervois, and to the south by a narrower littoral zone with frequent sandy intercalations, which indicate the approach of the first Pyrenean reliefs. A deeper area occupied the basin centre where terrigenous sedimentation, mainly of Pyrenean origin, accumulated (Fig. 4). The slopes separating the shallowest areas from the central basin were likely located in the area of the Alaric Mountain on the northern side, and at the level of Coustouge in the south. Several deltaic cones occurred along the northern and southern slopes of the basin (Fig. 4) and *Solenomeris* bioconstructions are often associated with these, prior to deposition of the lower blue marls (Plaziat and Perrin 1992). Near the southern flank of Alaric Mountain, the existence of steeper palaeoslopes towards the south was suggested by the presence of slumped *Solenomeris* limestone blocks (environment of the Réqui site, see below). Sediment

transferred on these slopes often led to a strongly allochthonous nature of some fossils causing important faunal mixing, particularly along the southern edge of the bay (Plaziat 1984a). The deeper area of the basin stretched from Fontcouverte to Frabrezan, Camplong, Montlaur and Pradelles-en-Val in the south of the Alaric Mountain, and from Fontcouverte to Moux and Douzens in the north. The crinoid sites are located within this area. They are grouped at the outlets of three main deltaic cones whose nutrient supply are thought to have favoured planktonic and benthic production (Fig. 4).

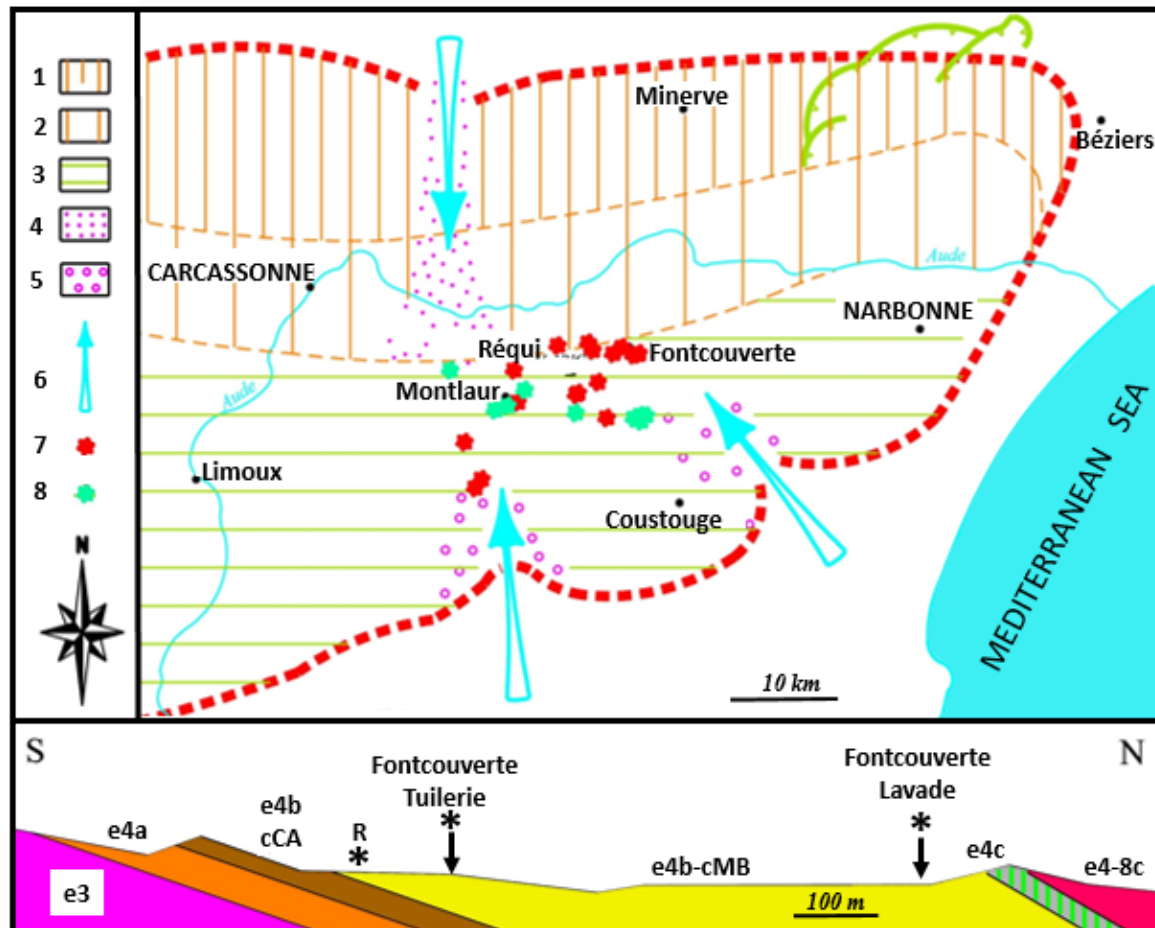


FIGURE 4. Simplified palaeogeographical map of the Gulf of Languedoc during the **middle** Ilerdian with the crinoid sites (**modified** after Plaziat 1981, 1984b) and geological section west of Fontcouverte. Map: 1: calcareous series, 2: mixed series with predominantly bioclastic limestones, 3: predominantly blue marls, 4: sandy facies, 5: facies with gravel and pebbles, 6: main deltaic axes, 7: crinoid sites studied, 8: other crinoid sites reported by Doncieux (1911). Geological section; e3-e4a: Paleocene, e4a: "lower Sparnacian", e4b-cCA: **early** Ilerdian (basal marine limestone), e4b-CMB: **middle** Ilerdian (lower and middle blue marls), e4c: **late** Ilerdian, e4-8c: **late** Ypresian to Bartonian (Carcassonne molasse), R: Stratigraphical **position** of the Réqui site located further west, near Montlaur. The **colours** and notations on the geological section are those of the Capendu geological map at 1/50.000 (Berger *et al.* 1990).

Location and inventory of outcrops with crinoids

Doncieux (1911) indicated a dozen sites with crinoids. Many of these are no longer accessible or no longer offer good outcrop conditions (see locations Fig. 4 and appendix). Most of these sites were in

the commune of Fabrezan, namely the Fontas, Bouffet and Bergès farmsteads, Bataille rivulet and north of Bellevue. Around Montlaur, Doncieux cited Le Plô, Terro Blanco and west of La Fraissinède. Near Fontcouverte, he only indicated a site to the southwest of the village and did not mention the ancient Tuilerie, where deposits are highly fossiliferous. One site was indicated to the north of Ribaute (Poux Estève Bas) and another near Pradelles-en-Val (La Bourdasse). The aboral cups and columnals that had been attributed to the genus "*Conocrinus*" and collected from all sites mentioned by Doncieux belong to *P. doncieuxi* (Roux 1978a). The site that we here name Les Lanes Sud likely corresponds to the site southwest of the village of Fontcouverte as indicated by Doncieux (1911).

The crinoids studied here originate from 22 sites, two exposing the middle blue marls, the others the lower, *Terebratulina*-rich blue marls (Fig. 4; Table 2). *Pseudoconocrinus* is the commonest genus (at 18 sites) and often the most abundantly represented. The Réqui site differs in having a diverse and peculiar crinoid fauna.

Sites studied	Taxon/taxa	Abundance	Type of ossicle
Coste de la Crabole (Douzens)	<i>Pseudoconocrinus doncieuxi</i>	few	Ac
Fontas (Fabrezan)	<i>Pseudoconocrinus doncieuxi</i>	abundant	Ac, Co
Lavade (Fontcouverte West)	? <i>Democrinus elongatus</i> , <i>Pseudoconocrinus lavadensis</i> <i>P. doncieuxi suboblongus</i> <i>Amphorometra atacica</i>	rare abundant few rare	Ac, Co? Ac, Co, Rh, Brax, Br Ac Cd, Br
Ancienne Tuilerie (Fontcouverte southeast, Mourrel de la Borio)	<i>Pseudoconocrinus doncieuxi</i> <i>P. doncieuxi suboblongus</i>	abundant rare	Ac, Co, Rh, Brax, Br Ac, Co
à l'Estagnol (Fontcouverte southeast)	<i>Pseudoconocrinus doncieuxi</i> <i>P. doncieuxi suboblongus</i>	abundant rare	Ac, Co Ac
La Caune (Fontcouverte southeast)	<i>Pseudoconocrinus doncieuxi</i>	few	Ac, Co
Les Lanes-Sud (Fontcouverte southwest)	<i>Pseudoconocrinus doncieuxi</i> <i>P. doncieuxi suboblongus</i> <i>Amphorometra atacica</i>	frequent few rare	Ac, Co Ac Cd
Le Coucou (Camplong d'Aude)	<i>Pseudoconocrinus doncieuxi</i> <i>P. doncieuxi suboblongus</i> <i>Amphorometra atacica</i>	abundant frequent frequent	Ac, Co, Rh, Brax, Br Ac Cd, Br, Ci
Ruisseau de Tourrent (Camplong)	<i>Pseudoconocrinus doncieuxi</i>	few	Ac, Co
Roc Fendu (Camplong d'Aude)	<i>Pseudoconocrinus doncieuxi</i>	abundant	Ac, Co
Le Cabagnol (Camplong d'Aude)	<i>Pseudoconocrinus doncieuxi</i>	frequent	Ac, Co, Rh, Brax
Les Vènes (Mayronnes)	<i>Pseudoconocrinus sp.</i>	few	Co
L'Auzerdier (Montlaur, Val de Dagne)	<i>Pseudoconocrinus doncieuxi</i>	abundant	Ac, Co, Rh, Brax
Commanderie (Montlaur, Val de Dagne)	<i>Pseudoconocrinus doncieuxi</i> <i>Amphorometra atacica</i>	abundant rare	Ac, Co, Rh, Brax Br
Terro Blanco (Montlaur, Val de Dagne)	<i>Pseudoconocrinus doncieuxi</i>	abundant	Ac, Co, Rh, Brax, Br
Réqui (Montlaur, Val de Dagne)	<i>Globulocrinus amphoraformis</i> <i>P. doncieuxi suboblongus</i> <i>Holopus plaziati</i> <i>Cherbonnierocrinus requiensis</i>	abundant abundant rare rare	Ac Ac, Co Brax, Br Ac
La Côte (Moux)	<i>Pseudoconocrinus lavadensis</i>	few	Ac, Co
Aigue Douce (Moux)	<i>Pseudoconocrinus doncieuxi</i>	few	Ac, Co
Les Côtes (Rieux-en-Val)	<i>Pseudoconocrinus doncieuxi</i>	few	Co
Montauriol (Serviès-en-Val)	<i>P. doncieuxi suboblongus</i>	few	Ac, Co
Les Rives (Ribaute)	<i>Pseudoconocrinus doncieuxi</i>	abundant	Ac, Co, Brax
La Prade (Arquettes-en-Val)	<i>Amphorometra atacica</i>	rare	Cd

TABLE 2. Sites with crinoids here studied with taxa, abundance and types of ossicles. For abbreviations, see Table 1.

Taphonomy and palaeoecology

Crinoids are rheophilic suspension feeders. The stalked forms that are fixed directly by their aboral cup belong to sciaphilous benthos. Their mode of life that allows them to filter food with their crown lifted up above the sea floor is consistent with weak to moderate laminar currents but is incompatible with strong turbulence induced by wave action (Roux 1987; Améziane and Roux 1997). Nowadays, they only colonise environments at depths of >100 meters sheltered from frequent storm waves. They are represented in the Ilerdian assemblages by Rhizocrinidae, most of which develop rhizoids penetrating muddy substrates. Holopodidae present at Réqui resemble barnacles. They are sessile with an aboral cup attached directly to hard substrates and with short arms that curl and retract into the calycinal cavity. Feather stars such as *Amphorometra* lose their stalk at an early post-larval stage and attach to various substrates using their cirri inserted on the centrodorsal plate. In contrast to other crinoids, many species of feather stars live in the euphotic zone.

The skeleton formed by numerous articulated ossicles dissociates more or less rapidly after death. The muscular joints, only present in the arms, are the first to dissociate. Columnals united by powerful ligaments dissociate later. In rhizocrinids, columnal facets of an articulation type named synarthry are not interlocked and dissociate as soon as the ligaments decay, while the aboral cup with its fused ossicles remains complete. Due to their low density, the isolated ossicles can be easily transported, even by weak currents. The sieve residues that yielded the various types of ossicles (Table 2) indicate rapid *in-situ* burial and absent or weak hydrodynamic selection after the dissociation phase. This is the case with *Pseudoconocrinus* from four sites: Lavade, the ancient Tuilerie de Fontcouverte, Le Coucou and Terro Blanco. However, brachials are few and underrepresented, probably because they are the first to dissociate, but also because the crown of arms is the preferred target of predators (Paschall and Waters 2016; Veitch and Baumiller 2021). At other sites (Le Cabagnol, La Commanderie, Les Rives and L'Auzerdier), hydrodynamic selection eliminated the smallest ossicles and only the largest brachials (IBr2ax), columnals and cups of *Pseudoconocrinus* remain present despite the abundance of material. The distal parts of the stalk with well-developed rhizoids are often partially buried in the mud during the animal's life. They can be preserved with connected ossicles in the absence of bioturbation (Merle and Roux 2018). This early burial limits the dissociation of distal columnals and increases the possible preservation of non-dissociated stalk segments. In Lavade, pluricolumnals represent ~30 % of columnals collected, 80% of pluricolumnals with two connected columnals and 1% with a maximum of 5 to 6 columnals. Most of the buried rhizoids escape hydrodynamic selection, which eventually eliminates the brachials. Their presence testifies to *in-situ* burial. For example, despite the abundance of material, all ossicles of *P. doncieuxi* from Les Rives near Ribaute were displaced and a hydrodynamic selection eliminated the smallest ones, such as non-axillary brachials, proximalmost columnals and rhizoids.

Under the best conditions of *in-situ* burial (Lavade, ancient Tuilerie de Fontcouverte), the ratio between the number of aboral cups and that of columnals articulated by synarthry (mesistele + dististele) should allow to reconstruct the average number of columnals per individual, thus the average stalk length in *Pseudoconocrinus* and the ratio of mesistele (erect part of stalk) to dististele (with rhizoids) length. The result (see below, under Taxonomy) shows an overrepresentation of dististele columnals (55% at Lavade). This is due to taphonomic bias: *in-vivo* burial of the dististele, hydrodynamic elimination of most of the small columnals of the proximal mesistele, but also to the mode of stalk growth with the permanent appearance of new columnals under the aboral cup and simultaneous progressive incorporation of the distalmost mesistele columnals into the dististele.

Three fossil assemblages have been distinguished: (1) one with *Pseudoconocrinus doncieuxi* predominating, which may include a few specimens of *P. doncieuxi suboblongus* **n. subsp.** and *Amphorometra atacica*; (2) one with *P. lavadensis* **n. sp.** predominating and *P. doncieuxi* var.

oblongus **n. var.**, ?*Democrinus elongatus* and *A. atacica* as accessory forms; (3) one with *Globulocrinus amphoraformis* **n. gen., n. sp.** and *P. doncieuxi suboblongus* **n. subsp.**, accessory with *Cherbonnierocrinus requiensis* **n. sp.** and *Holopus plaziati* **n. sp.** Assemblage 1 comes from almost monospecific populations that settled on a muddy sea floor and corresponds to an opportunistic phase of colonisation associated to a high morphological variability of *Pseudoconocrinus* aboral cups (Roux 1978a). This is the commonest assemblage in the lower blue marls (sites around Fontcouverte, except Lavade, Fabrezan, Camplong d'Aude, Montlaur except Réqui, Ribaute). Assemblage 2, which also inhabited muddy sea floor, is the result of a multispecific palaeobiocoenosis that was strongly dominated by one species of *Pseudoconocrinus* with a low range of morphological variation. This corresponds to the last crinoid community that survived in a stable environment prior to the infill of the basin (sites of Lavade and La Côte-Moux). Assemblage 3, specific to the site of Réqui, clearly differs from the other two in having a substantial and peculiar taxonomic diversity and a predominance of small individuals, resulting from mixing crinoids that lived on hard (*Globulocrinus*, *Holopus*) and muddy substrates (*Pseudoconocrinus* and *Cherbonnierocrinus*). At Réqui, slippery boulders of *Solenomeris* limestone are interbedded at the base of the lower blue marls. The apparent high diversity reflects the heterogeneity of the sea floor. The abundance of small specimens suggests populations with high rates of juvenile mortality in an unstable environment. *Pseudoconocrinus doncieuxi* is present at all sites with stalked crinoids; however, it should be noted that only the subsp. *suboblongus* has been recovered from Réqui, Montauriol and Lavade.

Palaeobathymetry and palaeogeography

Recent oceanographic investigations in bathyal environments conducted during last decades, notably direct observations from submersibles, have confirmed that most of the extant stalked crinoids are not relict forms and that their diversity and abundance are still largely underestimated (see, for example, Veitch *et al.* 2021 and Tunnicliffe *et al.* 2016). In the tropical western Atlantic, Rhizocrinidae are common only at depths >100 meters, although one species, *Democrinus rawsoni* (Pourtalès 1874) has been exceptionally reported at a depth of 66 meters (Meyer *et al.* 1978). Whether extant or fossil, an exceptional record of individuals beyond their usual range cannot be used as a generalisable reference. In the western Pacific, Rhizocrinidae have only been collected from depths >110 meters at all latitudes. *Democrinus japonicus* Gislén, 1927, the morphology of the aboral cup of which is close to that of *D. elongatus* and *P. doncieuxi suboblongus* **n. subsp.**, is abundant only between 140 and 170 meters (Gislén 1927). Extant *Cherbonnierocrinus* is known exclusively from the Bay of Biscay at a depth of ~500 meters. However, this fact cannot be used as a reference for interpreting a fossil biotope in view of the particularities of the bathymetric distribution of stalked crinoids in the northeast Atlantic province (Amézière and Roux 1997). The barnacle-like genus *Holopus* is known exceptionally from a depth of 100 meters, but has only been observed in numbers from 274 metres (Macurda and Meyer 1974) or at depths >400 meters (Syverson *et al.* 2015) on vertical or overhanging rocky walls, which suggest similarities with the site of Réqui. Boulders accumulated on the sea floor may have provided potential habitats for the settlement of sciaphilous species usually living in deeper environments. Although Holopodidae are not constrained by the hydrodynamic tolerance threshold of stalked crinoids, they have never been collected from circalittoral environments (Amézière *et al.* 1999). Roux *et al.* (2006) showed that the bathymetric distribution of stalked crinoids during the Eocene did not differ essentially from that in present-day oceans.

The proximity of the *Solenomeris* bioconstructions and the instability of the environment (inducing high juvenile mortality) lead us to consider the Réqui site (fossil assemblage of type 3) as one of the shallowest. It would have been situated at least at a depth of ~100 meters in reference to the

minimum depths at which extant *Holopus* lives. Adnet *et al.* (2010) also found at Réqui numerous juveniles in a selachian fauna where benthic forms predominated, and considered it to be the shallowest environment among the blue marl sites they analysed. The Lavade site (fossil assemblage of type 3), the youngest in the stratigraphical section, was a muddy sea floor favourable to laminar currents and the development of numerous specimens of *Pseudoconocrinus lavadensis* **n. sp.** of limited morphological variation and normal size. It lies 90 meters below the first emersion indices reported by Plaziat (1964), which corresponds to a thickness of decompacted sediment of >150 meters. In the section studied by Pirkenseer *et al.* (2013), it corresponded approximately to the uppermost strata in which planktonic foraminifera substantially predominated over benthic ones, and at the upper limit of the "outer neritic" biofacies with the ostracod *Krite angusta*. With reference to biotopes inhabited by the extant *Democrinus japonicus*, we can predict a depth of at least 140 meters for the environment corresponding to the sites with *P. lavadensis* **n. sp.** Those with fossil assemblage type 1, with abundant *Pseudoconocrinus doncieuxi* of highly variable aboral cups and reaching their maximum sizes, were probably shallower, closer to the hydrodynamic tolerance threshold of stalked crinoids, at a depth equal to or greater than 100 meters.

Plaziat (1984b) suggested that the palaeogeographical position of the Gulf of Languedoc could have sheltered it against too frequent storm waves and thus allow settlement of stalked crinoids at circalittoral sites. Although no similar example has been described from recent oceans, this hypothesis remains possible. It should also be noted that all the sites with nautiloid rhyncholites, as cited by Pacaud (2010), are localities that have yielded stalked crinoids.

Until now, the only diverse and abundant crinoid fauna known from the early Ypresian was described from the London Clay (Rasmussen 1972). It comprises one rhizocrinid [*Democrinus londinensis* (Forbes, 1852)], two isocrinids [*Isselocrinus subbasaltiformis* (Miller, 1821) and *Cainocrinus tintinnabulum* Forbes, 1852] and one feather star (*Amphorometra ornata* Rasmussen, 1972). This fauna inhabited depths that were at least 150-300 meters (see discussion in Merle and Roux 2018) deeper than that of the Corbières fauna. The two faunas differ mainly by the absence of isocrinids (notably of the genus *Isselocrinus*) in the Gulf of Languedoc and of *Pseudoconocrinus* in the London Clay. They have in common the genera *Democrinus* and *Amphorometra*. The Eocene of northeast Italy also has a highly diverse and occasionally abundant crinoid fauna the taxonomy of which is in need of revision. The crinoid-rich horizon of Monte Spilecco near Bolca contains rhizocrinids, holopodids and isocrinids (Munier-Chalmas 1891; Oppenheim 1902; Fabiani 1915; Manni 2005). Often attributed to the Ypresian, in several localities this horizon is in fact poorly dated and now assumed to be sometime younger (L. Giusberti, pers. comm.). In the same area, a similar, yet more diverse, crinoid fauna dated as Lutetian is likely to have belonged to an epibathyal environment (Frisone *et al.* 2020).

For the late Ypresian of Gan (Pyrénées Atlantiques), Merle and Roux (2018) described an environment estimated at a depth of 150-300 meters, with *D. londinensis* previously known from the London Clay and the oldest representative of the genus *Eocenocrinus* also present in the Lutetian of northeast Italy. During the Eocene, the sea that occupied the Pyrenean domain was wide open to the Atlantic Ocean via the Bay of Biscay, but closed on the eastern side. Direct faunal exchanges with the Paratethys marine domain (southeast France, northeast Italy) were thus excluded. As numerous genera among the Corbières fauna have Cretaceous–Danian ancestors (e.g., *Holopus*, *Pseudoconocrinus* and *Amphorometra*), the geographical distribution of Eocene crinoid taxa suggests a faunal heritage rooted in the Late Cretaceous, so common in the boreal basins of England, the Netherlands-Belgium and Denmark, as well as with those of the Paratethys. Breton and Vizcaino (1997) also reported that several asteroid taxa of the Corbières fauna seemed to have been derived from boreal Late Cretaceous ancestors. The abundance of *Pseudoconocrinus* in the Pyrenean domain during the Ilerdian illustrates

the maximum development of a lineage that first appeared in the Campanian and seems to have died out at the end of the Eocene (Roux *et al.* 2019).

Taxonomy

Phylogenetic analyses of DNA markers carried out on extant crinoids (Hemery 2011; Hemery *et al.* 2013; Rouse *et al.* 2013) have demonstrated the importance of morphological convergences and iterations during their evolution (Roux *et al.* 2013). Numerous families classically defined on the basis of external morphological traits have been found para- or polyphyletic. Recent revisions modifying the usual hierarchy of characters (Roux *et al.* 2019; Améziane *et al.* 2021) have led to changes in the classification proposed by Hess and Messing (2011). Amongst crinoids with a xenomorphic stalk, the family Rhizocrinidae now appears to be clearly distinct from both Bourgueticrinidae and Bathyocrinidae.

Family Rhizocrinidae Jaekel, 1894

Remarks. The distal face of the radial circlet (Fig. 2B) and the presence or absence of axillary brachials (Fig. 2D) have been shown to be highly useful for distinguishing the various rhizocrinid genera (Roux *et al.* 2019). Those authors subdivided *Conocrinus* (sensu lato) into three genera, namely *Conocrinus* (sensu stricto), *Paraconocrinus* and *Pseudoconocrinus*. Although appearing as early as the Ypresian, *Conocrinus* (sensu stricto) was not found in Ilerdian strata of Corbières. The proximal columnals that constitute the proxistele of rhizocrinids are more or less thick and disc shaped, usually with flat and smooth facets. They are rare or absent in the screen-washed residues that we picked by hand. The columnals of the mesistele and dististele have synarthrial articulations with a central ligamentary fossa that has a figure-8 shape. The fulcral ridges change orientation from one joint to the next, giving the columnals a twisted appearance (Fig. 2E-F). Most rhizocrinids are fixed by rhizoids developed from the distal part of the stalk (dististele). In the fauna described here, the columnal characters do not allow a clear distinction between the different genera. The external morphology of juvenile aboral cups occasionally shows clear, discriminating characters, which tend to disappear later during growth by morphological convergence (homoplasy; for example, see Fig. 14A-I). The abundance of material from some outcrops has allowed the recognition of juveniles and the reconstitution of ontogenic trajectories that have proved instrumental in clarifying the taxonomy (see Fig. 9, for example).

Stratigraphical distribution. Campanian-Recent.

Genus *Pseudoconocrinus* Roux, Eléaume and Améziane, 2019

Type species. *Conocrinus doncieuxi* Roux, 1978a, lower Ypresian.

Emended diagnosis. Aboral cup shape highly variable but never inverted conical, except in some juveniles; sutures between aboral cup ossicles often conspicuous. Distal face of radial circlet with small central depression (ratio to radial circlet diameter 0.20–0.30), long conspicuous interradianal crests separating large subtrapezoidal muscular synarthries, arm sockets about as wide as radials, muscular areas moderately concave with inner side slightly erect or not at all. Arms divided at IBr2ax, synostomial symmorphy at IBr1+2 without trifascial pattern, IBr1 short and substantially wider than

high, IBr2ax regularly pentagonal, occasionally two kinds of axillaries found in association with aboral cups: a large one which is wider than tall, and a smaller one which is substantially taller than wide, suggesting change during growth ontogeny or possible additional branching, free arms with frequent brachial pairs (two IIBr united by flat synostosis). Occasionally proxistele well differentiated with thick discoidal columnals, progressive transition from mesistele to dististele with numerous columnals bearing thin rhizoids.

Remarks. *Pseudoconocrinus* differs mainly from other Eocene and Recent rhizocrinid genera in having arms dividing at IBr2ax.

Stratigraphical distribution. Danian–Ypresian.

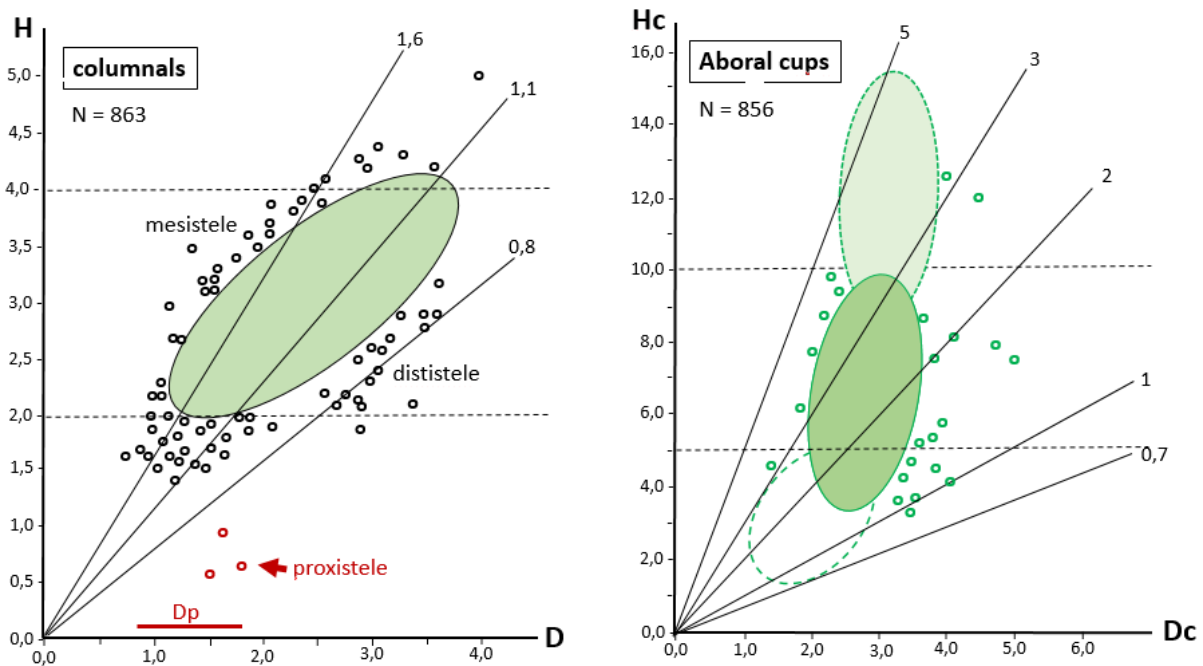


FIGURE 5. Variations in the shape of columnals and aboral cups of *Pseudoconocrinus doncieuxi* (sites near Fontcouverte, with the exception of Lavade). The colour envelopes cover more than 90% of specimens; black lines indicate the values of H/D (left) and Hc/Dc (right). Values in mm, except for ratios (black straight lines). See Fig. 2 for abbreviations.

***Pseudoconocrinus doncieuxi* (Roux, 1978a)**

Figs. 5-7, 8A-F, J-Q

Synonymy. *Conocrinus pyriformis* Doncieux, 1911: 157; *Conocrinus thorenti* Doncieux, 1911: 159; *Conocrinus* sp. Doncieux, 1911: 159; *Conocrinus doncieuxi* Roux, 1978a: 797-800, figs 1, 2a. - 1978b: 219, 226, fig. 12a, pl. 2-2. - Roux and Plaziat, 1978: 301; *Pseudoconocrinus doncieuxi* Roux *et al.*, 2019: 66-67, 79, fig. 8A-F, K-N.

Type material. The type series is housed in the palaeontological collections of the Claude Bernard University Lyon 1, and comprises 20 aboral cups and 20 columnals (UCBL-FSL 170248a) selected from a sample of 160 aboral cups and 460 columnals (UCBL-FSL 170248) with the mention "Fontcouverte, sud-ouest du village" (i.e., the outcrop here called Les Lanes Sud). The holotype is an aboral cup whose adoral face was illustrated in the original paper (Roux 1978a, fig. 2a).

Material examined. Three aboral cups from the Bories Collection (Fig. 6A-F, I); 4 columnals from the Plaziat Collection (Fig. 8J-M, O-Q). Numerous columnals and aboral cups from various sites in the Martinez Collection (see Table 2), numerous brachials (Figs. 6J-T and 7) and rhizoid fragments from the Martinez Collection from the ancient Tuilerie de Fontcouverte and Ribaute; specimens here figured are housed at the MNHN (see catalogue numbers, Tables 1, 3-4).



FIGURE 6. Aboral cups and axillary primibrachials of *Pseudoconocrinus doncieuxi*. Provenance: A-I, M-T: Tuilerie de Fontcouverte, J-L: Ribaute. A-C: MNHN.F. A69944a, A: lateral view showing sutures between basals, B: oblique view of radial circling, C: distal face of radial circling; D-F: MNHN.F.A81993, D: oblique view showing distal face of radial circling, E: aboral face with proximalmost columnals preserved; F: distal face of radial circling; G-H: MNHN.F. A81996, G: view of small stalk insertion, H: slightly oblique lateral view showing radial circling; I: MNHN.F. A69944b, slightly oblique lateral view showing distal face of radial circling; J-L: MNHN.F.A81997, IBr2ax of large specimen; J: external view, K: distal view showing muscular synarthrial facets, L: oblique view showing concave proximal synostosis facet; M-T: MNHN.F.A81994, axillary brachials. M-P: IBr2ax of medium-sized specimens, M: external view, N: inner/lateral view of same Br, O-P: another Br, O: inner view, P: inner/lateral view; Q-T: juvenile IBr2ax or IIBrax, Q: oblique inner-proximal view, R-S: another Br, R: external view, S: inner view, T: distal muscular synarthrial facets. Scale bars equal 1 mm (A–P) and 0.5 mm (Q–T).

Type stratum. Lower blue marls of middle Ilterdian age (early Ypresian), NP10–lower NP11.

Type locality. Les Lanes Sud, southwest of the village of Fontcouverte (Aude).

Diagnosis. Aboral cup of highly variable shape (usually $1.2 < Hc/Dc < 2.8$, which can vary from 1.0 to 5.0), variation due to basal height without correlation with Dc growth; maximum value of Dc in aboral third or at mid-height, more rarely proximally; always $Dr < Dc$, Dc reaching 5 mm and Hc 15.3 mm; constriction at radial/basal boundary or proximally absent or weak; adoral face of radial circling forming more or less marked pyramid, central depression often star shaped, $Dd < 0.26 Dr$; sutures between basals occasionally conspicuous even in large specimens, aboral face with stalk insertion of variable size (Dp reaching 0.54 Dc, sometimes < 0.30). Arms divided at IBr2ax, as high (sometimes less) as wide, synostosis at IBr1+2ax with lumen of neural canal subcircular, presence of small IIBrax substantially higher than wide, free arms composed mainly of succession of brachial pairs with alternating synostoses and muscular synarthries. Very rare flat-faceted discoid columnals of proxistele, less than half of other columnals with mid-height swelling, most often moderate; ~50% of the columnals with rhizoid insertions, less than half with 2 insertions (rarely 3) and $H < D$; columnals without rhizoid most often with $H/D > 1.5$.

Specimen	Figure	Hc	Dc	Dr	Dp	Dd	Wr	Hc/Dc	Dr/Dc	Dp/Dc	Dd/Dr
F.A81993	6D-F	7.70	3.60	2.91	<1.80	0.70	1.62	2.14	0.81	<0.50	0.24
F.A69944a	6A-C	7.21	3.43	2.58	1.63	0.53	1.31	2.10	0.75	0.48	0.21
F.A81996	6GH	6.32	3.90	2.50	0.90	0.60	1.05	1.62	0.64	0.23	0.25
F.A69944b	6I	6.40	3.16	2.55	0.93	0.64	1.27	2.03	0.81	0.29	0.25
F.A81998*	8A-C	5.13	2.90	1.90	1.00	0.47	1.10	1.77	0.66	0.34	0.25
F.A81999*	8D-E	6.76	2.72	2.07	1.34	0.52	1.00	2.49	0.76	0.49	0.25
F.A82000*	8F	5.83	2.68	2.03	1.10	0.60	1.07	2.18	0.76	0.41	0.30

TABLE 3. Quantitative characters of aboral cups of *Pseudoconocrinus doncieuxi* here figured. Catalogue numbers are those of MNHN. * = *P. doncieuxi suboblongus* n. subsp., Dp: diameter of stalk insertion, Wr: width of distal articular facet of one radial; other abbreviations see Fig. 2. Values in mm, except for ratios.

Description. Roux (1978a, b) presented a brief description, outlining the main quantitative characters of the aboral cups and columnals belonging to historical specimens from MNHN and UCBL-FSL collections and more recent collections by J.C. Plaziat. Here we provide additional data on the aboral cups, particularly on their extremes in variation. Screenwashing at the ancient Tuilerie de Fontcouverte and its immediate surroundings has provided numerous other ossicles, notably brachials and rhizoids.

Aboral cups (Figs. 5, 6A-I, 8A-F; Table 3): Hc up to 15.5 mm, but usually <8.5 mm, equal Dc or up to five times that (Fig. 5), shape variation due to lengthening of basal circler independent of diameter growth, tendency to elongation increasing during growth in most specimens with $2.5 < Dc < 4.0$ mm (Fig. 5), Dc usually <4.0 mm and rarely reaching 5.0 mm; maximum value of Dc in aboral third or at mid-height (Fig. 6A, D), more rarely above (Fig. 6H-I), usually $Dr/Dc < 0.8$, always $Dr \ll Dc$; constriction at radial-basal transition or at level of radial circler absent or weak; adoral face of radial circler forming more or less marked pyramid, each articular facet mainly occupied by ligament areas, more or less rectilinear interradian ridges sometimes terminated by abrupt widening on inner end (Fig. 6F), more or less star-shaped central depression with $Dd/Dr < 0.26$; sutures between basals may be conspicuous even in large specimens (Fig. 6A); aboral face with insertion of stalk generally well defined, often relatively large but highly variable ($0.3 < Dp/Dc < 0.5$, $0.35 < Dp/Dr < 0.7$).

Specimen	Place in arm	Wd	Wp	H	Wm	Wd/Wp	H/W'	remarks
Martinez Coll.	I Br2ax	2.08	1.58	1.67	1.15	1.32	0.80	Not figured
Martinez Coll.	I Br2ax	1.95	1.57	1.48	1.18	1.24	0.76	Not figured
F.A82994a	I Br2ax	1.82	1.41	1.18	1.12	1.29	0.65	Fig. 6O-P
F.A81997	I Br2ax	1.73	1.31	1.59	0.97	1.32	0.92	Fig. 6J-L
Martinez Coll.	I Br2ax	1.65	1.22	1.21	0.96	1.35	0.73	Not figured
F.A82994b	I Br2ax	1.41	1.18	1.23	0.79	1.19	0.87	Fig. 6M-N
Martinez Coll.	I Br2ax	1.00	0.84	1.06	0.52	1.19	1.06	Juvenile?
Martinez Coll.	I Br2ax	0.85	0.85	0.88	0.44	1.00	1.04	Juvenile?
F.A81995a	II Br1	1.20	1.17	0.77	-	1.03	0.64	Fig. 7A-C
F.A81995b	II Br1	0.90	0.95	0.50	-	0.95	0.56	Fig. 7E-F, H
F.A81995c	II Br1	0.85	0.75	0.60	-	1.00	0.71	Fig. 7G, I
F.A81995d	II Br prox. ?	0.95	1.00	0.81	-	0.95	0.81	Fig. 7D
F.A81995e	II Br hypo	1.07	1.10	0.65	-	0.97	0.61	Fig. 7R
F.A81995f	III Br hypo	0.75	0.80	0.47	-	0.94	0.63	Fig. 7L
F. A81995g	III Br hypo	0.67	0.75	0.35	-	0.89	0.47	Fig. 7K
F.A81995h	II Br epi	1.08	0.97	0.70	0.62*	1.11	0.65	Fig. 7O
F.A81995i	II Br epi	0.80	0.73	0.57	0.37*	1.10	0.71	Fig. 7P-Q
F.A81995j	II Br epi	0.55	0.50	0.37	broken	1.10	0.67	Fig. 7M-N
F.A81995k	II Br epi	0.55	0.50	0.30	0.30*	1.10	0.55	Fig. 7J
F.A82994d	II Brax	0.97	0.79	1.18	0.51	1.23	1.22	Fig. 6R-T
F.A82994c	II Brax	0.74	0.63	1.10	0.40	1.17	1.49	Fig. 6Q
Martinez Coll.	II Brax	0.62	0.52	0.77	0.31	1.19	1.24	Not figured

TABLE 4. Main quantitative characters in brachials of *Pseudoconocrinus doncieuxi*. Br infra: hyposynostosal brachial, Brsupra: episynostosal brachial with pinnule insertion, H: height, Wd: width of distal facet or maximum distal width of axillaries, Wm: width of one distal muscular synarthry in axillary, Wm*: width of pinnule socket in non-axillary brachial, Wp: width of proximal facet, W': maximum value of width (Wd or Wp). Values in mm, except for ratios.

Brachials (Figs. 6J-T, 7A-R; Table 4): Quantitative characters of different types of brachials given in Table 4. Robust axillary primibrachial (I Br2ax) (Fig. 6P), subpentagonal with concave aboral distal edges, often almost as wide as high (Fig. 6J, M), sometimes clearly wider than high with H/W' down to 0.65, pentagonal shape little marked in juveniles, well developed distal muscular synarthries forming marked protuberance at junction on the inner brachial side (Fig. 6J, O-P); subrectangular axillary secundibrachials (II Br2ax) with angle formed by distal articular facets poorly marked (Fig.

6R-S), aboral ligamentary depressions of distal muscular synarthries deep and narrow (Fig. 6T), wide adoral groove (Fig. 6Q); proximal synostoses of axillary concave with circular neural canal. Non-axillary brachials with muscular synarthry on one side and synostosis with circular neural canal on other, aboral (external) surface often with discrete ornamentation (Fig. 7I); no IBr1 observed; IIBr1 with adoral (inner) face concave probably corresponding to overhanging of adjacent tegmen (Fig. 7C, G), largest IIBr1 observed (Fig. 7A-C) with narrow, asymmetrical proximal facet, reduced muscular areas and slightly oblique fulcral ridge; other IIBr smaller, less asymmetrical, distal facet more or less

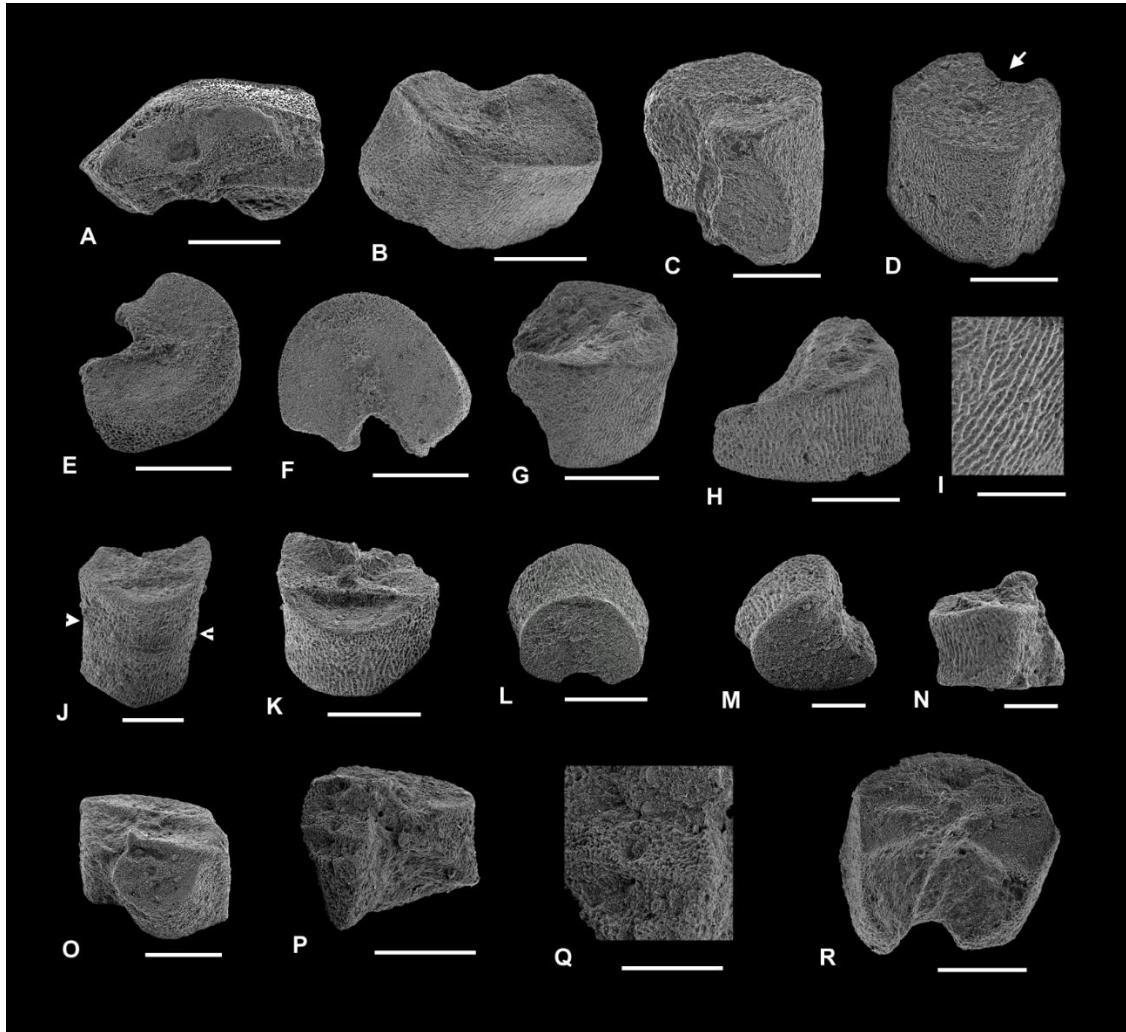


FIGURE 7. Non-axillary secundibrachials of *Pseudoconocrinus doncieuxi* from the Tuilerie de Fontcouverte (MNHN.F.A81995). A-C: IIBr1 of a large individual, A: proximal muscular synarthry, B-C: distal synostosis, B: oblique external view, C: oblique inner view; D: IIBr3, distal synostosis, oblique external view, arrow indicating inner axial gutter; E-F: IIBr, distal face with rudimentary axial ligament synarthry, E: oblique lateral view; G-I: IIBr1 of medium-sized individual, G: oblique lateral-distal view, H: oblique lateral-proximal view, I: detail of ornamentation of external surface; J-N: proximal IIBr without pinnular insertion, J: external oblique view of pair of IIBr joined by synostosis indicated by arrow heads, K-N: brachials of dissociated pairs, K: oblique view of muscular synarthrial facet, L-M: oblique views of synostiosal facet, N: lateral view; O-Q: IIBr with pinnular insertion, O: episynostiosal IIBr, P-Q: free Br with two muscular synarthrial facets, Q: detail of pinnular insertion; R: proximal muscular synarthrial facet of hyposynostiosal IIBr. Scale bar equals 0.5 mm, except in I, J and Q, where it equals 0.25 mm.

concave with occasional trace of axial fulcral ridge (Fig. 7E-F); one IIBr probably belonging to second pair of pinnuleless IIBr (IIBr3+4), with rectangular (external) aboral face, concave adoral (internal) face forming broad groove, synostosal facet almost flat with circular axial canal (Fig. 7D); other non-axillary brachials (Fig. 7J-R) with flat synostosal facet of width less than that of muscular articular facet, some IIBr with $Wd > 1$ mm, H and pinnule insertion > 0.6 mm; smallest Br (IIIBr?) with $Wd < 0.9$ mm, $H < 0.6$ mm and pinnule socket < 0.45 mm.

Columnals (Fig. 5, 8J-Q): Proximal columnals present but rare, some remaining attached to base of aboral cup (Figs. 6E, 8C), discoid with flat facet, D 1.49-1.84 mm, H/D 0.36-0.59. Mesistele columnals without rhizoids substantially higher than wide, $H/D > 1.2$, usually $1.0 < D < 2.5$ mm; most often minimum diameter at mid-height (Fig. 8J), fulcral crest with more or less regular secondary crenularium separated by axial groove (Fig. 8K). Columnals of distal part of stalk recognisable by rhizoid insertions starting from one or both ends of fulcral ridge of proximal facet (Fig. 8L-M); $H/D < 1.3$ decreasing to 0.6, usually $25 < D < 34$ mm, largest columnals with H 50 mm and D 40 mm; columnal body developing bulge with diameter greater than d (Fig. 8M), rarely than D (Fig. 8O), ~25% of columnals with well-marked bulge; fulcral ridge with regular secondary crenularium in parallel lines separated by groove or more rarely by dense calcite band (Fig. 8P-Q); few distal columnals showing depressed ligament area on each side of fulcral ridge segments (Fig. 8N); pluricolumnals of 2 to 4 ossicles with well-developed cirrus insertions as well as ~50% of isolated columnals. Rhizoids similar to those described below for *P. lavadensis* n. sp.

Remarks. Most non-axillary brachials have a synostosal facet, which indicates that the arms were mainly composed of a succession of brachial pairs, like in most extant rhizocrinids, at least proximally. About a quarter of brachials collected do not have a pinnule socket, the first pinnule was carried by an IIBr which was likely located beyond the two proximal pairs. As IIBrax are relatively rare and small, second divisions appear to be occasional and also located beyond the second pair of IIBr. Within the morphospace describing the shape of aboral cups, a group of specimens is set aside and attributed herein to a new subspecies, *P. doncieuxi suboblongus* n. subsp. Aboral cups within this variety tends to be very elongated and display a general oblong shape. Moreover this is the only shape collected in some of the explored outcrops (Table 2, see below).

Screenwashing at the Tuilerie de Fontcouverte has provided 387 columnals (excluding proxistele columnals) and 7 aboral cups, i.e., an average of 55 columnals per individual suggesting a stalk length of approximately 165 mm. Half of these columnals have well-developed rhizoid sockets and correspond to the distal stalk. The erect part should, on average, be in the order of 80 to 90 mm (about 30 columnals excluding proxistele). Gislén (1927) described a population of the extant rhizocrinid, *Democrinus japonicus*, with one phenotype converging with that of *P. doncieuxi*: highly variable aboral cup with Hc/Dc up to 4.5, proxistele restricted to the transition with the mesistele, rhizoids appearing near the thirtieth columnal for preserved stalk lengths varying from 50 to 100 mm with 35 to 61 columnals articulated by synarthries ($H/D \sim 1.6-1.7$).

Occurrence. Early Ypresian (Ilerdian, NP10-11), north Pyrenean basin especially in Corbières (Roux and Plaziat 1978; present study) and south Pyrenean basin of Graus-Tremp (Gaemers 1978; Leturcq 1999).

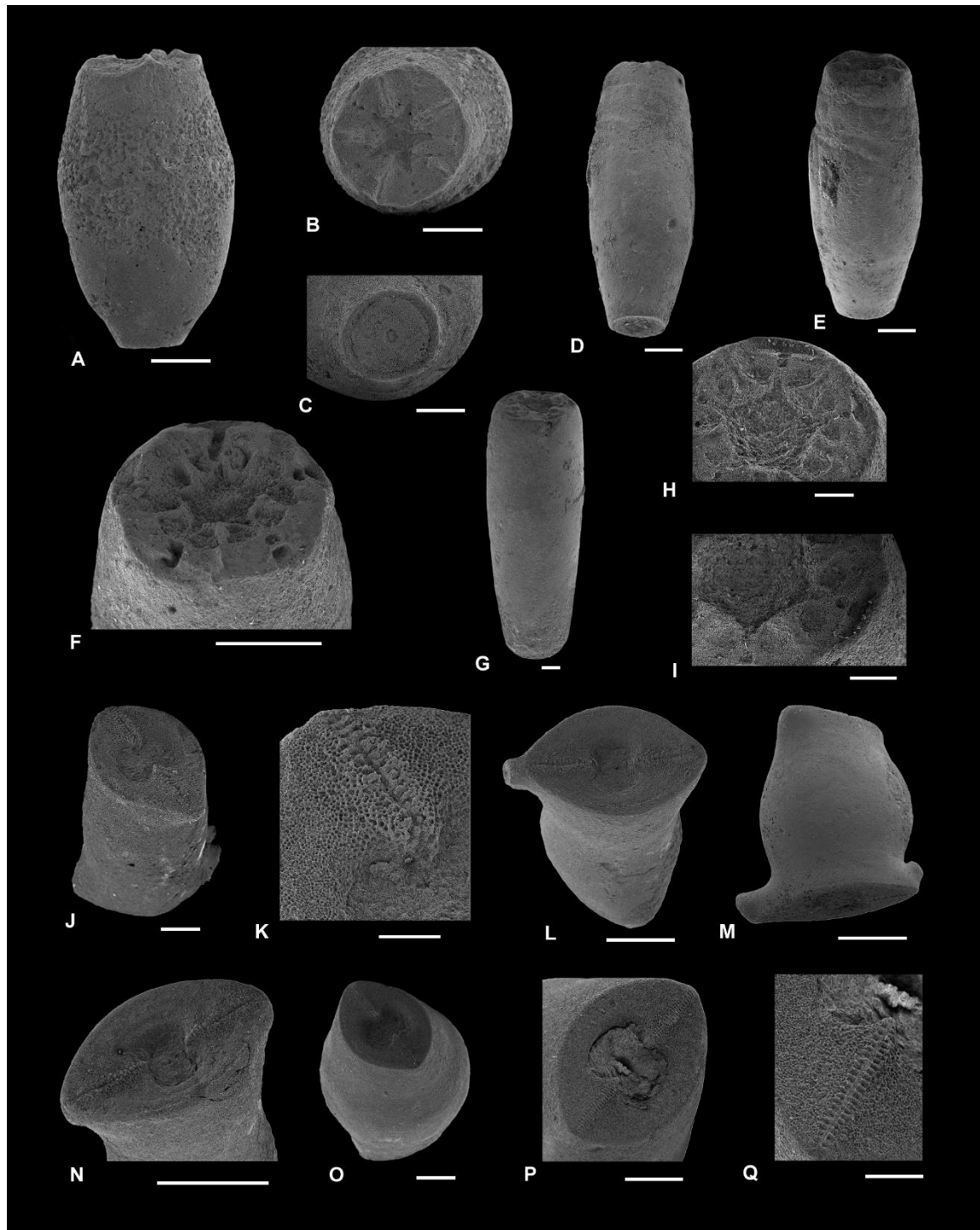


FIGURE 8. Aboral cups and columnals of *Pseudoconocrinus doncieuxi* and aboral cup of *?Democrinus cf. elongatus*. A-F: *P. doncieuxi suboblongus* n. subsp.; A-C: holotype from Fontcouverte à l'Estagnol (MNHN.F.A81998), A: lateral view, B: distal face of radial circling, C: aboral face with stalk insertion with proximalmost columnals preserved; D-F: paratypes, D-E: from Lavade (MNHN.F.A81999), F: from Réqui (MNHN.F.A82000), D: oblique lateral view showing stalk insertion, E: oblique lateral view of same specimen showing proximal face of radial circling, F: distal face of radial circling; G-I: *?D. elongatus* from Lavade (MNHN.F.A82010), G: lateral view, H: distal face of radial circling, I: detail of H showing interradianal crest and muscular synarthrial facet; J-Q: columnals of *P. doncieuxi* from Fontcouverte à l'Estagnol (MNHN.F.A69946), J-K: columnal of middle mesistele, K: detail of fulcral ridge; L-N: columnals of dististele, L: oblique proximal view, M: lateral view, N: distal facet, O-Q: columnal of distal mesistele, Q: detail of fulcral ridge. Scale bar equals 1 mm (A-B, D-F, G), 0.5 mm (C, H-I, L-P), 0.25 mm (J, Q) and 0.12 mm (K).

Pseudoconocrinus doncieuxi suboblongus n. subsp.

Figs. 8A-F, 9

Type-material. Holotype (MNHN.F.A81998; Fig. 8A-C, Plaziat Collection), from Fontcouverte (à l'Estagnol); paratype A (MNHN.F.A81999; Fig. 8D-E), from Fontcouverte (Lavade); paratype B (MNHN.F.A81999; Fig. 8F) from Montlaur (Réqui).

Etymology. In reference to the oblong shape of the aboral cup.

Material examined. In addition to the type series, 10 aboral cups from the Tuilerie de Fontcouverte (in UCB-FSL 170248b, and Martinez Collection); 125 aboral cups and 238 columnals from Réqui, some aboral cups and columnals from other sites (see Table 2) in the Martinez and Vizcaïno collections.

Diagnosis. Variety with often very elongated aboral cup, Hc up to 155 mm, H/D most often > 2.5 and sometimes up to 5.7, Dc maximum located in central or adoral third, aboral third in inverted truncated cone with base corresponding to stalk insertion, adoral third truncated conical or subcylindrical in shape, distal face of radial circlet almost flat with marked star-shaped central depression in largest specimens, stalk insertion wide ($Dp/Dr > 0.50$), columnals usually without marked bulge at mid-height.

Description. Quantitative characters of the three aboral cups of the type series listed in Table 3. Holotype: aboral cup with maximum Dc in central swollen third (Fig. 8A); adoral third in truncated cone, distal surface flat entirely occupied by insertion of arms, strongly star-shaped central cavity (Fig. 8B); aboral third in inverted truncated cone with flat base entirely occupied by stalk insertion housing proximalmost discoid columnals (Fig. 8C). Paratype A: aboral cup similar in shape to holotype but more elongated (H/D 2.5) and illustrating general trend of aboral cups from the Lavade and Requi sites (Fig. 8D-E). Paratype B: exceptionnally well-preserved, almost flat adoral face showing moderately protruding interradial ridges, with large, slightly star-shaped central cavity, and aboral and inner ligament areas of synarthries better developed than muscular areas (Fig. 8F).

Characters	Hc	Dc	Dr	Dp	Hc/Dc	Dr/Dc	Dp/Dc	Dp/Dr
Minimum	1.65	0.93	0.91	0.72	1.32	0.58	0.43	0.55
Maximum	11.4	2.94	2.45	1.81	5.73	1.00	0.89	0.94
Mean	4.52	1.80	1.53	1.13	2.45	0.86	0.64	0.75

TABLE 5. Quantitative characters of a sample of 125 aboral cups of *P. doncieuxi suboblongus n. subsp.* from Réqui near Montlaur (Martinez and Vizcaïno collections). For abbreviations, see Fig. 2. Values in mm, except for ratios.

Characters	H	D	d	d'	H/D	D/d	d'/D	d'/d
Minimum	0.95	0.56	0.26	0.37	0.91	1.02	0.50	0.75
Maximum	3.49	3.00	2.25	2.40	2.95	1.78	1.11	1.40
Mean	1.95	1.31	1.08	1.07	1.55	1.22	0.81	0.98

TABLE 6. Quantitative characters of a sample of 238 rhizocrinid columnals from Réqui near Montlaur (Martinez and Vizcaïno collections) in a bed with abundant aboral cups of *Pseudoconocrinus doncieuxi suboblongus n. subsp.* For abbreviations, see Fig. 2. Values in mm, except for ratios.

Tables 5 and 6 list the general quantitative characters of aboral cups and columnals from the Réqui site where this variety strongly predominates; these specimens display a much smaller size than those of *P. doncieuxi* from the Tuilerie de Fontcouverte and a tendency towards greater and earlier elongation (Hc/Dc from 2.5 to 5.73 for $1.7 < Dc < 3.0$ mm) (Fig. 8).

Remarks. *Pseudoconocrinus doncieuxi suboblongus n. subsp.* is present at numerous sites, but with widely varying frequencies. In the particular environment of Réqui (see above), this variety strongly predominates in several of the marl layers sampled. Aboral cups with $Dc > 1.7$ mm have a much less variable shape than those with $Dc > 2.5$ from the Tuilerie de Fontcouverte (Fig. 9). This suggests a tendency for elongation during ontogeny that was channeled by environmental factors early during growth. At Réqui, the absence of brachials and rhizoid segments, the abnormal relative abundance of aboral cups compared to columnals (about 3 columnals per 1 aboral cup), as well as the poor preservation due to attrition and biocorrosion indicate a displacement of the ossicles that does not allow us to estimate average stalk length.

Occurrence. Early Ypresian (middle Ilerdian, NP 10-11), Corbières.

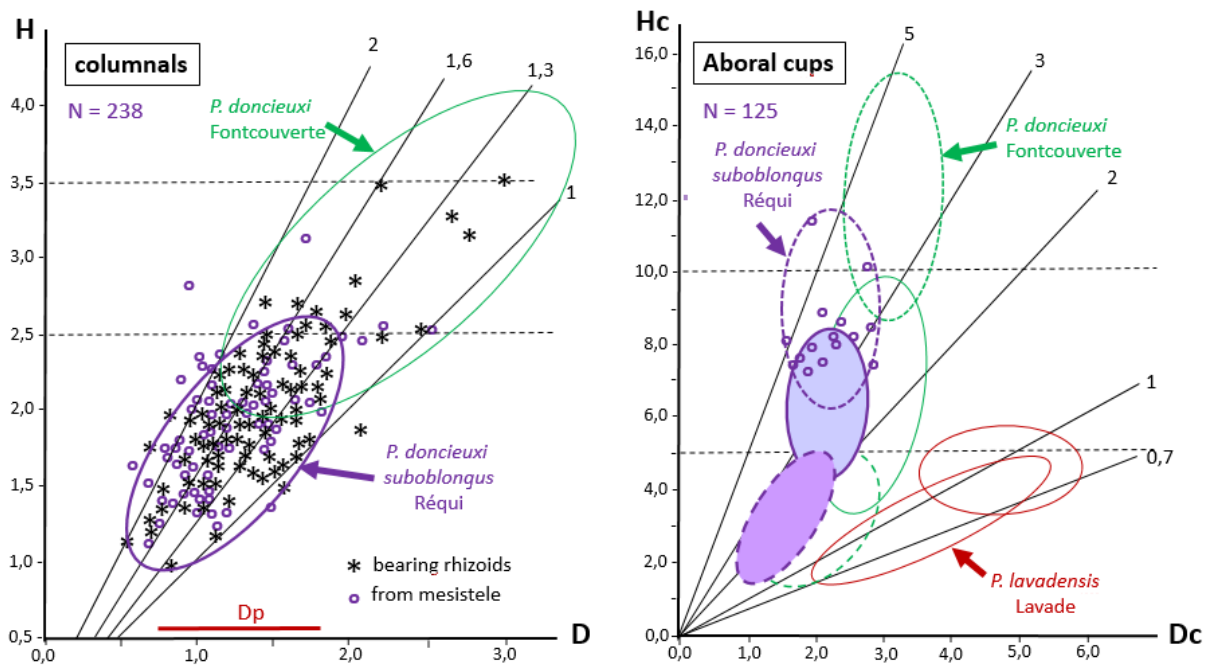


FIGURE 9. Variations in main quantitative characters related to columnal shape and aboral cups of *P. doncieuxi suboblongus n. subsp.* from Réqui. The coloured envelopes cover more than 90% of specimens; straight lines indicate values of H/D (left) and Hc/Dc (right) (in purple: specimens from Réqui, and, for comparison, in green: *P. doncieuxi* from the Fontcouverte sites, except for Lavade, in red: *P. lavadensis n. sp.* from Lavade). D_p and red bar: range of stalk insertion diameter (= proximalmost stalk diameter) measured on aboral cups from Réqui. Values in millimeters, except for ratios (black straight lines). See Fig. 2 for abbreviations.

***Pseudoconocrinus lavadensis* n. sp.**

Figs. 10-13

Type material. The type series, deposited in the collections of the Muséum national d'Histoire naturelle de Paris (see Table 1), comprises a selection of 15 aboral cups, 7 of which are figured (Fig. 10), including the holotype (Fig. 10A-B), 7 brachials including 2 figured (Fig. 11A-C), 35 columnals of the proxistele, including 4 figured (Fig. 11D-G), 40 columnals of the mesistele and more distal ones, including 3 figured (Fig. 11H-L) and 10 fragments of rhizoids including 3 figured (Fig. 11M-O).

Etymology. From Lavade near Fontcouverte (Aude), where the type series and abundant material were collected.

Material examined. Numerous ossicles in sieving residues (20 kg of sediment) from Lavade (113 aboral cups, 3,656 columnals, numerous brachials), and 3 aboral cups and 29 columnals from La Côte (Moux). Those that were not selected to constitute the type series, are in the Martinez Collection.

Diagnosis. Aboral cup often subspherical, more or less flattened both aborally and adorally, with distal face displaying a low to moderate relief, central star-shaped depression equal to or less than one third of distal diameter of radial circlet, ratio D_c/H_c between 0.64 and 1.33 (mean 0.88), ratio of diameter of stalk insertion to D_c most often between 0.30 and 0.50. IBr_1 1.5 times wider than high, distal facet convex. IBr_{2ax} pentagonal; proximal facet very concave with neural canal lumen subrectangular, distal muscular synarthries lateral edges juxtaposed to form very marked medial crest. $IIBr_{ax}$ unknown; numerous brachial pairs. Well-differentiated proxistele; proximalmost discoid columnals with flat facets, becoming thicker distally with concave facets devoid of a fulcral ridge and maximum diameter at mid-height. Proximal mesistele columnals with external surface usually strongly convex and almost as high as wide ($H/D < 1.5$); distal columnals displaying the same general shape and lateral convexity often only marked at mid-height or fading; 2 to 4 rhizoid insertions per columnal, occasionally 5.

Type stratum. middle blue marls of middle Ilerdian age, upper NP11.

Type locality. Lavade near Fontcouverte (Aude).

Description of aboral cups of type series. Holotype (MNHN.A82001) (Fig. 10A-B) subspherical, slightly flattened along adoral-aboral axis (HC/D_c 0.81), smooth external surface, indistinct sutures; aboral diameter (stalk insertion) $1/3 D_c$; distal face of radial circlet wide (Dr/D_c 0.90) and low relief with moderately developed central star-shaped cavity (Dr/D_c 0.26), discrete rectilinear interradian ridges and articular facets mainly occupied by ligament areas. Quantitative characters of the 15 aboral cups of type series given in Table 7. General shape varying from slightly pyriform (Fig. 10C, G) to strongly flattened (Fig. 10I), stalk insertion deeply concave with edges usually well-marked (Fig. 10E); relief of the distal face of radial circlet of highly variable, occasionally almost flat (Fig. 10I) or with interradian ridges ending in strong widening at edge of central cavity forming more pronounced relief (Fig. 10F, J); central cavity circular (Fig. 10F), pentagonal (Fig. 10J), occasionally star shaped as in the holotype, most often $D_d/Dr < 0.35$; sutures between basals always indistinct except sometimes towards aboral end. Paratype 11 with three IBr_1 still attached to aboral cup (Fig. 10K-L). Paratype 8 with one radial recessed, smaller than others, but without trace of predatory attack.

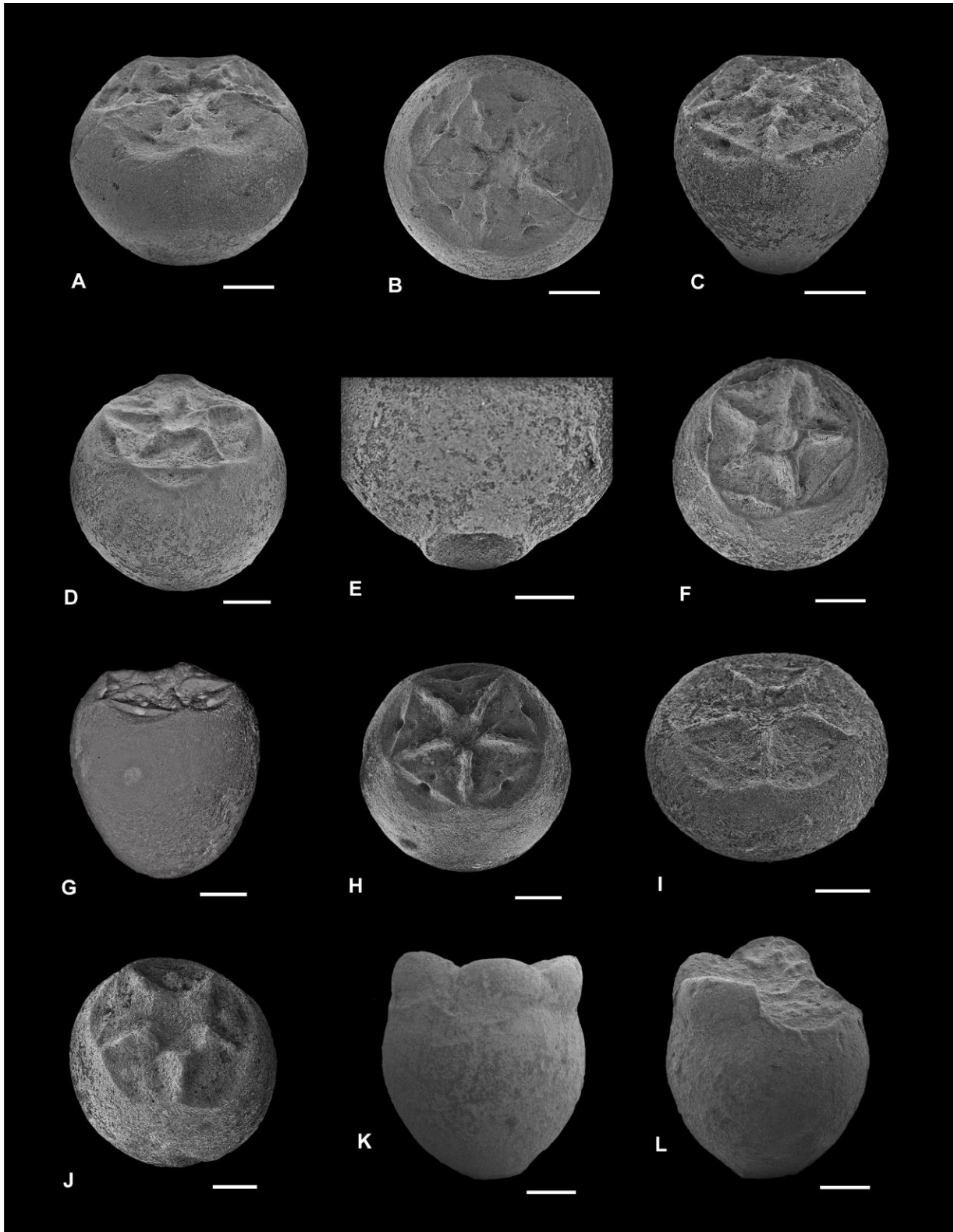


FIGURE 10. Aboral cups of the type series of *Pseudoconocrinus lavadensis* n. sp. from Lavade (Fontcouverte), documenting intraspecific morphological variations. A-B: holotype (MNHN.F.A82001); C-L: paratypes (MNHN.F.A82002), C: paratype 2, D-F: paratype 5, G-H: Paratype 6, I: Paratype 7, J: Paratype 4, K-L: Paratype 11; A, C, D, F, H-J: distal oblique views; B: distal face of radial circling; E: oblique view of aboral face with stalk insertion; G, K-L: lateral views; K-L: specimen preserved with three IBr1, two of which in process of dissociation (K) and one remaining in place (L). Scale bar equals 1 mm.



FIGURE 11. Brachials, columnals and rhizoids of the type series of *Pseudoconocrinus lavadensis* n. sp. from Lavade. A-C: IBr2ax (MNHN.F.A82004), A: oblique external view, B: same specimen, detail of proximal synostosis, C: other IBrax, inner view; D-G: proxistele columnals (MNHN.F.A82006); F-G: proxistele-mesistele transition; H-L: distal stalk columnals and rhizoid segments (MNHN.F.A82008), H: columnals without swollen body, I-L: columnals with swollen body, K: detail of fulcral ridge of J; M-O: rhizoid fragments. Scale bar equals 1 mm, except for K where it equals 0.5 mm.

Specimen (Figure)	Hc	Dc	Dr	Dp	Dd	Wr	Hc/Dc	Dr/Dc	Dp/Dc	Dd/Dr
Paratype 9	1.79	2.10	2.03	0.85	-	1.06	0.85	0.97	0.40	-
Paratype 8	2.09	2.74	2.15	0.70	0.52	1.05	0.76	0.78	0.26	0.24
Paratype 10	2.30	2.94	2.45	1.10	0.65	1.30	0.78	0.83	0.37	0.26
Paratype 2 (10C)	3.50	3.55	3.10	1.60	1.00	1.72	0.99	0.87	0.45	0.32
Paratype 3	3.35	3.89	3.15	1.47	0.73	1.75	1.00	0.81	0.38	0.23
Paratype 11 (10K-L)	4.15	4.10	3.74	1.66	1.15	2.10	1.01	0.91	0.40	0.29
Paratype 6 (10G-H)	4.65	4.14	3.50	1.52	0.80	1.80	1.12	0.84	0.37	0.23
Paratype 4 (10J)	4.30	4.28	3.60	1.58	1.35	2.19	1.00	0.84	0.37	0.37
Paratype 7 (10I)	2.94	4.43	3.78	0.80	0.66	1.90	0.66	0.85	0.18	0.17
Paratype 12	4.12	4.51	4.04	1.50	1.20	2.15	0.95	0.90	0.33	0.30
Paratype 1	5.40	4.57	3.75	1.40	1.15	1.95	1.18	0.82	0.31	0.31
Paratype 5 (10D-F)	4.32	4.64	3.45	1.60	1.20	2.00	0.93	0.76	0.34	0.35
Holotype (10A-B)	3.85	4.73	4.25	1.57	1.11	2.05	0.81	0.90	0.33	0.26
Paratype 14	4.10	5.67	4.13	2.05	1.25	2.15	0.72	0.73	0.36	0.30
Paratype 13	4.88	5.73	4.97	1.82	-	2.40	0.85	0.87	0.32	-

TABLE 7. Quantitative characters of aboral cups of the type series of *Pseudoconocrinus lavadensis* **n. sp.** by order of size (Dc used as growth index). For abbreviations, see Fig. 2 and Table 3. Values in mm, except for ratios.

Description of brachials, columnals and rhizoids of type series. Quantitative characters of primibrachials of type series given in Table 8. Three IBr1 still attached to paratype 11 (Fig. 10K-L), two of them slightly dissociated from adjacent radials, convex and spindle-shaped outer surface, almost 1.5 times wider than high, very convex distal outer border, distal facet convex but poorly preserved. Thick, subpentagonal IBr2ax with rectilinear or slightly concave distal outer edges (Fig. 11A), proximal facet strongly concave with subrectangular neural canal (Fig. 11B), broad adoral axial gutter (Fig. 11C).

Specimen	Figure	Brachial	Wd	Wp	H	Wm	Wd/Wp	H/W'
Paratype 16	-	IBr1	1.37	1.62	0.90	-	0.85	0.56
Paratype 19	-	IBr2ax	2,29	1,8	1,71	1,32	1,27	0,75
Paratype 21	-	IBr2ax	2,45	1,8	1,73	1,52	1,36	0,71
Paratype 22	11A-B	IBr2ax	2.45	1.82	1.85	1.57	1.35	0.76
Paratype 20	-	IBr2ax	2,35	1,84	1,82	1,3	1,28	0,77
Paratype 12	11K-L	IBr1	1.65	2.10	1.10	-	0.79	0.52
Paratype 17	11C	IBr2ax	2.71	2.16	2.14	1.68	1.25	0.79
Paratype 18	-	IBr2ax	3,42	2,75	2,3	1,8	1,24	0,67

TABLE 8. Main quantitative characters of primibrachials of the type series of *Pseudoconocrinus lavadensis* **n. sp.** H: height, Wd: width of distal facet or maximum width on distal part of axillaries, Wm: width of distal axillary muscular synarthry, Wp: width of proximal facet, W': maximum width value (Wd or Wp). Wp used as growth index. For abbreviations see Fig. 2 and Table. 4. Values in mm, except for ratios.

Articular facet	Outer surface	Values	H	D	H/D	location
Flat or slightly concave	Straight or ± convex	Minimum	0.16	1.00	0.16	the most proximal
		Maximum	0.91	1.82	0.50	
		N. columnals	8	8	8	
concave	convex	Minimum	0.70	1.07	0.45	other part of proxistele
		Maximum	1.44	2.27	0.89	
		N. columnals	19	19	19	
± flat with rudimentary fulcral ridge	Straight or convex	Minimum	0.97	1.40	0.49	proxistele - mesistele transition
		Maximum	2.15	1.88	1.04	
		N. columnals	8	8	8	

TABLE 9. Columnal characters in the proxistele of the type series of *Pseudoconocrinus lavadensis* n. sp. For abbreviations see Fig. 2. Values in mm, except for ratios.

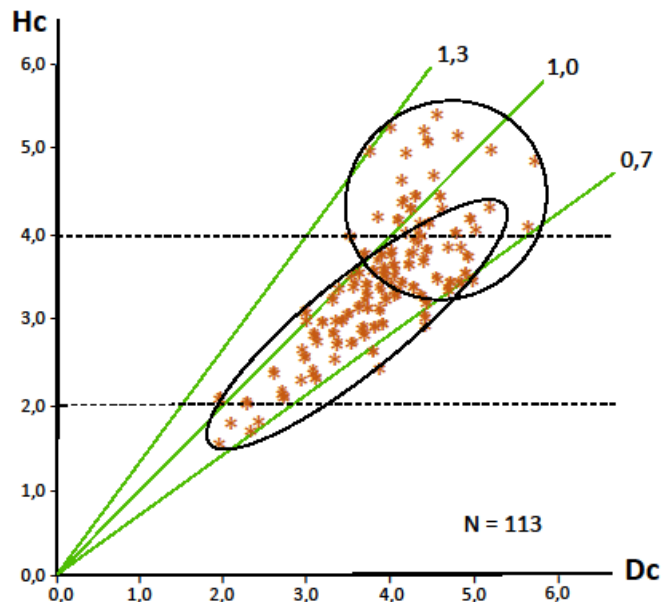


FIGURE 12. Variations in main quantitative characters related to aboral cup shape of *Pseudoconocrinus lavadensis* n. sp. from Lavade. Values in millimeters, except for ratios HC/DC (green straight lines). See Fig. 2 for abbreviations.

Quantitative characters of the columnals of the proxistele given in Table 9. Most proximal columnals cylindrical and flat faced, occasionally with slightly raised perilumen (Fig. 11D-E), most frequent proximal columnals from a more distal position in the proxistele with higher values of H and displaying concave facets without a fulcral ridge and external surface usually markedly convex (Fig. 11F), proxistele-mesistele transition identified by appearance of rudimentary fulcral ridge (Fig. 11G) and H/D values reaching 1. Columnals articulated by synarthries showing lateral bulge at mid-height (Fig. 11I) or not (Fig. 11H); 8-shaped ligament fossa well developed without extension on either side of fulcral ridge, fulcral ridge with regular secondary crenulation and more or less marked axial groove (Fig. 11J-K). Distal columnals with rhizoid socket diameter <0.6 mm (Fig. 11H-L). Rhizoid segments up to 7.5 mm long with diameter between 0.41 and 1.42 mm, ossicles of highly variable height

($0.7 < H < 7.7$), largest unbranched H 4.5 mm and D 1.3 mm, fragments of proximal rhizoids with clear articular sutures (synostoses) and often with large branch at one end (Fig. 11M-N), more distal fragments with fused ossicles and multiple insertions of small rhizoids (Fig. 11-O).

Description of other ossicles. Variations of aboral cups collected at Lavade summarised in Table 10; general shape variations moderate ($0.7 < Hc/Dc < 1.33$) within a group composed of some of the largest specimens, and relatively restricted in others ($0.7 < Hc/Dc < 1.0$) (Fig. 12). IBr1 very rarely found; one isolated IBr in Martinez Collection showing proximal facet with protruding fulcral ridge and large, deep muscular areas. IIBr2ax unknown, despite abundance of material collected. Other brachials with characters similar to those of *P. doncieuxi*. Washing of 20 kg of sediment provided 35 columnals of circular facets belonging to proxistele (0.96%) and 3,621 columnals articulated by oval synarthries of

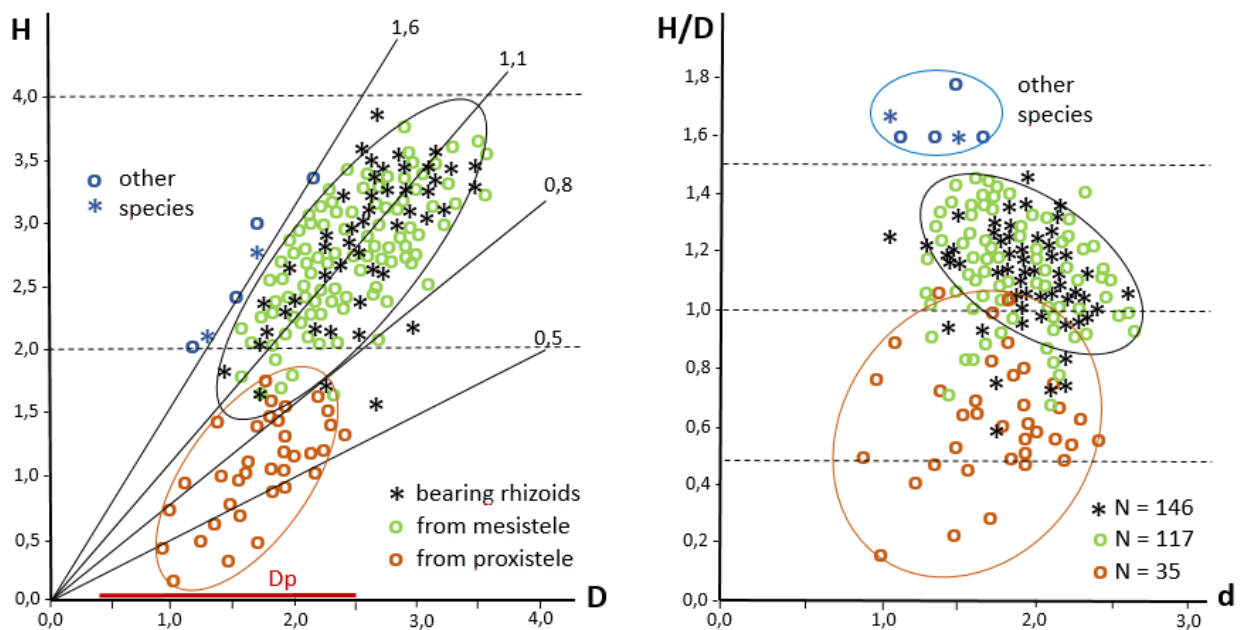


FIGURE 13. Variation in main quantitative characters of columnals from Lavade. Other species: columnals that can be attributed to *?Democrinus elongatus*. To make the scatter plot clearer, only ~50% of columnals bearing rhizoids were represented. Envelopes encompass at least 90% of all groups of columnals. D and d used as growth index. Values in millimeters, except for ratios H/D (black straight lines at left). See Fig. 2 for abbreviations.

Characters	Hc	Dc	Dr	Dp	Dd	Wr	Hc/Dc	Dr/Dc	Dp/Dc	Dd/Dr
Minimum	1.52	1.95	1.95	0.45	0.52	1.05	0.64	0.89	0.20	0.17
Maximum	5.40	5.73	4.66	2.56	1.95	2.95	1.33	1.00	0.76	0.58
Mean	3.46	3.94	3.59	1.73	1.31	2.28	0.88	0.92	0.44	0.35
N aboral cups	113	113	112	112	38	87	113	112	112	38

TABLE 10. Quantitative characters of the 113 aboral cups of *Pseudoconocrinus lavadensis* n. sp. from Lavade near Fontcouverte. For abbreviations see Fig. 2 and Table 3. Values in mm, except for ratios.

Characters	H	D	d	d'	H/D	d/D	d'/D	d'/d
Minimum	1.46	1.26	1.06	0.91	0.58	0.57	0.66	0.86
Maximum	3.85	3.56	2.65	3.79	1.46	0.98	1.27	1.69
Mean	2.76	2.45	1.89	2.32	1.13	0.78	0.95	1.22

TABLE 11. Variations in quantitative characters in a sample of 263 columnals articulated by synarthries of *Pseudoconocrinus lavadensis* n. sp. from Lavade. For abbreviations, see Fig. 2. Values in mm, except for ratios.

which 2,385 (65.23%) bearing one or more rhizoid sockets. Measurements were made on a randomly selected sample out of 263 columnals articulated by synarthry (Table 11; Fig. 13) with usually $0.85 < H/D < 1.45$, H/D remaining highly variable during growth, quantitative characters alone not allowing to distinguish columnals from mesistele and dististele; frequent lateral bulging at mid-height (48% with $d'/d > 1$). 20, 28 % with $d/D > 1.0$); 70 % of synarthries with $1.15 < D/d < 1.50$; distal pluricolumnals from 2 to 5 columnals, rhizoid insertions per columnal in variable number (35% 1 insertion on 1 facet, 50% 2 insertions on 1 facet, others >2 insertions up to 5), maximum diameter 1.25 mm for columnal with D 2.9 mm and d 2.15 mm.

Remarks. Sediment samples from Lavade have yielded 33 columnals (excluding proxistele) per aboral cup, 65% of which bear rhizoid sockets. This suggests a much shorter stalk (mean 92 mm) in *P. lavadensis* n. sp. than in *P. doncieuxi* (mean 165 mm). In *P. lavadensis* n. sp. the relatively high frequency of columnals from the proxistele indicates a more developed and well-differentiated proxistele composed of columnals with markedly concave facets and devoid of a fulcral ridge; these features are unknown in *P. doncieuxi*. The subspherical shape of aboral cups in *P. lavadensis* n. sp. corresponds to an increase in height delayed in favour of an increase in diameter during the ontogeny

Species of <i>Pseudoconocrinus</i>		<i>P. doncieuxi</i>	<i>P. lavadensis</i> n. sp.
Aboral cup	Shape	Tendency to elongation, strong variations in shape, $Dr/Dc < 0.8$, $0.8 < Hc/Dc < 5$ (mean 2.0)	Subspherical± flattened, weak variations in shape, $Dr/Dc > 0.8$, $0.6 < Hc/Dc < 1.3$ (mean 0.88)
	Size	Hc up to 15.3 mm (mean 6.1) Dc up to 5.0 mm (mean 3.2)	Hc up to 5.4 mm (mean 3.4) Dc up to 5.7 mm (mean 3.9)
Axillary Br	I _{Br} 2ax	Proximal facet moderately concave with subcircular lumen	Proximal facet strongly concave with subrectangular lumen
	II _{Br} ax	Present	Unknown
Stalk	Estimated length	Mean >15 cm About 1/2 proximal erected	Mean <10 cm About 1/3 proximal erected
	Stalk insertion	Dp/Dr 0.55-0.94 (mean 0.75)	Dp/Dr 0.24-0.77 (mean 0.48)
Columnals	Proximal (proxistele)	Rare, not differentiated with flat facets	Present, differentiated with concave facets
	Without rhizoids	About 50 % of columnals usually $H/D > 1.5$	About 40 % of columnals always $H/D < 1.5$
	With rhizoids	$< 50\%$ with 2 rhizoid sockets (rarely 3)	$>50\%$ with 2 rhizoid sockets or more (up to 5)
	All columnals	$<50\%$ with $d'/D > 0.9$	$>50\%$ with $d'/D > 0.9$

TABLE 12. Main characters distinguishing the two species of *Pseudoconocrinus* from the Ilerdian of Corbières.

of the basal circlet (Fig. 12), which is the contrary of what is observed in *P. doncieuxi* (Fig. 5). The two species of *Pseudoconocrinus* from Corbières clearly differ in the opposite ontogenic trajectory of their aboral cup (Fig. 9). Table 12 summarises the main characteristics that distinguish *P. lavadensis* n. sp. from *P. doncieuxi*.

Occurrence. Early Ypresian (middle Ilerdian, upper NP 11) in Corbières, only known from Lavade (Fontcouverte) and La Côte (Moux).

Genus *Democrinus* Perrier, 1883

Type species. *Democrinus parfaiti* Perrier, 1883, Recent.

Remarks. In the absence of precise information on brachials and columnals that could clearly be attributed to them, and in view of the great variability of known external morphology in extant species (Roux 1978b), the attribution of fossil species to this genus is based solely on the morphology of the proximal face of the radial circlet (Roux *et al.* 2019). We consider that this generic attribution needs confirmation, awaiting data on brachials and columnals; for this reason, we here use open nomenclature, as *?Democrinus*.

Stratigraphical distribution. Ypresian–Recent, possibly already from Danian.

?Democrinus elongatus (Roux, 1978c)

Fig. 8G-I

Synonymy. *Conocrinus elongatus* Roux, 1978c: 265-266, fig. 1A ; Roux *et al.* 2019: 66, 77; *Bourgueticrinus* sp. Zamora *et al.* 2018: 788, 791, fig. 10G ; *?Democrinus elongatus* Roux *et al.* 2019: 67, fig. 8G-J.

Type material. The holotype (UCBL-FSL 19210A) is from the Bartonian at Biarritz (Côte des Basques, Villa Marbella).

Material examined. 4 aboral cups from Lavade; specimen A (MNHN.F.A82010) is Fig. 8G-I, the other three are in the Martinez Collection.

Locality. Lavade near Fontcouverte (middle Ilerdian, NP11).

Specimen	Hc	Dc	Dr	Dp	Dd	Wr	Hc/Dc	Dr/Dc	Dp/Dc	Dd/Dr
A	5.42	1.72	1.39	0.72	0.56	0.70	3.15	0.81	0.42	0.40
B	4.25	1.84	1.64	1.27	0.65	0.80	2.31	0.89	0.69	0.40
C	8.90	2.86	2.45	2.00	0.97	1.21	3.11	0.86	0.70	0.40
D	11.17	3.03	2.15	1.50	0.90	0.95	3.69	0.71	0.50	0.42

TABLE 13. Variations in the main quantitative characters of Lavade aboral cups attributed to *?Democrinus elongatus*. Dp: diameter of the stalk insertion, Wr: width of the articular facet distal to a radial; for other abbreviations see Fig. 2. Dc used as growth index. Values in mm, except for ratios.

Description. Main variations in quantitative characters of aboral cups given in Table 13. Very elongated aboral cup, with $H/D > 3.1$, except in specimen B, maximum D in upper third, progressive variation of D along height in smallest specimen (Fig. 8G), very weak in others; adoral face with wide, pentagonal central cavity ($Dd/Dr \sim 0.40$), muscular areas more developed than ligament areas, discrete interradial crest with marked bending of inner side of radials (Fig. 8H-I), stalk insertion occupying aboral face. Specimen C with additional circle of plates (H 1.25 mm) prolonging basals, likely resulting from regeneration.

Remarks. Distal face of aboral cup of specimens here attributed to *?Democrinus elongatus* show same characters as those from Bartonian of Biarritz (Roux *et al.* 2019: fig. 8G-J). It can be distinguished from *Pseudoconocrinus doncieuxi suboblongus* **n. subsp.** by radial cirlet with adoral face having muscular areas more developed than ligament areas and interradial bending of the lateral edges of muscular fossae, absence of conspicuous interradial crests and wide, pentagonal to slightly star-shaped central cavity as observed in extant *Democrinus* (Roux *et al.* 2019). Lacking these characters, these two species cannot be separated when aboral cups are very elongated. Mesistele columnals from Lavade with no mid-height swelling and with $H/D \sim 1.6$ (Fig. 13) could belong to this species. Similarly, rare distal columnals from the Tuilerie de Fontcouverte show an extension of ligament depressions on either side of the fulcral crest (Fig. 8E) as observed in some extant species of *Democrinus* (Roux 1977); but no aboral cup of *?D. elongatus* has ever been identified at this site despite the abundance of material. Excess basals due to regeneration anomaly, as observed in specimen C, are frequent in extant *Democrinus japonicus* (Gislén, 1927). The aboral cup of *?D. elongatus* is easily distinguished from that of *D. londinensis* (Forbes, 1852), a Ypresian species from the London Clay whose sutures between plates are conspicuous and $Hc/Dc < 1.20$ (Rasmussen 1972). Zamora *et al.* (2018) attributed to *Bourgueticrinus* sp. an elongated aboral cup from the middle Ilerdian of Puebla de Roda (Graus-Tremp basin, Spain). The distal face of this cup has the typical characters of *?Democrinus elongatus*, which attests to the presence of this species in the south Pyrenean Ilerdian basin. Klikushin (1982) referred to a fragment of an aboral cup from the Upper Eocene of Crimea as "*Conocrinus*" cf. *elongatus*, but failed to present any conclusive character to confirm such an attribution.

Occurrence. Early Ypresian (Ilerdian) of the French-Spanish Pyrenean basin (bays of Languedoc and of Graus-Tremp); Bartonian of Biarritz (Côte des Basques, Villa Marbella).

Genus *Globulocrinus* nov.

Type species. *Globulocrinus amphoraformis* **n. gen, n. sp.**; lower Ypresian.

Etymology. In reference to the basal cirlet of globular feature, at least in juveniles.

Diagnosis. More or less urn- or amphora-shaped aboral cup, oblong to globular basal cirlet, distinct radial cirlet generally subcylindrical to slightly flare and of much smaller diameter than upper part of basal cirlet; distal face of radial cirlet with wide central depression and discrete interradial ridges. Brachials and columnals not yet identified.

Remark. *Conocrinus globulosus* Roux, 1978c is known to the Bartonian of Biarritz (Côte des Basques) only from a small, more or less crushed aboral cup that could correspond to a juvenile

specimen (Roux *et al.* 2019). We prefer to designate as the type species of the genus, *G. amphoraformis* **n. gen., n. sp.**, whose type series illustrates the variability and shape modifications of the aboral cup during growth.

Included species. *Conocrinus globulosus* Roux, 1978c and *Globulocrinus amphoraformis* **n. gen., n. sp.**

Stratigraphical distribution. Eocene (Ypresian–Bartonian).

***Globulocrinus amphoraformis* n. gen., n. sp.**

Figs. 14-15

Type material. 10 aboral cups from Réqui, illustrating the main morphological variations, including the holotype (MNHN.F.A82011) (Fig. 14G) and 9 paratypes (MNHN.F.A82012).

Etymology. In reference to the aboral cup which usually is amphora shaped.

Material examined. In addition to the type series, 158 aboral cups from Réqui in the Martinez and Vizcaino collections.

Diagnosis. Aboral cup covered by fine granulation with variable external morphology. In juveniles, aboral cup urn-shaped with neck formed by radial circlet, $1.0 < Hc/Dc < 1.7$, usually strong constriction between basal and radial circlets, radials occasionally relatively high (Hr/Hc up to 0.44), radial circlet more or less flared, external face of each ossicle often very convex, conspicuous ossicle sutures, stalk insertion pentagonal. Juvenile characters fading or disappearing in largest specimens, with elongation of basals giving an amphora shape to aboral cups (as in holotype), $Hc/Dc > 2$ and reaching almost 3; relative height of radials ($Hr/Hc < 0.2$) decreasing to 0.08 in largest specimens, radials substantially wider than high, stalk insertion becoming circular. Distal face of radial circlet with large central depression, pentagonal to slightly star-shaped. Brachials and columnals unknown.

Type stratum. Base of blue marls of the middle Ilerdian, above *Solenomeris* limestones, late NP10, but maybe already NP11.

Type locality. Réqui, north of Montlaur (commune de Val de Dagne, Aude).

Description of type series. Quantitative characters of aboral cups of type series given in Table 14. Holotype illustrating the amphora shape of aboral cup with neck formed by radial circlet (Fig. 14G), intermediate between globular urn shape of juveniles (Fig. 14A-E) and oblong shape of larger specimens (Fig. 14H-I). Smallest paratype (Fig. 14A) with a flared radial circlet and a large adoral cavity, constriction at basal-radial transition well-marked, maximum diameter at mid-height of basal circlet, very convex outer ossicle surfaces, very conspicuous sutures. All characters highly variable and may become less pronounced during growth: radials becoming markedly shorter than wide, radial circlet more or less flared (Fig. 14A, E, G), straight (Fig. 14C-D, F, I) or more or less conical (Fig. 14B, H) limiting diameter of adoral cavity; constriction between basal and radial circlets reduced (Fig. 14C), rarely disappearing (Fig. 14H); during growth, elongation of basals with disappearance of sutures and maximum diameter in adoral third (Fig. 14F-I); sutures between radials rarely disappearing (Fig. 14H), stalk insertion pentagonal in juveniles (Fig. 14K-L), becoming circular later.

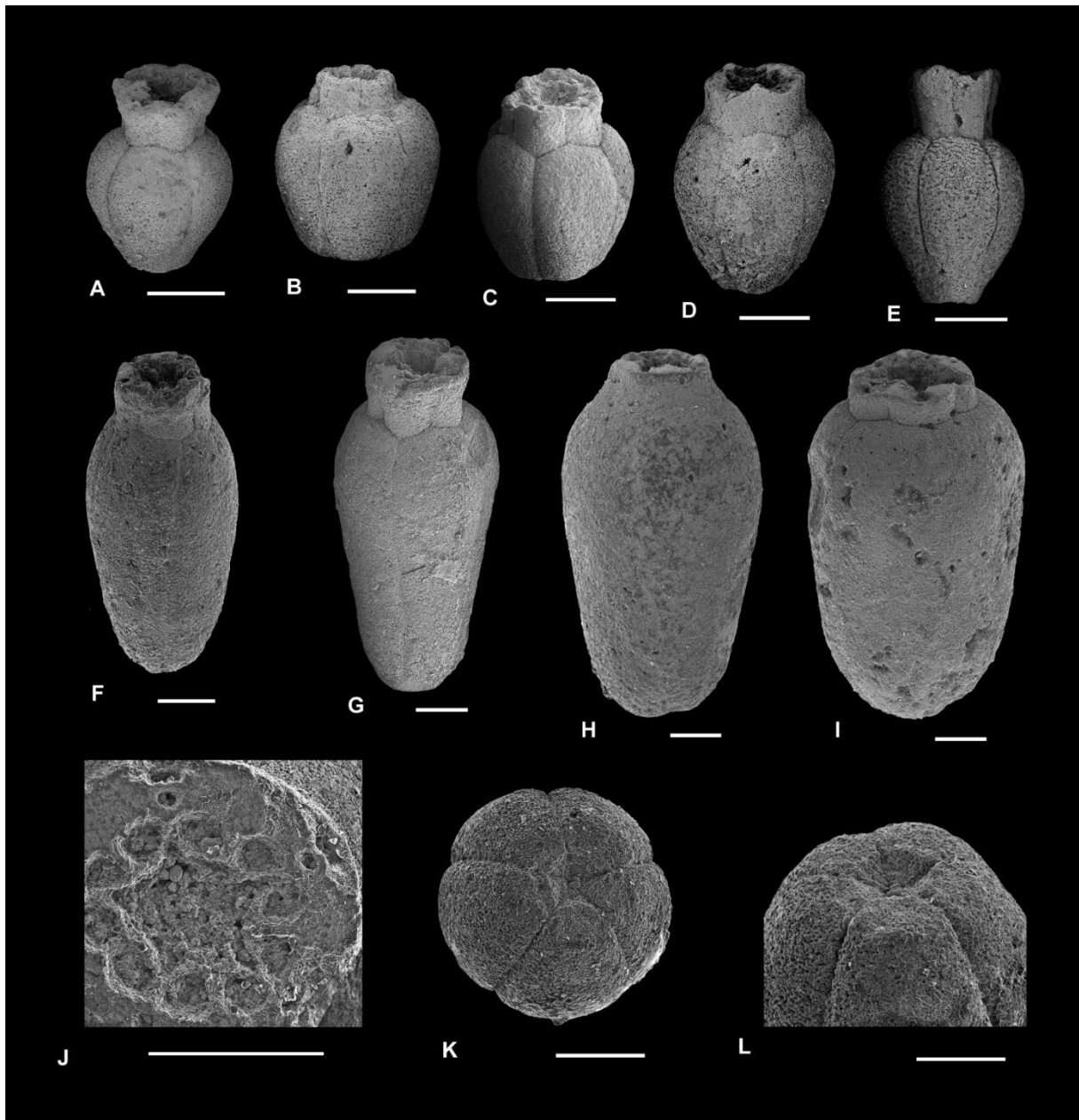


FIGURE 14. Aboral cups of type series of *Globulocrinus amphoraformis* n. gen., n. sp. from Réqui. A-I: lateral views showing variations and changes in morphology during ontogeny, G: holotype (MNHN.F.A82011); A-F, H-L: paratypes (MNHN.F.A82012), A: paratype 1, B: paratype 2, C and K-L: paratype 3, D: paratype 4, E: paratype 5, F: paratype 6, H: paratype 7, I: paratype 8, J: distal face of radial cirlet of paratype 9; K-L: aboral views of basal cirlet of paratype 3, showing pentagonal depression corresponding to stalk insertion. Scale bar equals 0.5 mm.

Adoral face of radial cirlet most often incompletely preserved, fragile interradial crests, marked but not inducing any relief on outer edge of radial cirlet; paratype 9 with worn or broken interradial crests, central pentagonal star-shaped depression with Dd/Dr about 0.4, muscular synarthries with narrow aboral ligament depression, deep subcircular muscle areas more or less equal in surface to internal ligament areas (Fig. 14J).

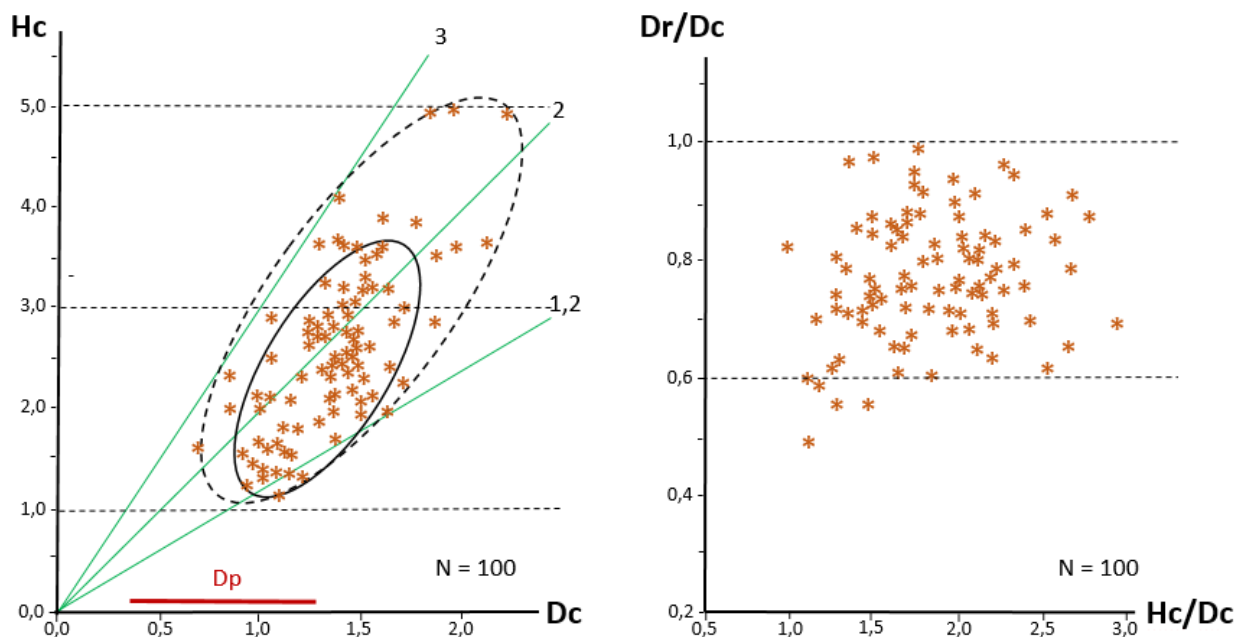


FIGURE 15. Variation in main quantitative characters related to aboral cup shape of *Globulocrinus amphoraformis* **n. gen., n. sp.** from Réqui. Dc used as growth index. Values in millimeters, except for ratios Hc/Dc (green straight lines). See Fig. 2 for abbreviations.

For all specimens, variation of main quantitative characters given in Table 15. About 90% of specimens with $Dc < 1.7$ mm or $Hc < 3.6$ mm, most with $1.2 < Hc/Dc < 2.5$, main ratios (Dr/Dc and Hc/Dc) uncorrelated leading to wide range of variation in aboral cup shape (Fig. 15). Radial circllet flared 50%, straight 40%, conical 10%, Dr always much smaller than maximum diameter of basal circllet.

specimen	Fig. 14	Hc	Hr	Dc	Dr	Dp	Hr/Hc	Hc/Dc	Hr/Dr	Dr/Dc	Dp/Dc
Paratype 1	A	1,22	0.33	0,95	0,7	0,35	0.27	1,28	0,47	0,74	0,37
Paratype 5	E	1,65	0.73	0,99	0,6	0,36	0.44	1,67	1,22	0,61	0,36
Paratype 3	C, K-L	1,34	0.40	1,15	0,8	0,4	0.30	1,17	0,50	0,70	0,35
Paratype 4	D	1,52	0.44	1,15	0,72	0,47	0.29	1,32	0,61	0,63	0,41
Paratype 2	B	1,35	0.35	1,19	0,58	0,4	0.26	1,13	0,60	0,49	0,34
Paratype 6	F	2,89	0.41	1,35	1,1	0,9	0.14	2,14	0,37	0,81	0,67
Holotype	G	3,49	0.60	1,57	1,08	0,9	0.17	2,22	0,56	0,69	0,57
Paratype 9	J	3.80	0.47	1.85	1.25	1.08	0.12	2.05	0.38	0.68	0.58
Paratype 7	H	3,59	0.28	1,98	1,58	1,24	0.08	1,81	0,18	0,80	0,63
Paratype 8	I	3,62	0.30	2,13	1,53	1,12	0.08	1,70	0,20	0,72	0,53

TABLE 14. Quantitative characters of the aboral cups of the type series of *Globulocrinus amphoraformis* **n. gen., n.sp.** Hr: height of radials; for other abbreviations see Fig. 2 and Table 3. Dc used as growth index. Values in mm, except for ratios.

Characters	Hc	Dc	Dr	Dp	Hc/Dc	Dr/Dc	Dp/Dc	Dp/Dr
Minimum	1.11	0.70	0.45	0.35	1.01	0.45	0.34	0.50
Maximum	4.95	2.22	1.58	1.27	2.95	0.98	0.84	1.07
Mean	2.49	1.35	1.03	0.82	1.83	0.77	0.61	0.79

TABLE 15. Variations of main quantitative characters in a sample of 167 aboral cups of *Globulocrinus amphoraformis* **n. gen., n. sp.** from Réqui. For abbreviations, see Fig. 2: Values in mm, except for ratios.

Remarks. Although highly variable, *G. amphoraformis* **n. gen., n. sp.** is easily recognised by its radial circlet that is well individualised with respect to the basal circlet. The shape of the larger aboral cups may converge with that of *Pseudoconocrinus doncieuxi* but their size remains much smaller. Compared to the ontogenic series of *G. amphoraformis* **n. gen., n. sp.**, the single known specimen of the Bartonian species *G. globulosus* with its aboral cup as high as wide may suggest that it is a juvenile. However, its maximum diameter of 3.8 mm, much larger than that of the largest specimens of *G. amphoraformis* **n. gen., n. sp.** and its sutureless basal circlet surmounted by a radial circlet that is very close to that of the largest aboral cups from Réqui (Fig. 14-I), suggest rather an adult specimen. If this is the case, *G. globulosus* would be distinguished principally by the absence of basal circlet elongation during growth. Brachials are unknown. Columnals are unidentified.

Occurrence. Early Ypresian (middle Ilerdian) of Corbières; species only known from Réqui near Montlaur (Val de Dagne, Aude).

Genre *Cherbonnierocrinus* Roux, Eléaume & Améziane, 2019

Type species. *Conocrinus cherbonnieri* Roux, 1976, Recent.

Stratigraphical distribution. Danian–Recent.

Cherbonnierocrinus requiensis **n. sp.**

Fig. 16A-G

Type material. 5 aboral cups, the best-preserved of which is designated holotype (MNHN.F.A82013) (Fig. 16E-G), the others are paratypes 1 to 4.

Etymology. From the type locality Réqui near Montlaur (Val de Dagne, Aude).

Specimen	Figure	Hc	Hr	Dc	Dd	Dp'	Wr	Hc/Dc	Hr/Hc	Dd/Dc	Dp'/Dc
Holotype	16E-G	1.36	0.36	0.71	0.34	0.36	0.33	1.91	0.26	0.49	0.51
Paratype 3	16D	1.09	0.47	0.78	-	0.37	0.33	1.40	0.43	-	0.47
Paratype 1	16A	1.03	0.38	0.79	-	0.40	0.31	1.30	0.37	-	0.51
Paratype 4	-	1.10	0.46	0.83	-	0.39	0.38	1.32	0.42	-	0.47
Paratype 2	16B-C	1.16	0.38	0.85	0.38	0.41	0.34	1.36	0.33	0.45	0.48

TABLE 16. Main quantitative characters of the aboral cups (type series) of *Cherbonnierocrinus requiensis* **n. sp.** Dp': aboral diameter. Dc is used as growth index. For abbreviations, see Fig. 2. Values in mm, except for ratios.

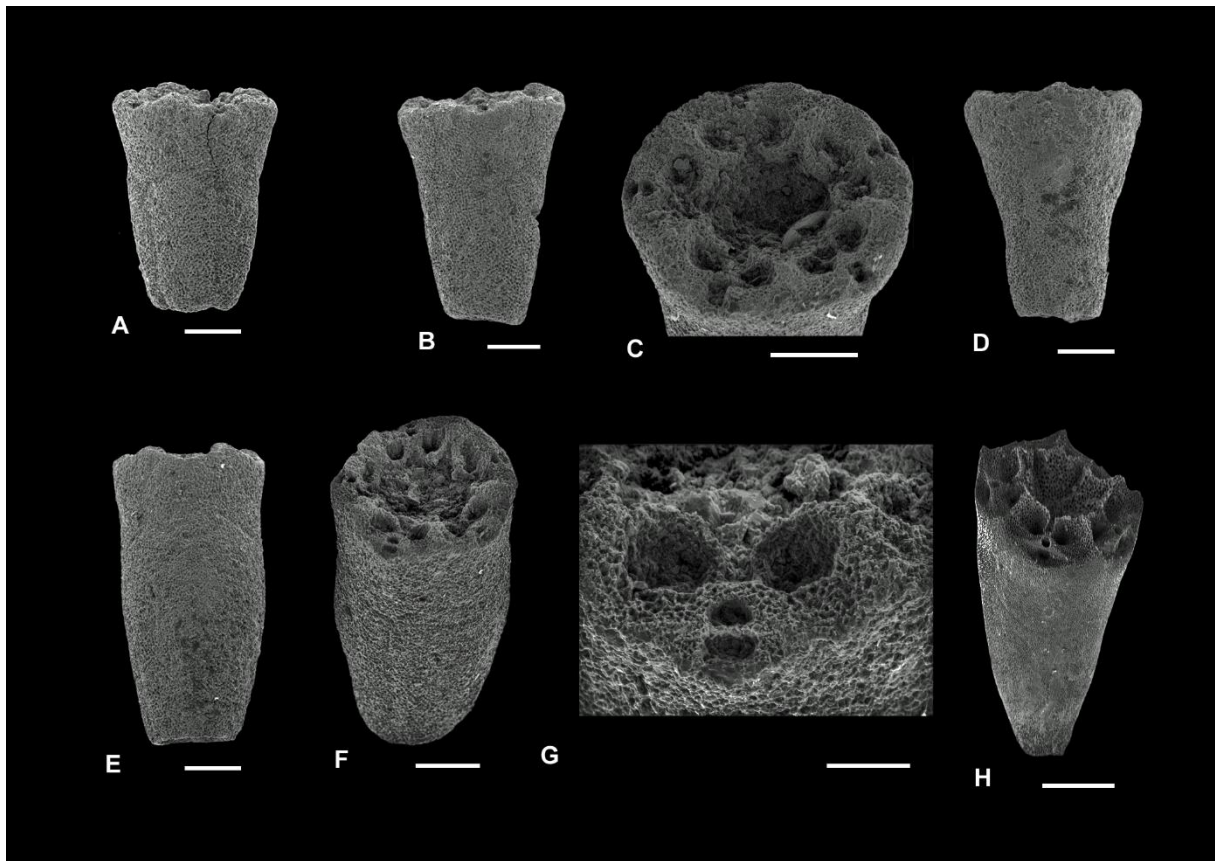


FIGURE 16. Aboral cups of type series of *Cherbonniericrinus requiensis* n. sp. A-D: paratypes (MNHN.F.A82014); E-G: holotype (MNHN.F.A82013), G: detail of muscular synarthry of distal face; H: aboral cup of *Ch. cherbonnieri*, Recent, Bay of Biscay, (MNHN.IE.2016.748). Scale bar equals 0.5 mm (A-F, H) and 0.25 mm (G).

Type stratum. Base of the blue marls of the middle Ilerdian, above the *Solenomeris* limestones, late NP10, but maybe already NP11.

Type locality. Réqui near Montlaur (Val de Dagne, Aude).

Diagnosis. Small species; aboral cup an inverted truncated cone in shape, external surface slightly concave to convex; sutures between plates variable, weakly marked between basals; aboral end diameter equal to or slightly less than 0.5 Dc; adoral face of radial circlet with discrete interrarial crests, muscular synarthries as wide as radials, broad central cavity.

Description of type series (Fig. 16). Quantitative characters of aboral cups of type series given in Table 16. Holotype (Fig. 16E-G) with aboral cup almost twice as high as wide, slightly swollen in upper half of basal circlet, lower part of basal circlet moderately inverted conical, slight constriction at basal-radial transition, basals about three times higher than radials, sutures between basals discrete or inconspicuous, marked sutures between basal and radial circlets and between radials. Aboral end diameter half of the maximum diameter of cup (D_p/D_c 0.49). Adoral face of radial circlet with slight marginal interrarial tips but without conspicuous interrarial ridges, muscular synarthries with reduced aboral ligament fossa and well-developed muscular fossae with lateral edges erected (Fig. 16G), broad

central cavity (Dd/Dc 0.49); pattern similar to that of extant specimen (Fig. 16H). Paratypes with aboral cup of variable flare and height, lateral profile slightly convex (Fig. 16A) to markedly concave (Fig. 16D); sutures between basals conspicuous (Fig. 16A) to absent (Fig. 16B); distal face of radial circlet imperfectly preserved in largest paratype (Fig. 16C).

Remarks. The aboral cup of the holotype of *C. requiensis* (Fig. 16E-G) is the closest to those of the extant species *C. cherbonnieri* (Roux, 1976) (Fig. 16H), both lacking sutures between basals. The paratypes (Fig. 16A-D) have an aboral cup general shape that is similar to those from the Danian of Denmark, attributed to ?*Cherbonniericrinus* sp. (Roux *et al.* 2019), which differ, however, by a larger adoral cavity like in the extant species. Columnals are unknown. The extant species *C. cherbonnieri* is anchored to the substratum by rhizoids penetrating into the sediment (Roux 1977).

Occurrence. Early Ypresian (middle Ilerdian) of Corbières; species known only from Réqui near Montlaur (Val de Dagne, Aude).

Famille Holopodidae von Zittel, 1879

Remarks. This family of sessile crinoids displays a morphological and functional convergence with barnacles. The aboral cup restricted to the radial circlet is fixed to the substrate by an incrusting base with parallel growth lines more or less developed. The relatively short arms curl inwards and retract into the calceal cavity with the proximal brachials forming a protective roof at rest. Study of extant species (Améziane *et al.* 1999) has clarified the major characters that distinguish *Holopus* and *Cyathidium*, the only two known extant genera attributed to this family (Table 17).

Stratigraphical distribution. Late Cretaceous (Cenomanian)–Recent, possibly since Late Jurassic (Sieverts-Doreck 1951).

	Characters	<i>Cyathidium</i>	<i>Holopus</i>
Closed crown	Convexity	Weak to moderate	Strongly marked
	IIBr visible	IIBr1 only	Beyond IIBr2
	Maximum diameter	Radial circlet	IIBr1 circlet
	Maximum IBr width	Proximal facet	Distal third
	Width/height of IBr	0.3 to 0.6	>0.5
	IBr shape	Subrectangular	Pentagonal
	IIBr1 shape	Trapezoidal to triangular	Subrectangular
Aboral cup	External surface	Radials indistinct, incrusting base more or less developed	Radials well-developed, incrusting base low or inconspicuous
	Apophyses or interradial crests on adoral face	Well-developed in adult with or without crenulations	Absent, muscular area often erected on adoral side

TABLE 17. Main characters differentiating the genera *Cyathidium* and *Holopus*.

Genus *Holopus* d'Orbigny, 1837

Type species. *Holopus rangii* d'Orbigny, 1837; Recent.

Stratigraphical distribution. Late Cretaceous (late Campanian)–Recent.

Holopus plaziati n. sp.

Fig. 17

Type material. The type series consists of 8 brachials, all figured as syntypes (MNHN.F.A82016) (Fig. 17).

Etymology. This species is dedicated to Jean-Claude Plaziat, author of many works on the Ilerdian in Corbières, who gave us the benefit of his knowledge of the field, especially concerning the site of Réqui.

Diagnosis. As description of the brachial type series; aboral cup unknown.

Type stratum. Base of blue marls of the middle Ilerdian above *Solenomeris* limestones, late NP10, but maybe already NP11.

Type locality. Réqui near Montlaur (Val de Dagne, Aude).

Description of type series. Quantitative characters of brachials of type series given in Table 18. Pentagonal axillary primibrachial (IBr1ax), external surface covered with coarse granulation, straight (Fig. 17A) to concave (Fig. 17F) lateral borders; internal face with Y-shaped neural groove, junction of two distal muscular synarthries forming conspicuous process (Fig. 17B, E), neural groove closing only at level of distal muscular synarthries; distal muscular synarthry with narrow, protruding fulcral ridge, inner edge of fulcral ridge with regular, well-marked crenulation, aboral ligament area slightly concave with narrow fossa of same size as neural canal, adoral ligament area beveled (Fig. 17J), muscular area oval towards central lumen and forming series of small fossae running along adoral ligament area opposite the lumen (Fig. 17D, G, J); proximal muscular synarthry often poorly preserved with linear fulcral ridge sometimes narrow, bordered by a reduced aboral ligament area and a deep adoral ligament area covered with elongated crenulations (Fig. 17K); variable lateral faces often narrow without crenulations (Fig. 17C) or wide with field of long crenulations on one of faces

Syntype	Figure	Place in arm	Wd	Wp	H	Wm	Wd/Wp	H/W'
8	17M-O	IIBr proximal	1.82	1.91	1.59	-	0.95	0.83
7	17K-L	IBr1 bivium	2.17	1.42	1.68	1.13	1.53	0.77
2	17B, J	IBr1 trivium	2.87	1.91	2.26	1.52	1.50	0.79
6	17C	IBr1 trivium	2.80	1.98	2.03	1.67	1.41	0.72
4	17G	IBr1 trivium	3.06	2.06	2.37	1.75	1.48	0.77
5	17H-I	IBr1 bivium	3.15	2.09	2.15	1.65	1.51	0.68
3	17D-F	IBr1 trivium	3.09	2.13	2.21	1.74	1.45	0.71
1	17A	IBr1 trivium	4.08	2.92	3.00	2.23	1.40	0.73

TABLE 18. Quantitative characters of brachials in the type series of *Holopus plaziati* n. sp. Wp used as growth index for IBr1. For abbreviations see Fig. 2 and Tables 4 and 9. Values in mm, except for ratios.

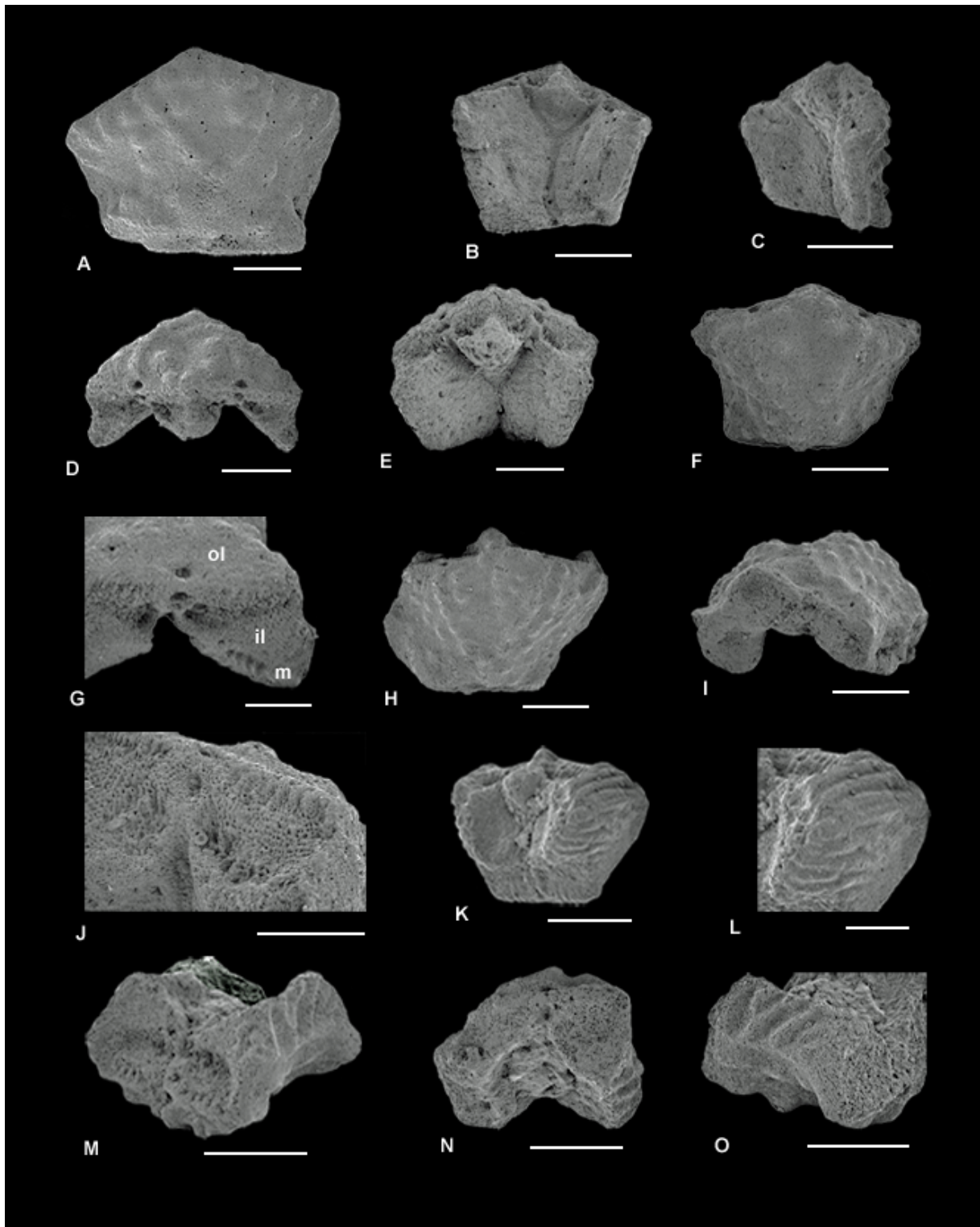


FIGURE 17. Brachials of type series of *Holopus plaziati* n. sp. from Réqui (MNHN.F.A82016). A-L: IBr1ax, M-O: proximal IIBr, A: aboral view of syntype 1; B: adoral view of syntype 2, C: lateral adoral view of syntype 6; D-F: syntype 3, D: distal view, E: adoral view, F: aboral view; G: detail of distal muscular synarthry of syntype 4 (il: inner ligament, m: muscular area, ol: outer ligament); H-I: syntype 5, H: aboral view, I: proximal view; J: detail of distal muscular synarthry of B, adoral view; K-L: syntype 7, K: lateral-adoral view, L: detail of lateral crenulations; M-O: syntype 8; M: lateral-proximal view; N: distal-adoral view, N: lateral-proximal view, O: lateral-distal view. Scale bar equals 1 mm, except for G, J and L, where it equals 0.5 mm.

(Fig. 17K-L). Some smaller, irregularly shaped IBr1ax with occasionally curved proximal face and muscular synarthry offset on one side (Fig. 17H-I). Proximal subrectangular secundibrachials subrectangular, wider than high, 3 to 5 strong lateral crenulations on each side (Fig. 17M, O), muscular synarthry symmetrical with respect to axial plane (Fig. 17M), no synarthry observed on opposite facet, possibly a synostosis, but feature probably related to poor preservation (Fig. 17N-O).

Remarks. The extant species, *H. rangii*, often shows a crown with a trivium of three large pentagonal IBr and well-developed arms and a bivium of two smaller IBr, sometimes irregularly shaped and with shorter arms (Carpenter 1884). The bivium is on the inside of the crown curvature and the trivium on the outside. This more or less marked arrangement is independent of the position of the anus (Grimmer & Holland 1990). It is thought to develop during growth under the influence of a unidirectional current (Donovan 1992). In *H. plaziati* n. sp., large pentagonal IBrax with few or no lateral crenulations (Fig. 17A-F) and those smaller, with widely developed lateral crenulations (Fig. 17K-L) or irregularly shaped (Fig. 17H-I), suggest the presence of a trivium and a bivium, respectively (Table 18). All other fossil species of *Holopus* are known only by their aboral cup. The oldest specimen has been recorded from Late Campanian chalk in northern Germany (Jagt *et al.* 2010). Manni (2005) and Frisone *et al.* (2020) confirmed the presence of the genus in the Eocene of northeast Italy. The Réqui site provided the first examples of brachials of an extinct species of *Holopus*. The corresponding aboral cup remains to be discovered.

Occurrence. Early Ypresian in Corbières (middle Ilerdian), species only known from Réqui near Montlaur (Val de Dagne, Aude).

Family Conometridae Gislén, 1924

Stratigraphical distribution. Late Cretaceous–Miocene.

Genus *Amphorometra* Gislén, 1924

Type species. *Glenotremites conoideus* Goldfuss, 1839; Late Cretaceous (Campanian–Maastrichtian).

Stratigraphical distribution. Cenomanian–Chattian.

Remark. The stratigraphical distribution of the genus has been extended to the Chattian by the discovery of a new species in New Zealand (Eagle 2009).

***Amphorometra atacica* (Doncieux, 1911)**

Fig. 18

Synonymy. *Antedon atacicus* Doncieux, 1911: 160-161, pl. 15, fig. 28a, b; Biese and Sieverts-Doreck, 1939: 79; *Glenotremites atacicus* Gislén, 1924: 125, 127, 191; Biese and Sieverts-Doreck, 1939: 95; Jagt *et al.*, 2002: 88.

Type material. Holotype, a single centrodorsal belonging to the Bories Collection housed in the palaeontological collections of the Paul Sabatier University of Toulouse under the catalogue number UPS BO-347.

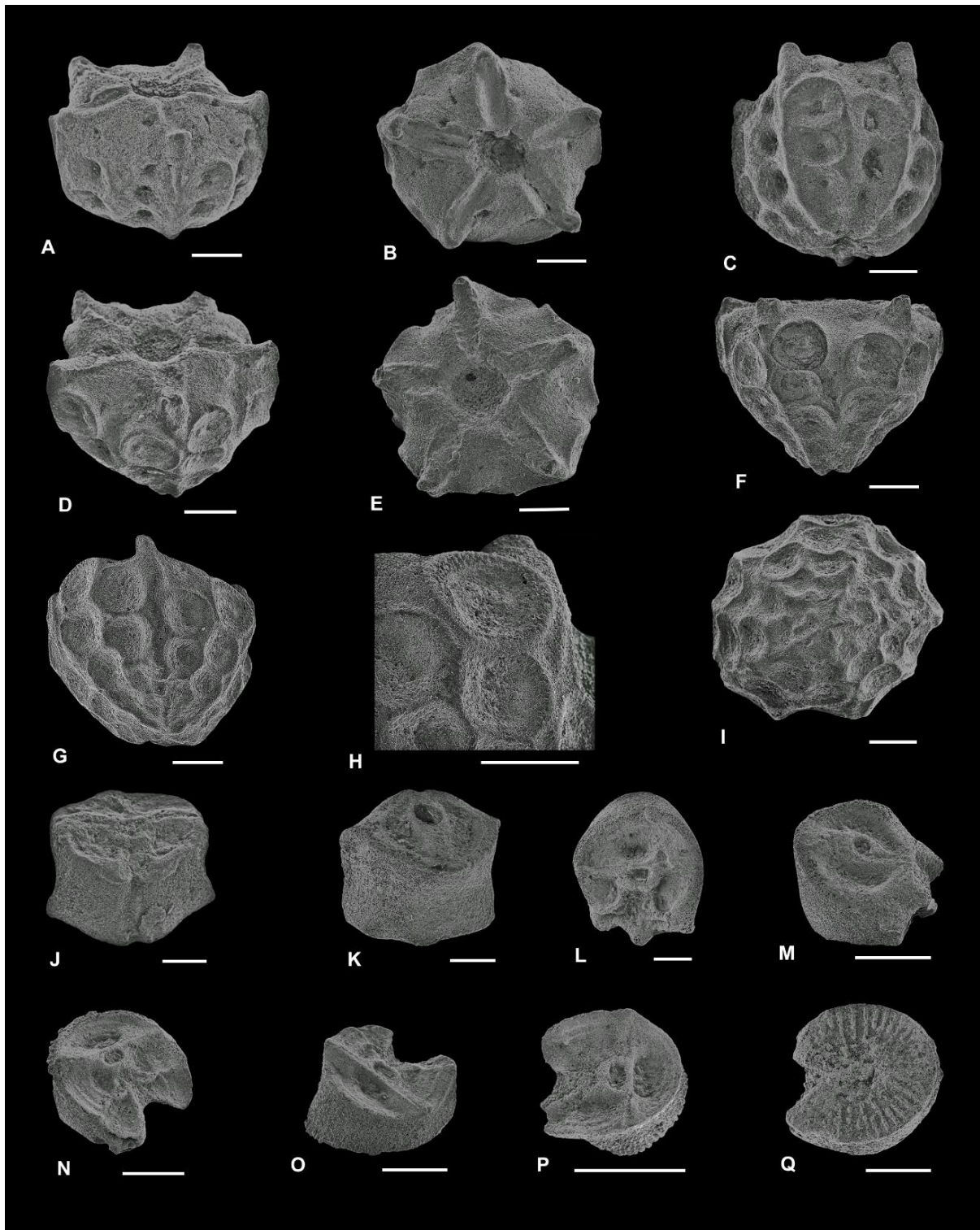


FIGURE 18. Centrodorsals (A-I) and brachials (J-Q) of *Amphorometra atacica*. A-F: specimens from Le Coucou (MNHN.F.A82017), G-Q: specimens from Lavade (MNHN.F.A82018); A and D: oblique-adoral views, B and E: adoral face, C and G: lateral-aboral views, F: lateral view, I: aboral view, H: detail of cirrus sockets; J-K: IBr1, J: proximal facet, K: distal facet; L-M: IIBr1, L: proximal facet, M: distal facet; N-O: free IIBr, N: distal facet, O: proximal facet; P: proximal facet of another free IIBr; Q: distal facet of hypozygial IIBr. Scale bar equals 1 mm.

Material examined. 15 centrodorsals in the Martinez Collection, 11 from Le Coucou including 2 here figured (Fig. 18A-F) (MNHN.F.A82017), 2 from Lavade, including 1 here figured (Fig. 18G-I) (MNHN.F.A82018a), 1 from La Prade (Arquettes-en-Val), 1 from Montauriol; 1 IIBr and 2 cirrals from Le Coucou; 9 brachials including 5 here figured (Fig. 18J-Q) (MNHN.F.A82018b) from Lavade, 1 brachial from La Commanderie.

Emended diagnosis. Centrodorsal hemispherical to inverted conical ($0.62 < H/D < 1.04$); lateral faces with interrarial crests often protruding and converging towards apex, rendering star-like appearance, interrarial crests forming conspicuous projections on adoral face; cirri arranged in two columns of 3 or 4 cirrus sockets separated by interrarial crests, cirrus sockets subcircular in shape with marginal radiating crenulations; adoral face with depressed and smooth insertion areas of radials; basal insertions narrow and raised. Axial synarthry at IBr1+2 and IIBr1+2, other free IIBr with muscular synarthries, except for some pairs with IIBr joined by syzygy of radiating crenularium. Radial circlet, IBr2ax and distribution of syzygies along arms unknown.

Type stratum. Lower blue marls of the middle Eerdian (early Ypresian), NP10–lower NP11.

Type locality. Les Lanes Sud, southwest of the village of Fontcouverte.

Description. Main quantitative characters of centrodorsals and brachials given in Tables 19 and 20, respectively. General shape of highly variable profile, from inverted conical (Fig. 18F) to hemispherical (Fig. 18A), with very prominent (Fig. 18A, C) to discrete (Fig. 18G, I) interrarial ridges converging towards apex and rendering star-like appearance when not worn (Fig. 18I). Interrarial ridges terminating in marked projection on adoral side (Fig. 18A) corresponding to outer end of basal

specimen	H	H'	D	D'	Dci	D'/D	H/D	H/H'	Dci/D
C-a	3.44	3.18	3.62	0.68	0.86	0.19	0.95	1.08	0.24
L-a	3.71	3.50	4.29	0.86	1.21	0.20	0.86	1.06	0.19
C-Fig. 18A-C	3.47	3.16	4.35	0.91	0.92	0.21	0.80	1.10	0.21
C-f	3.88	3.18	4.36	0.82	1.12	0.19	0.89	1.22	0.26
C-b	4.56	3.74	4.38	0.82	1.34	0.19	1.04	1.22	0.31
L-Fig. 18G-I	3.36	2.96	4.39	1.05	1.09	0.24	0.77	1.14	0.25
C-Fig.18D-F	3.74	3.10	4.77	1.23	1.28	0.26	0.78	1.21	0.27
M-a	3.70	3.03	4.79	1.00	1.07	0.21	0.77	1.22	0.22
C-c	4.38	3.74	4.82	1.24	1.20	0.26	0.91	1.17	0.25
C-d	3.12	2.82	5.00	0.92	1.26	0.18	0.62	1.11	0.25
C-e	4.12	3.76	5.30	0.94	1.12	0.18	0.78	1.10	0.21
LS-Holotype	3.5	3.18	5.30	1.16	1.06	0.22	0.66	1.11	0.20
ALP	-	-	5.42	1.30	1.01	0.24	-	-	0.19
C-g	4.58	4.00	5.64	1.18	0.94	0.21	0.81	1.15	0.17
C-h	4.24	3.76	5.64	0.94	1.12	0.17	0.75	1.13	0.20
C-i	4.36	3.76	6.12	1.18	1.06	0.19	0.71	1.16	0.17
maximum	4.58	4.00	6.12	1.30	1.34	0.26	1.04	1.22	0.31
mean	3.90	3.41	4.86	1.00	1.00	0.21	0.82	1.15	0.23
minimum	3.12	2.82	3.62	0.68	0.86	0.17	0.62	1.06	0.17

TABLE 19. Main quantitative characters of centrodorsals of *Amphorometra atacica*. ALP: from Arquettes-en-Val (La Prade), C: from Le Coucou, LS: from Les Lanes Sud, L: from Lavade, M: from Montauriol. D is used as a growth index. For abbreviations, see Fig. 2. Values in mm, except for ratios.

insertion (Fig. 18B, C). Between two interradial ridges, two rows of 3 to 4 (rarely 5) circular cirrus sockets, wide, deep, and presenting marginal radiating crenulation (Fig. 18H), i.e., total number of 30 to 35 cirri. Cylindrical proximal cirrals wider than high with one of facets having perilumen markedly in relief. Aboral face of centrodorsal with smooth insertion surfaces of radials, depressed between interradial projections; narrow, slightly lanceolate, raised basal insertions bordered by fine symplexial crenularium observable on best-preserved facets (Fig. 18E), central cavity of variable diameter ($0.17 < D/D < 0.26$) subpentagonal to circular. Radials unknown. Symmetrical muscular synarthry articulating radial and IBr1 with large aboral ligament fossa and moderately developed muscle areas (Fig. 18J). Axial synarthry at IBr1+2 and IIBr1+2 with broad fulcral ridge encompassing neural canal and deep ligament depressions (Fig. 18K, M). IBr2ax unknown. Proximal muscular synarthry of IIBr1 asymmetrical (Fig. 18L). Muscular synarthry articulating two IIBr with fulcral ridge slightly oblique, aboral ligament area wide and deep, adoral ligament areas almost equal to or slightly wider than muscular areas, distal facet of proximal brachial having finely festooned border, making outer surface of arms slightly rough (Fig. 18N-P). Presence of IIBr pairs united by flat syzygy with 20 to 25 radiating crenulae (Fig. 18Q), IIBr with one syzygial facet less frequent than free IIBr with two muscular synarthries.

Remarks. *Amphorometra ornata* Rasmussen, 1972 from the lower Ypresian London clay is very close to *A. atacica*. Paul (1992) completed the description of that species on the basis of abundant material including in particular a theca with proximal arm segments still connected. In addition to a highly developed ornamentation, especially on the arms, this species differs from *A. atacica* in having a lower centrodorsal ($0.4 < H/D < 07$) (Fig. 19) with less differentiated interradial ridges, the proximal synarthry of IBr1 with more elongated muscular areas and the synarthries at IBr1+2 and IIBr1+2 with a narrower fulcral crest and deeper ligament depressions, and syzygies with <20 radiating crenulae. At a comparable centrodorsal diameter, the number of cirri is higher in *A. ornata*.

Occurrence. Early Ypresian of Corbières (middle Ilerdian, NP10–11).

Figure	Ossicule	H	W	Wa	H/W	Wa/W	Site
Fig. 18P	IIBr free	0.85	1.29	1.30	0.66	1.01	Lavade
not figured	IIBr epizygial	0.91	1.32	1.39	0.69	1.05	Lavade
not figured	IIBr hypozygial	0.75	1.38	1.50	0.54	1.09	Le Coucou
not figured	IIBr free	1.35	1.58	1.67	0.85	1.06	Lavade
not figured	IIBr epizygial	1.20	1.79	1.71	0.67	0.95	Lavade
Fig. 18L-M	IIBr1	1.26	1.85	2.05	0.68	1.11	Lavade
Fig. 18N-O	IIBr free	1.08	1.89	2.23	0.57	1.18	Lavade
not figured	IIBr free	1.28	2.06	2.45	0.62	1.19	Lavade
Fig. 18Q	IIBr hypozygial	1.19	2.25	2.37	0.53	1.05	Lavade
Fig. 18J-K	IBr1	2.28	3.41	2.48	0.67	0.73	Lavade

TABLE 20. Main quantitative characters of brachials in *Amphorometra atacica*. H: height, W: width along fulcral ridge, Wa: width along adoral-aboral axis, W is used as a growth index. For abbreviations, see Fig. 2. Values in mm, except for ratios.

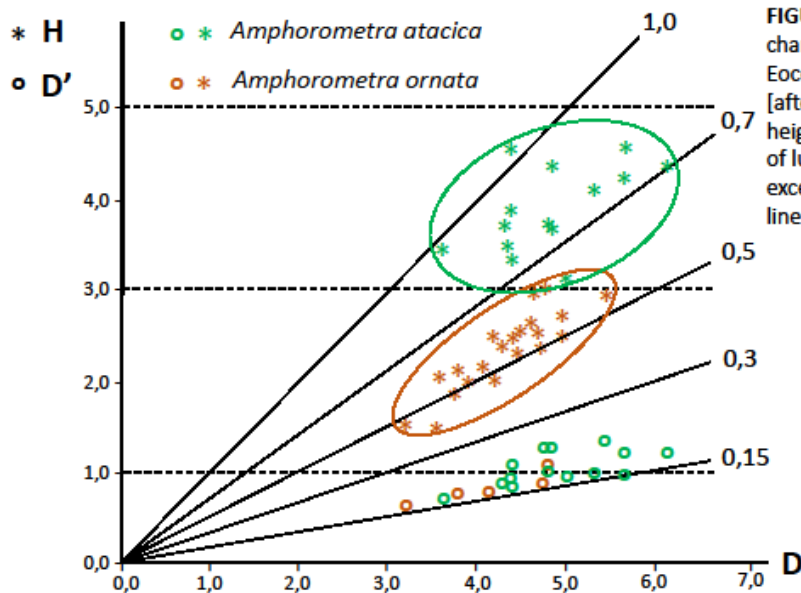


FIGURE 19. Variations in main quantitative characters of centrodorsals in two Early Eocene species of the genus *Amphorometra* [after Paul (1992) for *A. ornata*]. H: maximum height, D: maximum diameter, D': diameter of lumen of distal face. Values in millimeters, except for ratios H/D and D'/D (black straight lines). For abbreviations see Fig. 2.

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References

- Adnet, S., Louppe, V. & Martinez, A. (2010) Shark and rays from the confined Eocene gulf of Corbières (S. France). Review and relationships with the Atlantic fauna. *In*: 8th Congress of the European Association of Vertebrate Paleontology, Aix-en-Provence. *Mésogée*, 66, 9.
- Améziane, N., Bourseau, J.-P., Heinzeller, T. & Roux, M. (1999) Les genres *Cyathidium* et *Holopus* au sein des Cyrtocrinida (Crinoidea: Echinodermata). *Journal of Natural History*, 33, 139–170.
- 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. <https://doi.org/10.1007/s00435-020-00508-y>
- Améziane, N. & Roux, M. (1997) Biodiversity and historical biogeography of stalked crinoids (Echinodermata). *Biodiversity and Conservation*, 6, 1557–1570.
- Berger, G.M., Boyer, F. & Rey, J. (1990) Notice explicative de la feuille de Lézignan-Corbières à 1/50.000. *Carte géologique de la France à 1/50.000*, 1038. B.R.G.M., Orléans, 70 pp.
- Biese, W. & Sieverts-Doreck, H. (1939) Crinoidea caenozoica. *In*: Quenstedt, W. (Ed.), *Fossilium Catalogus, I: Animalia*, 80. W. Junk, 's Gravenhage, pp. 1–155.
- Bousquet, J.C. (1979) Approche paléocéologique de l'Ilerdien de la Montagne d'Alaric (Corbières septentrionales – Aude). *Géologie Méditerranéenne*, 6 (2), 369–378.
- Breton, G. & Vizcaino, D. (1997) Astérides (Echinodermata) de l'Ilerdien moyen (Yprésien) des Corbières (Aude, France). Taxonomie, relations paléobiogéographiques et évolutives. *Bulletin de la Société d'Études scientifiques de l'Aude*, 9, 11–28.
- Carpenter, P.H. (1884) Report upon the Crinoidea collected during the voyage of H.M.S. "Challenger" during the years 1873–1876. Part I, General morphology, with description of the stalked crinoids. *Report on the scientific results of the exploring voyage H.M.S. Challenger*, Zoology, (11) 32, 1–440.
- 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.
- d'Orbigny, A. (1837) Mémoire sur une seconde espèce vivante de la famille des Crinoïdes ou Encrines, servant de type au genre nouveau *Holope* (*Holopus*). *Magazine de Zoologie*, (7) 10, 1–8.
- Doncieux, L. (1911) Catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Hérault. Deuxième partie (Fascicule II). Corbières septentrionales. *Annales de l'Université de Lyon*, série 1, 30, 1–161.
- Donovan, S.K. (1992) SEM study of the living cyrtocrinid *Holopus rangii* (Echinodermata, Crinoidea) and implications for its functional morphology. *Journal of Paleontology*, 66 (4), 665–675.
- Eagle, M.K. (2009) New comatulid crinoids from the Meyers Pass Limestone Member (Waitakian (Chattian)) of the Pentland Hills and Hurstlea, South Canterbury, New Zealand. *Records of the Auckland Museum*, 45, 101–129.
- Fabiani, R. (1915) Il Paleogene del Veneto. *Memorie dell'Istituto di Geologia della Regia Università di Padova*, 3, 1–336.
- Forbes, E. (1852) Monograph of the Echinodermata of the British Tertiaries. Palaeontographical Society, London, 36 pp.
- Frisone, V., Preto, N., Pisera, A., Agnini, C., Giusberti, L., Papazzoni, C.A., De Angeli, A., Beschin, C., Mietto, P., Quaggiotto, E., Monaco, P., Dominici, S., Kiessling, W., Luciani, V., Roux, M. & Bosellini, F.R. (2020) A first glimpse on the taphonomy and sedimentary environment of the Eocene siliceous sponges from Chiampo, Lessini Mts., NE Italy. *Bollettino della Società paleontologica Italiana*, 59 (3), 299–313.

- Gaemers, P.A.M. (1978) Biostratigraphy, palaeoecology and palaeogeography of the mainly marine Ager Formation (Upper Paleocene–Lower Eocene) in the Tresp Basin, Central–South Pyrenees, Spain. *Leidse Geologische Mededelingen*, 51, 151–231.
- Gély, J.P. & Sztrakos, K. (2000) L'évolution paléogéographique et géodynamique du Bassin aquitain au Paléogène: enregistrement et datation de la tectonique pyrénéenne. *Géologie de la France*, 2, 31–57.
- Gislén, T. (1924) Echinoderm studies. *Zoologiska Bidrag fran Uppsala*, 9, 1–316.
- Gislén, T. (1927) Japanese crinoids. Papers from Dr Th. Mortensen's Pacific Expedition 1914-16, 37. *Videnskabelige Meddelelser fra det Dansk naturhistorisk Forening*, 83, 1–69.
- Goldfuss, G.A. (1826) Petrefacta Germaniae, divisio secunda. Radiarorum reliquiae. Vol. 1. Arnz & Co, Düsseldorf, pp. 115–221.
- Grimmer, J.C. & Holland, N.D. (1990) The structure of a sessile, stalkless crinoid (*Holopus rangii*). *Acta Zoologica*, 71 (2), 61–67.
- Hemery, L.G. (2011) *Diversité moléculaire, phylogénie et phylogéographie des Crinoïdes (Echinodermes) dans un environnement extrême: l'océan Austral*. Unpubl. PhD thesis, Muséum national d'Histoire naturelle, Paris, 381 pp.
- Hemery, L. G., Roux, M., Améziane, N. & Eléaume, M. (2013) High-resolution crinoid phyletic inter-relationships derived from molecular data. *Cahiers de Biologie marine*, 54, 511–523.
- Hess, H. & Messing, C.G. (2011) *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Revised Crinoidea, Vol. 3*. University of Kansas, Paleontological Institute, Lawrence, Kansas, pp. 1-261.
- Jaekel, O. (1894) Entwurf einer Morphogenie und Phylogenie der Crinoiden. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1894, 101–121.
- Jagt, J.W.M., Neumann, C. & Girod, P. (2010) First record of a holopodid crinoid from the Late Campanian white chalk facies of northern Germany. In: Reich, M., Reitner, J., Roden, V., Thuy, B. (Eds.), *Echinoderm Research 2010, 7th European Conference on Echinoderms*, Abstract volume, p. 59, Universitätsdrucke, Gottingen.
- Jagt, J.W.M., Deckers, M.J.M. & Parren, J. (2002) Notes on North Sea Basin Cainozoic echinoderms, Part 1. Miocene comasterid crinoids from central Limburg, the Netherlands. *Cainozoic Research*, 1 (for 2001), 83–90.
- Klikushin, V.G. (1982) Cretaceous and Paleogene Bourgueticrinina (Echinodermata, Crinoidea) of the USSR. *Geobios*, 15 (6), 811–843.
- Leturcq, T. (1999) *Dynamique récifale à l'Ilerdien: exemple du bassin de Graus-Tresp (Pyrénées, Espagne)*. Unpubl. PhD thesis, Université P. et M. Curie, Paris, n°: 99 PA06 6303, 2 vol., 376 pp.
- Macurda Jr, D.B. & Meyer, D.L. (1974) Feeding posture of modern stalked crinoids. *Nature*, 247, 394–396.
- Manni, R. (2005) The non-isocrinid crinoids of the Michelotti collection. *Bollettino della Società Paleontologica Italiana*, 44 (3), 211–218.
- Martín-Martín, M., Rey, J., Alcalá-García, F.J., Tosquella, J., Deramond, J., Lara-Corona, E., Duranthon, F. & Antoine, P.O. (2001) Tectonic controls on the deposits of a foreland basin: an example from the Eocene Corbières-Minervois basin, France. *Basin Research*, 13, 419–433.
- McInerney, F.A. & Wing, S.L. (2011) The Paleocene-Eocene Thermal Maximum: a perturbation of carbon cycle, climate and biosphere with implications for the future. *Annual Review of Earth and Planetary Science*, 39, 489–516.
- Merle, D. & Roux, M. (2018) Stalked crinoids from Gan (Late Ypresian, southwestern France): exceptional stereom preservation, paleoecology and taxonomic affinities. *Swiss Journal of Palaeontology*, 137, 225–244.
- Meyer, D.L., Messing, C.G. & Macurda Jr, D.B. (1978) Zoogeography of tropical western Atlantic Crinoidea (Echinodermata). *Bulletin of Marine Science*, 28 (3), 412–441.
- Miller, J.S. (1821) *A natural history of the Crinoidea or lily-shaped animals, with observations on the genera Asteria, Euryale, Comatula, and Marsupites*. C. Frost, Bristol, 150 pp.

- Munier-Chalmas, E. (1891) *Etude du Tithonique du Crétacé et du Tertiaire du Vicentin*. Salvy, Paris: 185 pp.
- Oppenheim, P. (1902) Revision der tertiären Echiniden Venetiens und des Trentino, unter Mittheilung neuer Formen. *Zeitschrift der deutschen geologischen Gesellschaft*, 54, 159–283.
- Pacaud, J.-M. (2010) Description des rhyncholites des Nautilus (Mollusca, Cephalopoda) du Paléogène des bassins de Paris et d'Aquitaine et des Corbières (France). *Geodiversitas*, 32 (1), 121–156.
- Paschall, O.C. & Waters, J.A. (2016) Estimated predation rate on the stalked bourgueticrinid (Crinoidea) *Democrinus* from Roatan, Honduras. *Geological Journal*, 52 (5), 727–732.
- Paul, C.R.C. (1992) *Amphorometra* (Crinoidea, Echinodermata) from the London Clay of Aveley, Essex. *Tertiary Research*, 13, 117–124.
- Perrier, E. (1883) Sur un nouveau Crinoïde fixé, le *Democrinus* parfait, provenant des dragages du «Travailleur». *Comptes Rendus de l'Académie des Sciences, Paris*, 96, 450–452.
- Pirkenseer, C.M., Steurbaut, E., Abels, H.A., King, C. & Speijer, R.P. (2013) An expanded lower Eocene shelf sequence from the eastern Aquitaine Basin, SW France: biostratigraphy, biofacies, and stable carbon and oxygen isotopes. *Newsletters on Stratigraphy*, 46 (3), 339–361.
- Plaziat, J.C. (1964) Pistes d'oiseaux et remaniements synsédimentaires dans le Lutétien du détroit de Carcassonne (Aude). *Bulletin de la Société géologique de France*, (7) 6, 289–293.
- Plaziat, J.C. (1981) Late Cretaceous to Late Eocene palaeogeographic evolution of southwest Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 36 (3-4): 263–320.
- Plaziat, J.C. (1984a) Paléobiocénoses et déplacements massifs d'organismes littoraux (Madréporaires, Mollusques, fruits de *Nypa*, en sédimentation vasosableuse pérideltaïque. Rôle des courants, des tempêtes et des séismes dans l'Ilerdien de Coustouges (Aude, France). *Geobios*, Mémoire spécial, 8, 301–312.
- Plaziat, J.C. (1984b) *Le domaine pyrénéen de la fin du Crétacé à la fin de l'Eocène. Stratigraphie, paléo-environnements et évolution paléogéographique*. Unpubl. PhD thesis, Université Paris-Sud, 1362 pp.
- Plaziat, J.C. & Perrin, C. (1992) Multikilometer-sized builds by foraminifera (*Solenomeris*) from the early Eocene of the Pyrenean domain (S. France, N. Spain). Palaeoecologic relations with coral reefs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 96 (3–4), 195–231.
- Pourtalès, L.F. de (1874) On a new species of *Rhizocrinus* from Barbados. *Harvard University, Museum of Comparative Zoology*, Memoir 4 (8), 27-31.
- Pujalte, V., Baceta, J.I., Schmitz, B., Orue-Etxebarria, X., Payros, A., Bernaola, G., Apellaniz, E., Caballero, F., Robador, A., Serra-Kiel, J. & Tosquella, J. (2009). Redefinition of the Ilerdian stage (early Eocene). *Geologica Acta*, 7 (1–2), 177–194.
- Rasmussen, H.W. (1972) Lower Tertiary Crinoidea, Asteroidea and Ophiuroidea from northern Europe and Greenland. *Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter*, 19 (7), 1–83.
- Rouse, G.W., Jermin, L., Wilson, N.G., Eeckhaut, I., Lanterbecq, D., Oji, T., Young, C.M., Browning, T., Cisternas, P., Helgen, L., Stuckey, M. & Messing, C.G. (2013) Fixed, free and fixed: the fickle phylogeny of extant Crinoidea (Echinoderma) and their Permian-Triassic origin. *Molecular Phylogenetics and Evolution*, 66, 161–181.
- Roux, M. (1977) Les Bourgueticrinina (Crinoidea) recueillis par la «Thalassa» dans le Golfe de Gascogne: anatomie comparée des pédoncules et systématique. *Bulletin du Muséum national d'Histoire naturelle*, (3) 426, Zoologie, 296, 25–83.
- Roux, M. (1978a) Importance de la variabilité de la forme du calice chez les Bathycrinidae (Echinodermes, Crinoïdes): l'exemple de l'espèce éocène *Conocrinus doncieuxi* nov. sp. *Comptes Rendus de l'Académie des Sciences Paris*, D287, 797–800.

- Roux, M. (1978b) Ontogenèse, variabilité et évolution morphofonctionnelle du pédoncule et du calice chez les Millericrinida (Echinodermes, Crinoïdes). *Géobios*, 11 (2), 213–241.
- Roux, M. (1978c) Les crinoïdes pédonculés (Echinodermes) du genre *Conocrinus* provenant de l'Eocène des environs de Biarritz. *Comptes Rendus de l'Académie des Sciences Paris*, D296, 265–268.
- 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*, 2. A.A. Balkema, Rotterdam/Brookfield, pp. 1–53.
- Roux, M., Cahuzac, B. & Sztrákos, K. (2006) Les paléoenvironnements éocènes à crinoïdes pédonculés des marnes de Miretrain (Angoumé, SW France): interprétations paléobathymétriques. *Comptes Rendus Géosciences*, 338, 262–271.
- Roux, M., Eléaume, M., Hemery, L.G. & Améziane, N. (2013) When morphology meets molecular data in crinoid phylogeny: a challenge. *Cahiers de Biologie Marine*, 54, 541–548.
- Roux, M., Eléaume, M. & Améziane, N. (2019) A revision of the genus *Conocrinus* d'Orbigny, 1850 (Echinodermata, Crinoidea, Rhizocrinidae) and its place among extant and fossil crinoids with a xenomorphic stalk. *Zootaxa*, 4560 (1), 51–84.
- 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. & Plaziat, J.C. (1978) Inventaire des Crinoïdes et interprétation paléobathymétrique de gisements du Paléogène pyrénéen franco-espagnol. *Bulletin de la Société géologique de France*, (7) 20 (3), 299–308.
- Sieverts-Doreck, H. (1951) *Cyathidium* im Tithon von Mähren? *Neues Jarbuch für Geologie und Paläontologie Abhandlungen*, 94 (1), 1–4.
- Syverson, V.J., Messing, C.G., Stanley, K. & Baumiller, T.K. (2015) Growth, injury, and population dynamics in the extant cyrtocrinid *Holopus mikihe* (Crinoidea, Echinodermata) near Roatan, Honduras. *Bulletin of Marine Science*, 91 (1), 47–61.
- Szczepanik, P. & Sawlowicz, Z. (2005) Pyritization of microfossils: crinoid remains from the Middle Jurassic of Ogrodzieniec (Kraków-Częstochowa Upland, Poland). In: Tyszka J., Oliwkiewicz-Miklasińska M., Gedl P. & Kaminski M. A. (Eds.), *Methods and applications in micropalaeontology. Studia Geologica Polonica*, 124, 37–52.
- Sztrakos, K., Gély, J.P., Blondeau, A. & Müller, C. (1998) L'Eocène du Bassin sud-aquitain: lithostratigraphie et analyse séquentielle. *Géologie de la France*, 4, 57–105.
- Sztrakos, K. & Gély, J.P. (2000) L'évolution paléogéographique et géodynamique du Bassin aquitain au Paléogène: enregistrement et datation de la tectonique pyrénéenne. *Géologie de la France*, 2, 31–57.
- Tunnicliffe, V., Roux, M., Eléaume, M. & Schornagel, D. (2016) The stalked crinoid fauna (Echinodermata) of the Molucca and Celebes seas, Indonesia: taxonomic diversity and observations from remotely operated vehicle imagery. *Marine Biodiversity*, 46, 365–388.
- Veitch, M.A. and Baumiller, T.K. (2021) Low predation intensity on the stalked crinoid *Democrinus* sp. (Echinodermata), in Roatán, Honduras, reveals deep water as likely predation refuge. *Bulletin of Marine Science*, 97, 22 p., one line. <https://doi.org/10.5343/bms.2020.0024>
- Yans, J., Marandat, B., Masure, E., Serra-Kiel, J., Schnyder, J., Storme, J.Y., Marivaux, L., Adnet, S., Vianey-Liaud, M. & Tabuce, R. (2014) Refined bio- (benthic foraminifera, dinoflagellate cysts) and chemostratigraphy ($\delta^{13}\text{C}_{\text{org}}$) of the earliest Eocene at Albas-Le Clot (Corbieres, France): implications for mammalian biochronology in southern Europe. *Newsletters on Stratigraphy*, 47 (3), 331–353.
- Zamora, S., Aurell, M., Veitch, M., Saulsbury, J., López-Horgue, M.A., Ferratges F.A., Arz, J.A. & Baumiller, T.K. (2018) Environmental distribution of post-Palaeozoic crinoids from the

Iberian and south-Pyrenean basins, NE Spain. *Acta Palaeontologica Polonica*, 63 (4), 779–794.

Zittel, K.A. von (1879) Holopidae. In: *Handbuch der Palaeontologie*, 1876-1880, 1, Palaeozoologie, 1. Oldenburg, München & Leipzig, 765 pp.