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***Discometra luberonensis* sp. nov. (Crinoidea, Himerometridae),
a new feather star from the Late Burdigalian**

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Abstract. Most fossil feather stars are known only from the centrodorsal often connected to the radial circle. This is the case for *Discometra rhodanica* (Fontannes, 1877), the type species of the genus *Discometra*, collected from the Late Burdigalian of the Miocene Rhône-Provence basin (southeastern France). The quarries operating in this area have exposed layers from the Late Burdigalian on the northern flank of the Lubéron anticline near Ménerbes (basin of Apt, Vaucluse, southeastern France). These layers contain exceptionally well-preserved echinoderms, among which are three specimens of a feather star with cirri and arms still connected to the centrodorsal. They are attributed to a new species: *Discometra luberonensis* sp. nov. (Himerometridae). The number of arms can reach 60, as in extant species of the genus *Himerometra*, but the pattern of arm divisions is closer to that of the genus *Heterometra*, which has no more than 45 arms in extant species. *Discometra luberonensis* sp. nov. differs from *D. rhodanica* by the characters of its centrodorsal. Here we redescribe the centrodorsal and radial circle of *D. rhodanica* based on previously and newly collected specimens. We designate a neotype for *D. rhodanica*, because the holotype is considered lost. Affinities between *Discometra*, *Himerometra* and *Heterometra* are discussed.

Keywords. Crinoidea, Himerometridae, *Discometra*, Miocene, southeastern France.

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Introduction

The family Himerometridae A.H. Clark, 1908 consists only of extant species, except for the genus *Discometra* Gislén, 1924, which dates to the Miocene, and is only known from centrodorsals and the

radial circlet. Gislén (1924: 180) erected this genus “at least temporarily” to group together Miocene species with insufficiently known centrodorsals and radial circlets, but differing from the other extant genera distinguished by A.H. Clark (1909, 1918). Isolated ossicles and calices found in the Eocene and Oligocene had been attributed to the extant genus *Himerometra* A.H. Clark, 1907, and *Discometra* was attributed to Himerometridae (Sieverts-Doreck 1961; Strimple & Mapes 1984; Rasmussen 1978; Hess & Messing 2011). Later, Taylor *et al.* (2017) removed all fossil species from *Himerometra* and assigned them to *Himerometroidea incertae sedis*.

On the northern flank of the Lubéron anticline (Apt basin, Vaucluse, SE France; Fig. 1), bioclastic limestones with the pectinid bivalve *Gigantopeecten restitutus* (Fontannes, 1884) dated to the Late Burdigalian contain accumulations of spectacular fossiliferous slabs exposed during the exploitation of quarries located on the Ménerbes-Lacoste Plateau (Bongrain 2013). The shells of *G. restitutus*, most often with connected valves, and the tests of the echinoid *Tripneustes planus* (Agassiz, 1840) preserved with their spines and dental apparatus are the most abundant taxa and are associated with complete large sea stars and brittle stars. These accumulations correspond to mass sediment flows on the unstable slopes of the northern flank of the Lubéron anticline. They led to the almost instantaneous burial of benthic

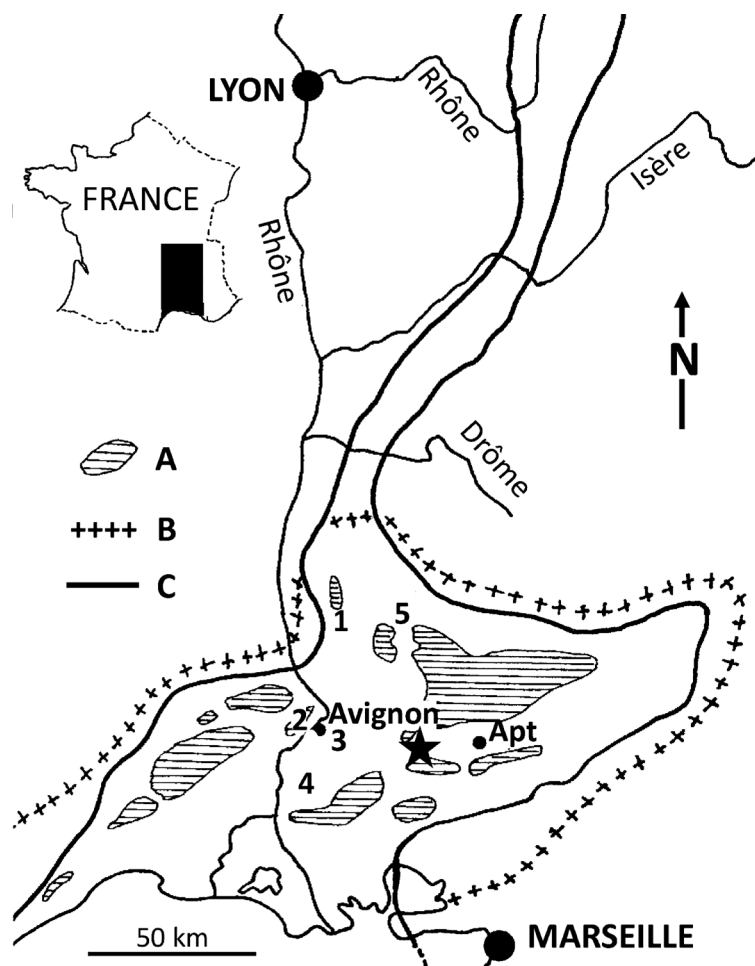


Fig. 1. The Miocene Rhône-Provence Gulf (modified from Philippe 1998: fig.1). A = submarine or emerging shoals; B = limit of the Rhône-Provence Gulf; C = estimated limit of the Burdigalian transgression. Sites with *Discometra* Gislén, 1924 cited in the text are indicated as follows: black star = Ménerbes-Lacoste Plateau; 1 = Bollène; 2 = Les Angles; 3 = Caumont-sur-Durance (Picabrier); 4 = Notre-Dame du Château; 5 = Entrechaux.

communities, with the result that some feather stars were exceptionally preserved. Centrodorsals, often with their radial circlet, were previously collected in the Late Burdigalian of the Rhône-Provence basin (Fontannes 1880; de Loriol 1897; Pellat 1897; Nicolas 1898; Joleaud 1907; Valette 1928; Philippe 1974). *Discometra rhodanica* (Fontannes, 1877) is the species that reaches the largest size.

Here we describe three specimens of a new species of Miocene feather star with arms connected to the calyx and with crowns well enough preserved to allow description of arm organization. The specimens were collected from Ménerbes in deposits that correspond to a thermal maximum at the Late Burdigalian-Langhian boundary (Demarcq 1984). In the Rhône-Provence Gulf, the Miocene Sea transgressed over a deformed and eroded substratum, leaving numerous submarine or emerging shoals separated by strongly incised valleys (Demarcq 1970; Besson 2005) (Fig. 1). Such a setting agrees with the distribution of extant species of Himerometridae, which are mainly found in shallow-water environments in the tropical western Pacific and northern Indian Ocean (Hess & Messing 2011). To determine whether or not our three specimens belong to *D. rhodanica*, we re-examined reference specimens in the collections of the museums in Lyon, Avignon and Saint-Rémy de Provence, and well-preserved specimens recently collected in Caumont-sur-Durance (Picabrier site).

Material and methods

The specimens of *D. luberonensis* sp. nov. (Fig. 2A–F) are preserved on three limestone slabs rich in echinoderms and *Gigantopecten* extracted from the Soubeyran quarry in Ménerbes and conserved at the Centre “Louis Lortet” de conservation et d’étude des collections (Musée des Confluences, Lyon). The slab MHNL 20.056151 (collected by R. Lacombe, now added to M. Philippe’s collection) was illustrated by Bongrain (2013: fig. 9b). Following the expansion of urbanization in the last decades, most of the ancient outcrops where *D. rhodanica* had been collected are no longer accessible (Bollène, Les Angles, Caumont-sur-Durance) with the exception of Notre-Dame du Château between Saint-Etienne du Grès and Saint-Rémy de Provence (northern slope of the Alpilles). It was therefore important to locate the specimens used for the first descriptions of the species. Those collected by E. Pellat and described by him (Pellat 1897) and de Loriol (1897) are housed in the collection of the Musée des Alpilles in Saint-Rémy de Provence. Those coming from ancient quarries of the Les Angles Plateau (west of Avignon) and described by Nicolas (1898) belonged to his own collection deposited in the palaeontological collection of the University Claude Bernard, Lyon I, and in private collections including the Châtelet’s collection, which has been partly deposited in the Musée Requien, Fondation Calvet (Musée d’Histoire naturelle) in Avignon. However, we were unable to find the calyx figured by Nicolas (1898: 403, fig. 1), or those figured by Fontannes (1880: pl. 2, figs 10–11). As a consequence, we consider them as lost. Measurements of these lost specimens (Table 2) are deduced from the original publications. The three calices from the Picabrier outcrops exposed in Caumont-sur-Durance were collected by one of us (MP). This site was studied by Ulysse (1968). The centrodorsal comes from the ‘Ferme Pie’ outcrops exposed near Entrechaux (Philippe 1974). The studied specimen of *Himerometra robustipinna* (Carpenter, 1881) (Fig. 2G) was collected during the Salomon 1 cruise (DW 1822, 9°51.08’ S, 160°51.8’ E, depth 51–54 m) and the studied specimen of *Heterometra savignii* (Müller, 1841) (Fig. 2H) during the R.P. Dollfus expedition to the Gulf of Suez. They are housed in the zoological collection of the Muséum national d’histoire naturelle in Paris.

The pictures in Figs 3, 5–6 were taken using a scanning electron microscope (SEM) type JEOL-840A at 15 kV (Electron Microscopy Platform of the Muséum national d’histoire naturelle in Paris). Ossicles from extant species were dissociated after a 12-hour bath in sodium hypochlorite, washed with distilled water and dried. All ossicles observed using SEM were coated with a colloidal platinum solution.

Table 1. List of fossil and extant specimens examined. In the ‘Remarks’ column, the names of the collectors are indicated (except for extant species and type specimens, see text). CD = centrodorsal; RR = radial circlet.

Taxon	Collection	Catalog #	Locality	Preservation	Figure	Remarks
<i>Heterometra savignii</i>	MNHN	MNHN-IE-2016-1381	W-Pacific	complete	2H	Recent
<i>Himerometra robustipinna</i>	MNHN	MNHN-IE-2012-862	W-Pacific	complete	2G	Recent
Unidentified Comatulidae	MASR	2020.5021	N.D. Château	RR	5D–E	Pellat
	MHNL	20.062689	Entrechaux	CD	5C	Philippe
<i>Discometra rhodanica</i>	UCBL	200025a	Les Angles	calyx	–	Nicolas
<i>Discometra rhodanica</i>	MRA	3.000.349	Les Angles	calyx	–	Châtelet
<i>Discometra rhodanica</i>	MRA	3.000.348	Les Angles	calyx	–	Châtelet
<i>Discometra rhodanica</i>	UCBL	200025b	Les Angles	CD	–	Nicolas
<i>Discometra rhodanica</i>	MASR	2020.5011	N.D. Château	calyx	5A–B	neotype
<i>Discometra rhodanica</i>	MHNL	20.062686	Picabrier	calyx	6A	Philippe
<i>Discometra rhodanica</i>	MHNL	20.062687	Picabrier	calyx	6C–D	Philippe
<i>Discometra rhodanica</i>	MHNL	20.062688	Picabrier	calyx	6B	Philippe
<i>Discometra luberonensis</i> sp. nov.	MHNL	20.056148	Ménerbes	complete	2C–D	paratype
<i>Discometra luberonensis</i> sp. nov.	MHNL	20.056151	Ménerbes	complete	2E–F	paratype
<i>Discometra luberonensis</i> sp. nov.	MHNL	20.062682	Ménerbes	complete	2A–B	holotype

Repositories

- MHNL = Centre “Louis Lortet” de conservation et d’étude des collections, Musée des Confluences (formerly Muséum d’Histoire naturelle de Lyon), Lyon
 MASR = Musée des Alpilles, Saint-Rémy de Provence
 MRA = Musée Requien, Fondation Calvet, Avignon
 MNHN = Muséum national d’histoire naturelle (zoological collection), Paris
 UCBL = Université Claude Bernard (palaeontological collections), Lyon I

Table 2. Quantitative characters of calices attributed to *Discometra* Gislén, 1924 from the Miocene of the Rhône-Provence basin. D1 = maximum diameter of centrodorsal; D2 = diameter of aboral cirrus-free depression; D3 = diameter of adoral cavity limited by radial circlet; Hca = calyx height (centrodorsal + radial circlet); Hcd = average of centrodorsal height. Specimens ordered by size at each site (D1 used as the age index). Specimen UCBL 200025b is an isolated centrodorsal. Parameters in mm. Ratios in **bold** type: D2/D1 = index of cirrus disappearance on aboral centrodorsal face; D3/D1 = degree of opening of the adoral calyx cavity; Hcd/Hca = relative centrodorsal height; Hcd/D1 = degree of centrodorsal flattening. * = neotype of *D. rhodanica* (Fontannes, 1877) (from de Loriol 1897: fig. 8); ** = holotype of *D. luberonensis* sp. nov. See Table 1 and text for more information on specimens.

Specimen	Location	D1	D2	D2/D1	D3	D3/D1	Hcd	Hca	Hcd/Hca	D1/Hcd
<i>Discometra rhodanica</i>										
Fontannes 1880: fig. 10	Bollène	~13.0	~7.2	~ 0.56	~3.0	~ 0.23	~2.0	~4.5	~ 0.44	~ 6.67
Fontannes 1880: fig. 11	Bollène	~8.5	?	–	~2.8	~ 0.33	~1.8	~5.0	~ 0.36	~ 4.76
Nicolas 1898: fig. 1	Les Angles	14.3	?	?	<5.0	< 0.35	~3.8	>7.5	< 0.51	~ 3.76
UCBL 200025a	Les Angles	14.0	<8.2	< 0.58	3.0	0.21	2.75	6.2	0.44	5.00
MRA 3.000.349	Les Angles	13.4	6.8	0.51	<3.7	< 0.28	2.8	5.8	0.48	4.78
UCBL 200025b	Les Angles	>12.0	5.0	< 0.42	–	–	2.65	–	–	< 4.54
MRA 3.000.348	Les Angles	7.85	–	–	–	–	1.8	>4.0	< 0.45	4.39
MASR 2020.5011 *	N.D. Château	8.3	2.1	0.3	1.9	0.23	2.2	4.6	0.48	3.85
MHNL 20.062686	Picabrier	12.0	7.5	0.62	>2.7	> 0.22	2.6	?	?	4.61
MHNL 20.062687	Picabrier	9.9	3.25	0.33	2.6	0.26	2.2	4.9	0.45	4.50
MHNL 20.062688	Picabrier	7.7	2.1	0.27	1.75	0.23	1.8	4.4	0.41	4.23
<i>Discometra luberonensis</i> sp. nov.										
MHNL 20.056148	Ménerbes	13.5	8.55	0.63	?	–	2.5	?	–	5.26
MHNL 20.056151	Ménerbes	12.5	8.3	0.66	?	–	1.9	?	–	6.67
MHNL 20.062682 **	Ménerbes	11.7	6.3	0.54	?	–	2.8	?	–	4.18

Abbreviations

- I, II, III, IV, V = brachitaxis position from proximal (I) to more distal (V)
 Ibr2ax = first brachitaxis composed of 2 brachials of which the second is an axillary
 br = brachial (when used without prefix refers to free arm; otherwise refers to a given brachial in a brachitaxis)
 - = synarthry (e.g., br1-2 refers to a synarthry between brachials 1 and 2 of free arm)
 + = syzygy (e.g., br3+4 refers to a syzygy between brachials 3 and 4 of free arm)
 c = cirral (e.g., c1-c5 indicate cirrals 1 to 5)
 P_{II} = exterior pinnule on the first or second ossicle of brachitaxis II (e.g., P_{II} on IIbr2)

Results

Class Crinoidea Miller, 1821
Subclass Articulata Zittel, 1879
Order Comatulida A.H. Clark, 1908
Superfamily Himerometroidea A.H. Clark, 1908
Family **Himerometridae** A.H. Clark, 1908

Remarks

Hess & Messing (2011) placed Himerometridae within the superfamily Mariametroidae A.H. Clark, 1909 (later changed to Himerometroidea by Taylor *et al.* 2017) in which rod-shaped basals are absent. All genera in Himerometridae (*Heterometra* A.H. Clark, 1909, *Himerometra*, *Craspedometra* A.H. Clark, 1909, *Amphimetra* A.H. Clark, 1909), except *Discometra*, show coelomic grooves on the adoral side of centrodorsal. *Amphimetra* has multiple radiate coelomic grooves while *Heterometra*, *Himerometra* and *Craspedometra* show Y-shaped grooves with more or less wide branches. In *Discometra*, such Y-shaped features are present as canals included in the stereom and located just beneath the surface of the proximal facet of radials (Fontannes 1880; Sieverts-Doreck 1961). As a consequence, coelomic grooves are absent from the adoral surface of the centrodorsal. In *Himerometra*, the aboral facet of each radial displays a pair of wide grooves running in parallel in the inner part and diverging in a Y shape in the outer part; this feature is also visible on the oral side of the centrodorsal (Fig. 3A). Coelomic groove patterns are very similar in *Himerometra* (Fig. 3A) and *Discometra* (Fig. 4) but differ markedly in each of the other genera (Rasmussen 1978: figs 593–594). The numerous radiating coelomic grooves (A.H. Clark 1915) distinguish *Amphimetra* the most from the other genera, and Hemery (2011), Summers & Rouse (2014) and Taylor *et al.* (2017) questioned its attribution to Himerometridae. In *Himerometra*, the general shape of the centrodorsal varies from hemispherical to almost discoidal. The insertions of cirri on the centrodorsal have a very variable aspect on the same individual, with or without a slight rectangular transverse relief (Fig. 3B). The radial circling delimits a more or less wide adoral cavity whose flanks corresponding to the inner face of the radials are sculpted by strong vermiculate figures (Fig. 3C). The distal articular facet of the radials is sub-trapezoidal, the internal (adoral) ligamentary areas, with no distinguishable limit adorally, are separated by a large depression, and the muscular areas are reduced and nearly inconspicuous (Fig. 3D).

Stratigraphical range

Miocene–Recent (Western Pacific), possibly since the Eocene.

Genus *Discometra* Gislèn, 1924

Type species

Eugeniocrinus? rhodanicus Fontannes, 1877.

Emended diagnosis

Centrodorsal hemispherical to low hemispherical or discoidal; cirrus-free aboral apex concave or flattened; adoral side with inter-radial ridges; cirrus sockets with or without low transverse rectangular ridge and closely placed, often in 3 (rarely 5) irregular rows. Cirrals without aboral spines. Radials with internal, Y-shaped coelomic canals just beneath proximal surface; radial circling nearly equal to or lower and narrower than centrodorsal; interarticular ligament fossae large, separated by wide midradial area. Rod-shaped basals absent. Numerous arms, up to about 60; brachitaxes with 2 or 4 ossicles (2 frequent beyond tertibrachitaxis); ligamentary synarthry at br1-2; syzygy with radiating crenularium at br3+4; ligamentary articulations irregularly placed beyond br5.

Remarks

Gislén (1924) designated *D. rhodanica* as the type species of the genus, so it is important to clarify and complete the description with the new data provided here. *Discometra* is mainly distinguished from all other genera of Himerometridae by its internal coelomic canals located near the aboral surface of the radials.

Geographical distribution

From southeastern France (this study) to northern and central Italy (Noelli 1900; Airaghi 1904; Albus 1930), central Europe and Poland (Sieverts-Doreck 1961; Radwańska 1987) as well as Algeria (Pomel 1885–1887) and possibly Egypt (cited by Fourtau 1920 but without illustration), in the Early and Middle Miocene.

Included species

Discometra eggenburgensis (Schaffer, 1912), *D. luberonensis* sp. nov., *D. michelottii* (Noelli, 1900), *D. rhodanica* (Fontannes, 1877) and *D. speciosa* (Pomel, 1885).

Discometra luberonensis sp. nov.

[urn:lsid:zoobank.org:act:2C82EC72-FEDC-4BCB-9716-88EEFDB0146D](https://zoobank.org/act:2C82EC72-FEDC-4BCB-9716-88EEFDB0146D)

Fig. 2A–F

Diagnosis

Robust species with arms up to 60 in number. Centrodorsal a rounded pentagonal, flattened, truncated cone; basal diameter up to 14.3 mm; aboral pole cirrus-free, flattened and slightly depressed, smooth or very slightly granular, reaching $\frac{2}{3}$ of centrodorsal diameter. Cirrus sockets in 2–3 irregular marginal rows. Cirri XXX–L of up to at least 30 never higher than wide cirrals, 27.5 mm long. Arm pattern with Ibr2ax, IIbr1-2 3+4ax; br1-2ax frequent up to fifth brachitaxis; ligamentary synarthry at br1-2; multiradiate syzygy at br3+4; very oblique muscular synarthries in proximal part of arms.

Etymology

The epithet refers to the Massif du Lubéron, a major mountain range in the Provence area where the specimens on which the description is based were collected. Lubéron is part of the greater administrative area (Région) called Provence-Alpes-Côte d'Azur in the southeast of France.

Material examined

Holotype

FRANCE • SE France, Vaucluse, Bassin d'Apt, Ménerbes-Lacoste Plateau; MHNL 20.062682.

Paratypes

FRANCE • same collection data as for holotype; MHNL 20.056148, 20.056151.

Locus typicus

“Calcaire de Ménerbes” (Demarcq 1970), facies with large pectinids (*Gigantopecten restitutensis*), quarries in Ménerbes-Lacoste Plateau (Bassin d'Apt, Vaucluse, southeastern France), Late Burdigalian.

Description

Holotype (Fig. 2A–B)

Specimen well exposed aborally, displaying centrodorsal, proximal part of three rays, about ten free arms visible in profile and recurved aborally, five cirri still attached to centrodorsal, and many fragments

of arms and isolated cirri. Centrodorsal a flattened truncated cone; apex broad, almost flat and smooth, devoid of cirrus sockets; cirrus sockets arranged in 2 to 3 irregular rows. Maximum length of complete attached cirrus 27.50 mm with 30 cirrals; cirrals subcylindrical; c1–c5 wider than high; following cirrals as high as wide; maximum cirral diameter 1.0 mm, average width of proximal half of cirri 2.0 mm, most frequent height of cirrals about 1 mm; terminal claw slightly curved and about twice as long as preceding segment. Radial circlet hidden. Arms divided 4 or 5 times; Ibr2 always axillary; secundibrachitaxes IIbr1-2 3+4ax (4 cases), IIbr undivided (1); pattern observed in the following brachitaxes: IIIbr1-2ax (5), IVbr 1-2ax (4), IVbr 1-2 3+4ax (1), IVbr undivided (1), Vbr1-2ax (2), Vbr1-2 then broken (2), Vbr1 2+3 4... (1), VIbr1-2 3+4... (2), estimated total number of arms close to 60. Non-muscular (ligamentary) articulations: ligamentary synarthry at 1-2 and syzygy with multiradiate crenularium at 3+4 (most often ankylosed at IIbr3+4); syzygies or synostoses irregularly arranged along free arms, separated by 4 to 8 muscular synarthries; br1-9 more or less rectangular, following brachials wedge-shaped. Maximum primibrachial width 7.10 mm; maximum primibrachitaxis length 6.30 mm; Ibr2ax height 3.42 mm; secundibrachial width 4.90 mm; IIbr1-2 height 3.35 mm; IIbr1-2 3+4ax maximum length 6.25 mm; IIIbr1-2 width 3.50 mm, height 3.35 mm; maximum height of tertibrachial axillary 2.0 mm; average width of proximal half of distalmost free arm 2.65 mm; longest isolated fragment of free arm 38 mm with 26 brachials; maximum length of an attached free arm 50.0 mm. Preserved pinnules rare, proximal part of P_{II} robust, composed of more or less squarish segments; more distal part of proximal pinnule getting thinner and flexible with relatively short pinnulars (less than twice as high as wide).

Paratypes

Specimen MHNL 20.056148 (Fig. 2C–D) with largest centrodorsal diameter, aboral cirrus-free depression flat and very slightly granular; about 30 cirri preserved around centrodorsal hiding proximal part of crown; complete cirrus with 25 cirrals, length 26 mm, longest cirrus fragment 27 mm with 28 cirrals. Specimen MHNL 20.056151 (Fig. 2E–F) with most flattened centrodorsal, aboral surface flat and smooth with two small pits; only $\frac{2}{3}$ of crown preserved, one brachitaxis visible, with same pattern as holotype; visible arms 38, allowing an estimated total number close to 60.

Discometra rhodanica (Fontannes, 1877)

Figs 3E, 4A, 5A–B, 6

Eugeniocrinus ? rhodanicus Fontannes, 1877: 669.

Antedon meneghinianus Fontannes, 1880: 412–413, pl. 2, fig. 11a–c.

Antedon rhodanicus – Fontannes 1880: 410–412, pl. 2, fig. 10a–c. — de Loriol 1897: 121–124, pl. 4, fig. 8 (non 9–10). — Nicolas 1897: 131–132, fig. 6; 1898: 398–399, 402–404, fig. 1. — Airaghi 1904: 44–45, figs 14–15. — Schütze 1904: 156–162, pl. 2, figs 4–5. — Albus 1930: 291–292, pl. 11, figs 5, 7.

Discometra rhodanica – Gislén 1924: 180–182. — Biese & Sieverts-Doreck 1939: 106–107. — Sieverts-Doreck 1961: 110–117, 124, text fig. 2. — Rasmussen 1978: T890, fig. 593-4a.

Antedon cf. rhodanicus – Valette 1928: 31–34, fig. 5.

Discometra meneghiniana – Biese & Sieverts-Doreck 1939: 105.

non *Antedon rhodanica* – Vadasz 1915: 89–90, pl. 7, figs 24–26.

non *Discometra rhodanica* – Rasmussen 1978: T890, fig. 593-4b–c. — Hess & Messing 2011: 107, fig. 52-3a–d.

Emended diagnosis

Species known only from its calyx (centrodorsal + radial circlet). Centrodorsal hemispherical, often more flattened in large specimens, diameter can reach 14 mm; lateral surface with large cirrus sockets arranged in up to 3 irregular rows, each at bottom of a more or less marked depression; aboral pole depressed, conical in smaller (young) specimens (to $\frac{1}{3}$ maximum centrodorsal diameter) and bordered

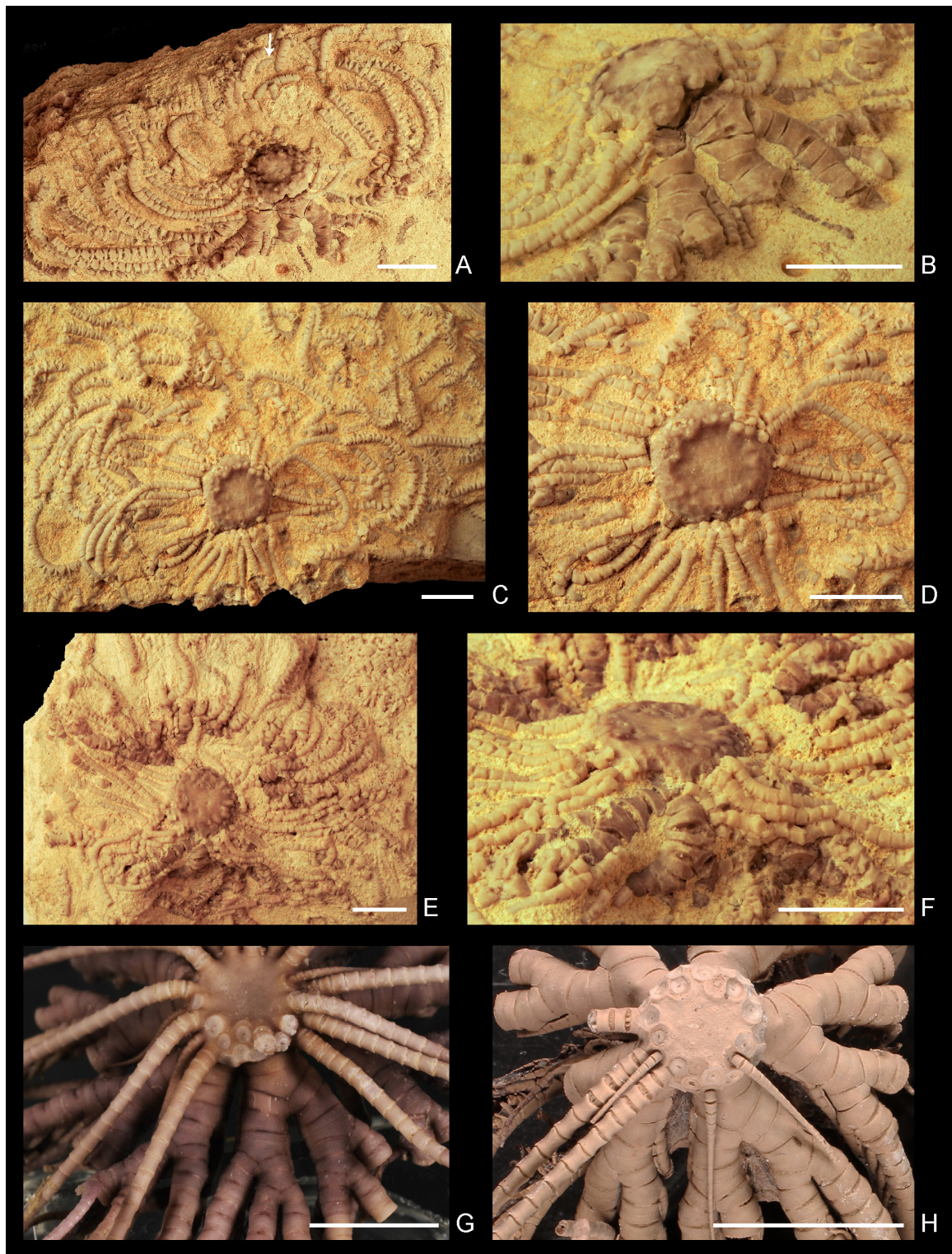


Fig. 2. Aboral view of the proximal crown and centrodorsal in three genera of Himerometridae A.H. Clark, 1908. **A–F.** *Discometra luberonensis* sp. nov., Late Burdigalian of Ménerbes-Lacoste Plateau. **A–B.** Holotype (MHNL 20.062682). **C–D.** Paratype (MHNL 20.056148). **E–F.** Paratype (MHNL 20-056151). **G–H.** Extant species of Himerometridae from western Pacific. **G.** *Himerometra robustipinna* (Carpenter, 1881) (MNHN-IE-2012-862). **H.** *Heterometra savignii* (Müller, 1841) (MNHN-IE-2016-1381). Scale bars: A–G = 10 mm; H = 5 mm.

by smaller apical cirrus sockets arranged in two irregular rows; apical depression becoming wider (to $\frac{2}{3}$ maximum diameter) and deeper with increasing centrodorsal diameter and with numerous radial grooves.

Material examined

Neotype

FRANCE • 1 calyx; Bouches du Rhône, Notre-Dame du Château near Saint-Etienne-du-Grès; MASR 2020.5011 (figured by de Loriol 1897: fig. 8).

Other material

FRANCE • 1 calyx; Gard, Les Angles; UCBL 200025a • 2 calices; same collection data as for preceding; MRA 3.000.348, 3.000.349 • 1 centrodorsal; same collection data as for preceding; UCBL 200025b • 3 calices; Vaucluse, Caumont-sur-Durance, Picabrier; MHNL 20.062686, 20.062687, 20.062688.

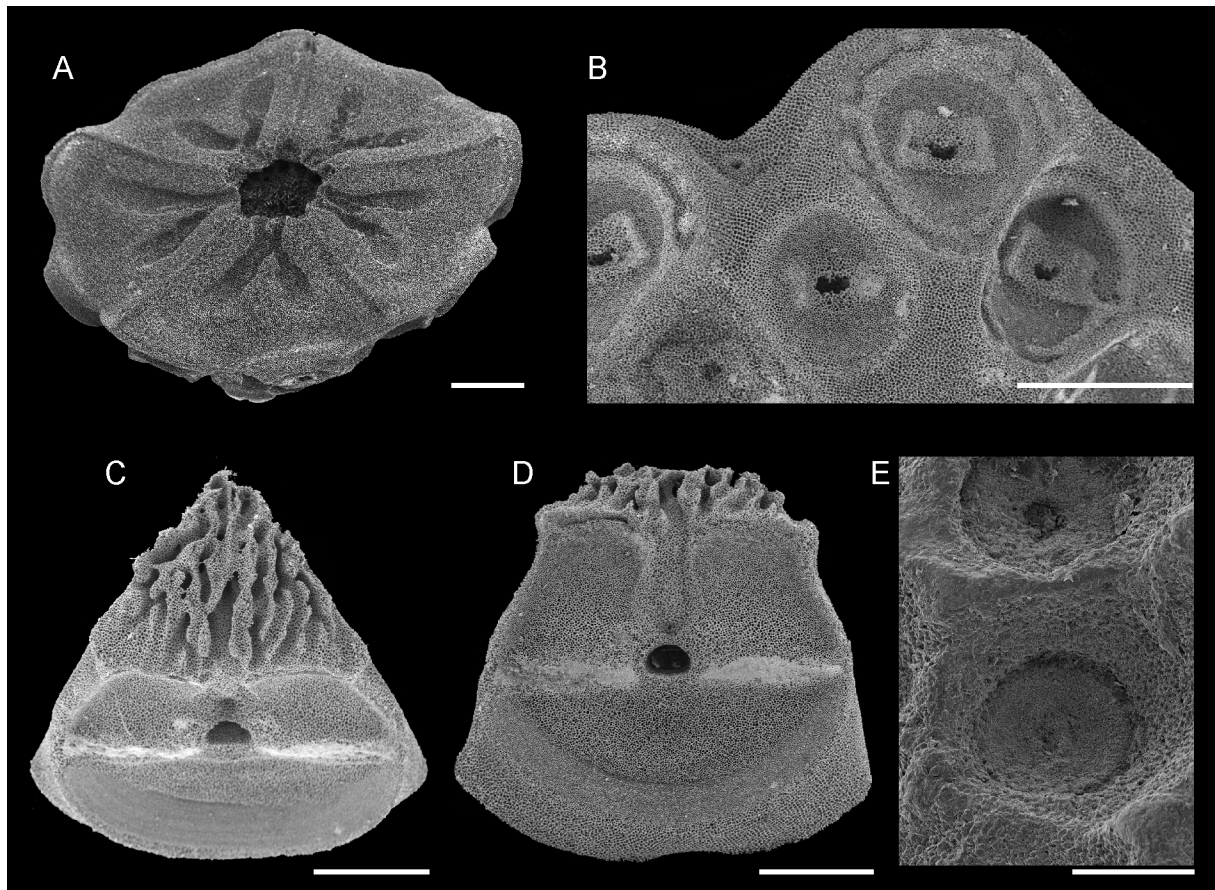


Fig. 3. Centrodorsal and radials in Himerometridae A.H. Clark, 1908. **A–D.** *Himerometra robustipinna* (Carpenter, 1881) (MNHN-IE-2012-862). **A.** Adoral side of centrodorsal. **B.** Cirrus sockets on lateral face of centrodorsal. **C–D.** Radials. **C.** Adoral view showing vermiculate grooves on inner face. **D.** Distal articular facet. **E.** *Discometra rhodanica* (Fontannes, 1877) from Picabrier (MHNL 20.062687), cirrus sockets on centrodorsal. Scale bars: A–D = 1 mm; E = 0.5 mm.

Locus typicus

Late Burdigalian, facies with *Chlamys praescabriuscula* (Fontannes, 1878), near Bollène (Vaucluse, southern France).

Description

Neotype

Extensive investigations in the collections of MHNL and MRA to retrieve the specimens used by Fontannes (1880) to describe *D. rhodanicus* and *D. meneghinianus* have been unsuccessful. They can be considered lost. Moreover, the locality from which they were collected, now located in an urbanized area, has now become inaccessible. The specimen illustrated by de Loriol (1897: fig. 8) from the Late Burdigalian of Notre-Dame du Château (east of Saint-Etienne du Grès), an outcrop still accessible, is housed in the collection of the Musée des Alpilles in Saint-Rémy de Provence (MASR 2020.5011). We designate this specimen as the neotype (Fig. 5A–B). Although smaller, its good preservation and its characters are similar to those of the specimen illustrated by Fontannes (1880: pl. 2, fig. 10a–c). This specimen consists of a hemispherical centrodorsal and radial circling. Its dimensions are given in Table 2. The aboral surface of the centrodorsal (Fig. 5A) shows a marked depression surrounded by small apical cirrus sockets (diameter <0.4 mm) partially worn out or biocorroded. The lateral surface is covered with larger cirrus sockets (diameter 0.5 to 0.9 mm) more or less oval and hollow; flattened socket floors sometimes displaying a roughly rectangular, low transverse ridge (Fig. 5B, arrow) like in extant Himerometridae (Fig. 3B). These larger cirrus sockets are arranged in up to three irregular rows. The maximum diameter of the radial circling is much smaller than that of the centrodorsal (ratio 0.82). Centrodorsal height almost equals that of the radial circling. Radial distal articular facet is almost entirely occupied by ligamentary areas, while muscular areas are comparatively inconspicuous. Its geometry is similar to that observed in *Himerometra* (Fig. 3D). Irregular radiating grooves can be seen on the walls of the central adoral cavity, which is partially filled with sediment. They correspond to the vermiculate grooves reported above in the extant species of Himerometridae (Fig. 3C).

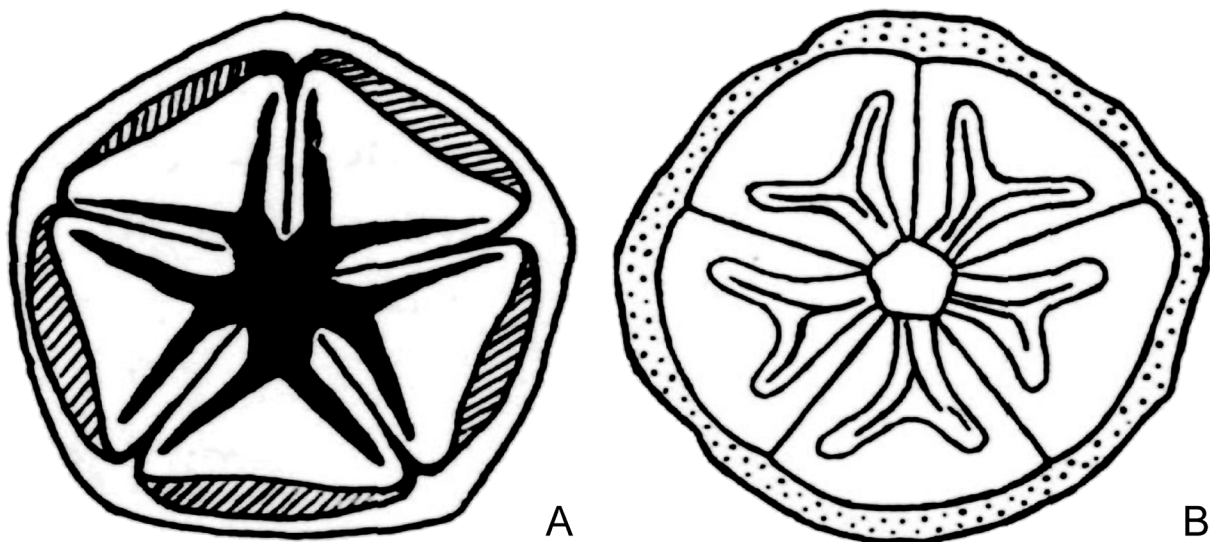


Fig. 4. Cross sections near aboral surface of radial circling showing Y-shaped coelomic canals in the genus *Discometra* Gislén, 1924. **A.** *Discometra rhodanica* (Fontannes, 1877). **B.** *Discometra eggenburgensis* (Schaffer, 1912). Modified from Sieverts-Doreck (1961) in which A was modified from Fontannes (1880).

Calices from the Picabrier deposit at Caumont-sur-Durance

Three calices illustrate morphological changes during growth (Fig. 6). Centrodorsal diameter of the smallest specimen (MHNL 20.062688) is hemispherical, 7.7 mm across (Fig. 6B), with an aboral face similar to that of the neotype. Centrodorsal of the largest specimen (MHNL 20.062686) is more discoidal, 12 mm across (Fig. 6A); its aboral depression deeper, $\frac{2}{3}$ of centrodorsal diameter; apex completely devoid of cirrus sockets and covered by numerous radial grooves, as in one of the specimens illustrated by Fontannes (1880) (Fig. 4A). Cirrus sockets more or less circular, slightly concave and well delineated, and each located at the bottom of a well-marked depression (Fig. 3E). These depressions become almost contiguous, separated by fragile, often worn out crests. Centrodorsal of specimen MHNL 20.062687 is 9.9 mm across; specimen shows an intermediate morphology (Fig. 6C–D).

Specimens from other sites

Most of the other specimens examined were collected in the Rhône-Provence basin by one of us (MP) and are represented by centrodorsals only or centrodorsal and radial circllets, often worn out or biocorroded. Nevertheless, some characters of the calyx, such as degree of centrodorsal flattening, broadening and deepening of aboral cirrus-free depression, centrodorsal/radial circllet height ratio, and flaring of adoral cavity delimited by the radial circllet, are still visible and prove to be very variable (Table 2). The ancient quarries of Les Angles, now inaccessible, provided many specimens partly described by Nicolas (1898). Those that we have found in older collections, including the largest known specimens (UCBL 200025a, MRA 3.000.348, MRA 3.000.349), are worn out and do not allow detailed observation.

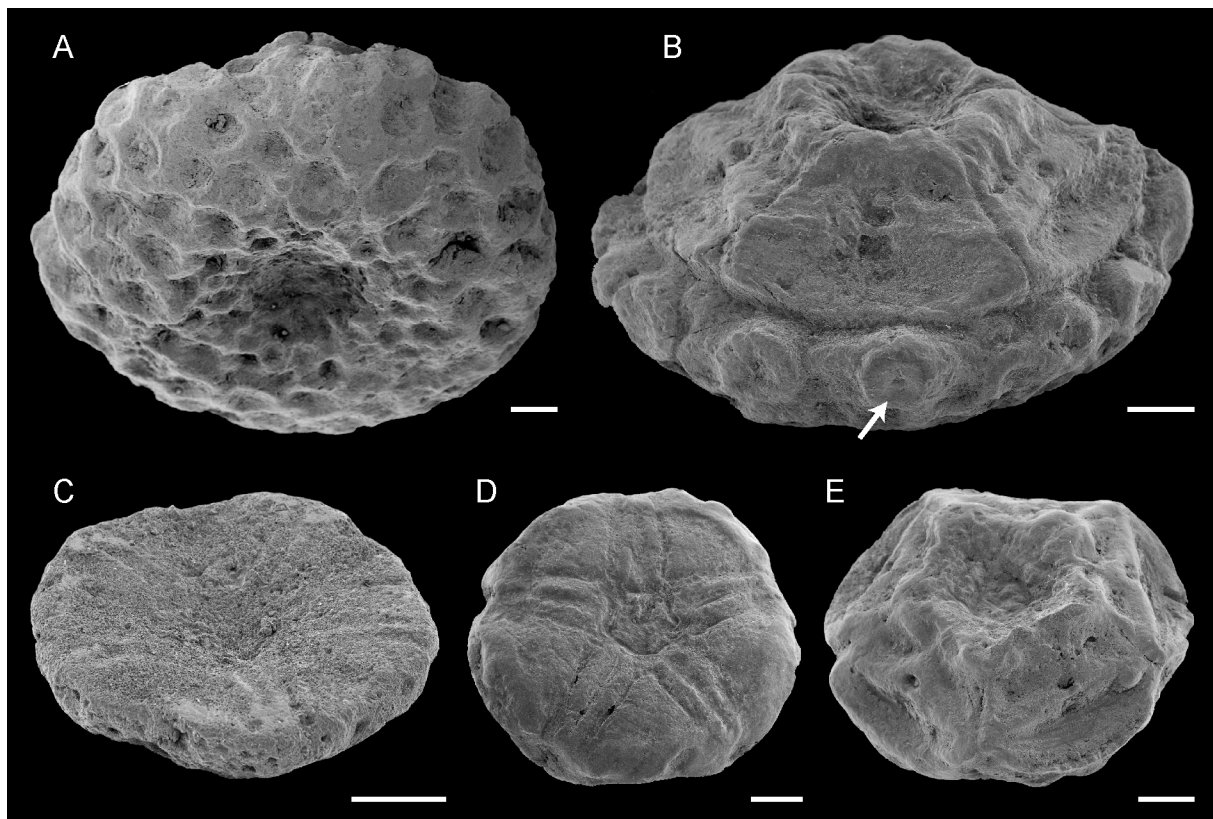


Fig. 5. Late Burdigalian specimens attributed to *Discometra rhodanica* (Fontannes, 1877) by de Loriol (1897). **A–B.** Neotype of *D. rhodanica* from Notre-Dame du Château (MASR 2020.5011). **A.** Oblique aboral view of centrodorsal. **B.** Oblique adoral view of calyx (arrow = sub-rectangular low ridge). **C–E.** Unidentified Comatulidae Fleming, 1928. **C.** Adoral face of a centrodorsal from Entrechaux – ‘Ferme Pie’ (MHNL 20.062689). **D–E.** Radial circllet from Notre-Dame du Château (MASR 2020.5021). Scale bars = 1 mm.

Remarks

Gislén (1924) pointed out the strong affinities between *D. rhodanica*, *D. eggenburgensis* and *D. meneghiniana* (Fontannes, 1880). *Discometra meneghiniana* is only known from the single calyx described by Fontannes (1880: pl. 2, fig. 11) and considered lost. It was collected from the same outcrops as the holotype of *D. rhodanica*. Fontannes's figure suggests that this specimen is strongly worn out; in particular the aboral depression of the centrodorsal displays an abnormally regularly circular appearance. It nevertheless falls within the field of variation of the species. We consider it to be a junior synonym of *D. rhodanica*.

Discussion

Genus *Discometra* Gislén 1924

Confirming the pioneering observations of Fontannes (1880) on the presence of Y-shaped coelomic canals in *Discometra*, Sieverts-Doreck (1961) transferred this genus to Himerometridae. Rasmussen (1978) and Hess & Messing (2011) adopted the same view.

However, Sieverts-Doreck (1961) had pointed out that the two specimens from Notre-Dame du Château attributed to *D. rhodanica* by de Loriol (1897: figs 9–10) could not belong to family Himerometridae. From these two specimens, we were successful in locating the specimen illustrated in fig. 9 only. This specimen consists of the radial circlet, which shows on its well-preserved aboral face traces of five rod-

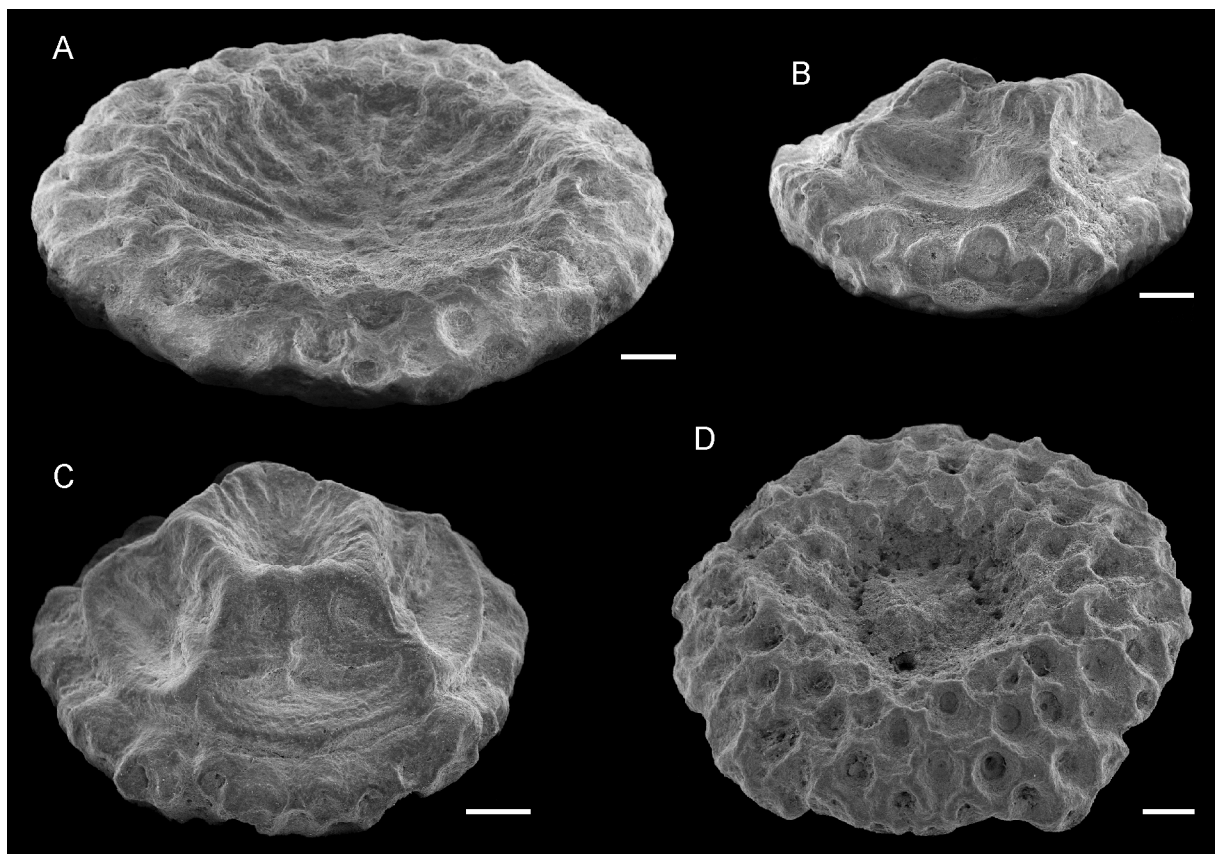


Fig. 6. Calices of *Discometra rhodanica* (Fontannes, 1877) from Picabrier. **A.** Aboral oblique view of centrodorsal, largest specimen (MHNL 20.062686). **B.** Adoral oblique view, smallest specimen (MHNL 20.062688). **C–D.** Specimen of intermediate size (MHNL 20.062687). **C.** Adoral oblique view. **D.** Aboral oblique view. Scale bars = 1 mm.

shaped basals (Fig. 5D). A corresponding structure is present on the adoral face of an isolated centrodorsal collected near Entrechaux (Ferme Pie) (Fig. 5C). Rod-shaped basals are absent in the superfamily Himerometroidea to which Himerometridae belongs (sensu Hess & Messing 2011). In addition, the distal articular facet of the radials has small but conspicuous and clearly delimited muscular areas and triangular interarticular ligament fossae. In the specimen attributed by Vadasz (1915: pl. 7, figs 24–26) to *D. rhodanica*, the distal articular facet of radials exhibits these same characters, which are incompatible with an attribution to Himerometridae according to Taylor *et al.* (2017). Unfortunately, Hess & Messing (2011: fig. 52-3a–d) used figures from these two specimens to illustrate the genus *Discometra*.

In calices from the Rhône-Provence Miocene basin, the main quantitative characters vary mainly with size within each site, but not when considering all the sites together. The ratios indicate a large variability independent of size (Table 2). This result suggests the influence of local environmental conditions. However, large specimens exhibit a marked tendency towards flattening of the centrodorsal and extension of the aboral cirrus-free apical depression. Regarding this variability, the quantitative data are too sparse to draw taxonomic conclusions. Only the qualitative characters of the centrodorsal aboral depression allow us to distinguish two species.

Jagt *et al.* (2002) recognized five species (*Discometra eggenburgensis*, *D. meneghiniana*, *D. michelottii*, *D. rhodanica* and *D. speciosa*) of Cenozoic feather stars attributed to the genus *Discometra*, among which *D. meneghiniana* is here considered to be a junior synonym of *D. rhodanica* (see below).

***Discometra luberonensis* sp. nov.**

Two genera of extant Himerometridae have a large number of arms: *Heterometra* with up to 48 arms and *Himerometra*, which reaches about 60 arms as in *D. luberonensis* sp. nov. *Himerometra* displays well separated primibrachitaxes (Fig. 2G), and tertibrachitaxes are of 2 brachials only. *Heterometra* has brachitaxes of 2 or 4 brachials and primibrachitaxes in lateral contact as in *D. luberonensis* sp. nov. (Fig. 2B), or separated (Fig. 2H) as in *Himerometra*. The centrodorsals of *D. luberonensis* sp. nov. differ from those of *D. rhodanica* and *D. eggenburgensis* in having a less hemispherical general shape, an aboral depression devoid of cirrus sockets, and a flatter and smoother aboral depression devoid of both cirrus sockets and radial grooves (Fig. 2B, D, F) as is common in other extant Himerometridae (Fig. 2G–H). Attribution of this new species to the genus *Discometra* needs to await confirmation of the presence of internal coelomic canals near the proximal surface of the radials.

***Discometra rhodanica* (Fontannes, 1877)**

By comparing calices from other sites with the growth series from Picabrier, it appears that the neotype from Notre-Dame du Château and the holotype from Bollène fit into this sequence in size and shape. The holotype of *D. meneghiniana* and the large specimens from Les Angles have their aboral depression moderately developed despite their large size. Some specimens of *D. eggenburgensis* (Sieverts-Doreck 1961: figs 3a, 4) have a broad aboral depression with radiate grooves, but more discrete than those observed in the largest specimen from Picabrier. In view of the morphological variations in *D. eggenburgensis* described by Sieverts-Doreck (1961) and our observations on *D. rhodanica*, we do not have a robust discriminating character to distinguish the two species based on the calyx alone. Pending additional data on the crown and cirri in the two species, we suggest that the distinction between them should be temporarily maintained.

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