

Research Article

An exceptionally well-preserved starfish fauna (Asteroidea, Echinodermata) from the Early Miocene of southeastern France

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<https://zoobank.org/09228051-8C7C-4A58-BAEA-44EB772062AD>

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Academic editor: Ben Thuy ♦ Received 24 May 2025 ♦ Accepted 24 November 2025 ♦ Published 3 February 2026

Abstract

A new starfish fauna from the Late Burdigalian (Early Miocene) of the Apt basin (Rhodano-Provençal gulf, southeastern France) is described here. This new starfish fauna comes from accumulation levels of marine invertebrates, including exceptionally well-preserved pectinid bivalves and echinoderms. Among the echinoderms, the sea urchins are the most abundant, closely followed by the starfish. This is the first time the starfish fauna is being studied in detail. Here are described twelve additional specimens of *Lacosteaster lauerorum* Gale & Ward, 2024 (Solasteridae, Valvatida) with the first description of the abactinal face of the species, an undetermined species of *Astropecten* (Astropectinidae, Paxillosida), and two new genera and species: *Cruciformaster pedicellarius* **gen. nov. et sp. nov.** (Oreasteridae, Valvatida) and *Menerbesaster bongrainae* **gen. nov. et sp. nov.** (Echinasteridae, Spinulosida).

Keywords

Apt basin, Asteroidea, Astropectinidae, Echinasteridae, exceptional preservation, Late Burdigalian, new taxa, Oreasteridae, Solasteridae

Introduction

The Calcaire de Ménerbes Formation attributed to the Late Burdigalian (Early Miocene) has been exploited in numerous quarries in the Ménerbes and Lacoste area (Apt basin, rhodano-provençal gulf, southeastern France) (Fig. 1). At different levels, it includes accumulation lenses of exceptionally well-preserved invertebrates, with skeletal elements still in articulation.

Bongrain (2013) gave a preliminary inventory of the taxa found in the accumulation lenses (bivalves, sea urchins, feather stars, sea stars and brittle stars) with particular attention to the large bivalve *Gigantopecten restitutensis* (Fontannes, 1884). Based on taphonomic

and paleoecological observations, she suggested that the fossil-rich lenses were the result of very rapid displacement and burial of two main benthic communities, one characterized by *Gigantopecten restitutensis* and the other by the regular echinid *Tripneustes planus* (Agassiz, 1840). Among the echinoderms, taxonomic studies were carried out by Philippe (1998) on the sea urchins and by Éléaume et al. (2020) on the feather stars. Bongrain (2013) proposed brief identifications of the sea stars. She assigned them to the genera *Solaster* Forbes, 1839, *Astropecten* Gray, 1840 and *Echinaster* Müller & Troschel, 1840.

The present study focuses on the asteroid fauna, mainly with taxonomic descriptions, including two new genera and species. Several asteroid assemblages from western

Europe have been described in the literature, but only a few have yielded exceptionally well-preserved specimens with their skeletal elements still in articulation. Remarkable examples include the Bajocian assemblage of Schinznach-Dorf (Aargau, Switzerland) described by Hess (1972), the Callovian assemblage of La Voulte-sur-Rhône (Ardèche, France) described by Villier et al. (2009), the Kimmeridgian assemblage of Cerin (Ain, France) described by Breton et al. (1994) and the Upper Cretaceous (Cenomanian-Maastrichtian) Chalk of southern England described by several authors (e.g. Sladen 1891, 1893; Spencer 1905, 1907, 1908; Gale 1987a, b, 1989; Breton 1992). Although consisting only of isolated elements and therefore not regarded as exceptionally preserved, the fauna firstly discovered by Hess (1966) and later described by Gale (2011b) is remarkable for its diversity, comprising eleven taxa from eight families from the Oxfordian of Savigna (Jura, France), an unusually rich assemblage that is rarely encountered in the fossil record. A few exceptionally well-preserved Miocene asteroids are known, for example *Kionaster petersonae* Blake & Portell, (2011) from the Lower Miocene of Florida, *Doraster consellatus* Kato & Oji, (2013) from the Miocene of Japan, and the comparatively poorly preserved material of ?*Ceramaster* sp. from the Miocene of Romania (Jagt and Codrea 2010). The assemblage described here is the first to provide a snapshot of the asteroid diversity during the Miocene of Western Europe.

Here are described four taxa, including two new genera and species: *Astropecten* sp.; *Cruciformaster pedicellarius* gen. nov. et sp. nov.; *Lacosteaster lauerorum* Gale & Ward, 2024; and *Menerbesaster bongrainae* gen. nov. et sp. nov. Each taxa represents a different family, highlighting an exceptional diversity: Astropectinidae, Echinasteridae, Oreasteridae, and Solasteridae. *Cruciformaster pedicellarius* gen. nov. et sp. nov. is the first fossil species belonging to the Oreasteridae. The Echinasteridae and Solasteridae were previously each represented by a single species in the fossil record. The Eocene echinasterid *Echinaster jacobsoni* Rasmussen, 1972 is known from Denmark (Rasmussen 1972), while the Jurassic solasterid *Plesiosolaster moretonis* (Forbes, 1856) is known from England and Switzerland (Hess 1972; Blake 1993). In contrast, the Astropectinidae are represented by numerous species in the fossil record (e.g. Heller 1858; Cavara 1886; Sacco 1893; Hess 1955; Borghi and Bajo Campos 2009; Jaselli and Collareta 2018).

Material and methods

The material examined here is housed in the Centre “Louis Lortet” de conservation et d’étude des collections, Musée des Confluences in Lyon; the Muséum d’Histoire Naturelle in Grenoble and the Muséum d’Histoire Naturelle in Geneva (Table 1). It includes sixteen asteroid individuals preserved on fifteen limestone slabs.

They were collected from the Calcaire de Ménerbes Formation located on the Lacoste plateau and in the north of the Petit Luberon Massif (Fig. 1). Nine specimens were extracted from the Soubeyran quarry. The remaining six specimens lack precise locality data. For four of them, only the collection village (Ménerbes or Lacoste) is known and for two of them, even the collection village is not known. In the Soubeyran quarry, where most of the starfishes studied come from, the echinoderm fauna is particularly rich and diversified, with representatives of four of the five extant classes: sea urchins, feather stars, sea stars and brittle stars.

Most of the asteroid ossicles are in connection which is exceptional in the fossil record. Some asteroids are incomplete due to the burying mode and the limestone cutting during the quarry exploitation. Asteroids show as much their abactinal face as their actinal face and sometimes both when they are oblique.

Asteroids are described following the terminology used by Fau and Villier (2018, 2020) and derived from Gale (2011a). They were photographed using a Nikon D5000 camera and an AxioCam MRc 5 camera mounted on a Zeiss Discovery V8 stereomicroscope at the Université de Claude Bernard Lyon 1. They were illustrated using the Inkscape ver. 1.3.2 software. For comparative purposes, scanning electron microscope (SEM) images of selected ossicles of the extant species *Oreaster reticulatus* (Linnaeus, 1758) were taken using a Zeiss EVO MA15 at the Scientific Imaging Lab of the National Museum of Natural History of the Smithsonian Institution. The specimen (USNM 7511) was dissected following the protocol described by Fau and Villier (2018, 2020).

Institutional abbreviations are as follows:

MDC	Musée des Confluences (Centre “Louis Lortet” de conservation et d’étude des collections) in Lyon, France;
MHNG	Muséum d’Histoire Naturelle in Geneva, Switzerland;
MHNGr	Muséum d’Histoire Naturelle in Grenoble, France;
LF	Lauer Foundation for Paleontology, Science and Education in Wheaton, Illinois, United States of America;
MCCB	Museo Civico Craveri in Bra, Italy;
MSNPI	Museo di Storia Naturale dell’Università di Pisa in Calci, Italy;
NHMW	Naturhistorisches Museum Wien in Vienna, Austria;
UNIBO	Università de Bologna, Italy;
UNIPR	Museo di Storia Naturale dell’Università degli Studi di Parma, Italy;
USNM	Smithsonian Institution, Natural History National Museum, Washington D.C., United States of America.

Morphological abbreviations are as follows:

Ab	abactinals;
Abact sp	abactinal spines;
Ac	actinals;
Ad	adambulacrals;
Ads	adambulacral spines;
Am	ambulacrals;
Fa	first ambulacrals;
Fr	furrow spines;
In	inferomarginals;
Marg sp	marginal spines;
Md	madreporites;
Ms	marginal spines;
Or	orals;
Os	oral spines;
Pn	pedicellariae notches;
Prox	proximal;
R	large radius, distance between the center of the disc and the end of an arm;

r	small radius, distance between the center of the disc and an interbranchial area;
Sb	subambulacral spines;
Su	superomarginals.

Geological and environmental settings

According to Demarcq (1962) and Germain et al. (1966), the Calcaire de Ménerbes Formation is a bioclastic limestone lens about 30 meters thick, extending from Oppède to Lacoste villages and resting on Cretaceous limestones or Eocene sands. This shallow-water sediment is poor in quartz, fairly fine, slightly vacuolated, rich in algae, bryozoans, mollusks and echinoderms.

Carbonnel (1969) correlated the Calcaire de Ménerbes Formation with nearby limestones attributed to the Late Burdigalian. Besson (2005) interpreted the Calcaire de Ménerbes Formation as deposited during his second transgressive depositional sequence, an

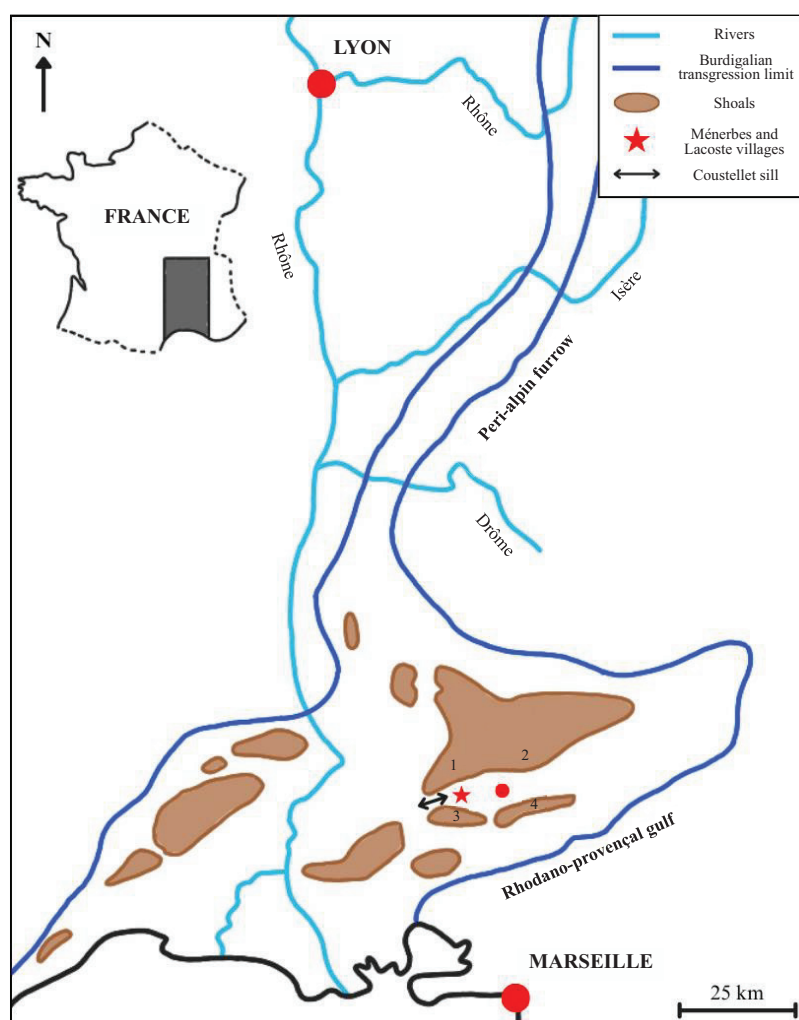


Figure 1. Map of the Miocene rhodano-provençal gulf (modified from Bongrain, 2013). 1: Mont Ventoux, 2: Montagne de Lure, 3: Petit Luberon and 4: Grand Luberon.

Table 1. List of specimens examined for the present study.

Genus and species	Catalogue number	Most precise location	Face	Type status
<i>Lacosteaster lauerorum</i>	MDC.20056003	Ménerbes	2 faces	
<i>Lacosteaster lauerorum</i>	MDC.20056007	Ménerbes	Actinal	
<i>Lacosteaster lauerorum</i>	MDC.20056147	Unknown	2 faces	
<i>Lacosteaster lauerorum</i>	MDC.20056149	Unknown	Abactinal	
<i>Lacosteaster lauerorum</i>	MDC.20056151	Soubeyran	Abactinal	
<i>Lacosteaster lauerorum</i>	MDC.20056152	Soubeyran	Actinal	
<i>Lacosteaster lauerorum</i>	MDC.20062672	Soubeyran	2 faces	
<i>Lacosteaster lauerorum</i>	MDC.20062673	Soubeyran	Abactinal	
<i>Lacosteaster lauerorum</i>	MDC.20062674	Soubeyran	Abactinal	
<i>Lacosteaster lauerorum</i>	MDC.20062675	Soubeyran	Actinal	
<i>Lacosteaster lauerorum</i>	MDC.20062676	Soubeyran	Actinal	
<i>Lacosteaster lauerorum</i>	MDC.20062677	Soubeyran	Actinal	
<i>Cruciformaster pedicellarius</i>	MHNG-GEPI-87379a	Ménerbes	Actinal	Holotype
<i>Cruciformaster pedicellarius</i>	MHNG-GEPI-87379b	Ménerbes	Abactinal	Paratype
<i>Astropecten</i> sp.	MHNGr.PA.2624	Lacoste	Abactinal	
<i>Menerbesaster bongrainae</i>	MDC.20055541	Soubeyran	Abactinal	Holotype

interpretation which is further supported by the occurrence of overlying Langhian to Serravallian deposits infilling incised valleys, consistent with a subsequent marine transgression. Bongrain (2013) noted that it contains invertebrates' assemblages characteristic of the thermal maximum reached at the boundary between the Burdigalian and Langhian (Demarcq 1984). However, the precise age of the Calcaire de Ménerbes Formation remains uncertain pending the discovery of reliable biostratigraphic markers.

Bongrain (2013) interpreted the exceptional accumulations observed in the Ménerbes and Lacoste area as the result of a sudden and massive mortality event. Nevertheless, she noted that quarry operating surfaces of abandoned quarries do not allow accumulation strata to be observed. In fact, in the quarry opened in Lacoste village, these surfaces show herringbone cross-stratifications, indicative of tidal currents, and erosional surfaces, above where the fossils are located, suggesting storm waves. This implies that the fossiliferous accumulations could be due to episodic storms (Besson 2005; Philippe Sorrel, Université de Claude Bernard Lyon 1, oral communication).

Systematic Paleontology

Class Asteroidea de Blainville, 1830
Superorder Valvatacea Blake, 1987
Order Valvatida Perrier, 1884

Family Solasteridae Viguiet, 1878

Diagnosis. Family with a large circular disc and five to fifteen long broad tapering arms. Abactinals bearing a cluster of spines often on a tall central column (metapaxillae) and forming a reticulated irregular mesh. Superomarginals sometimes discreet and metapaxilliform. Inferomarginals frequently conspicuous. Actinals rarely extending to the end of the arms. Adambulacrals bearing two series of spines,

the subambulacral spines perpendicular to the groove and the furrow spines parallel to the groove (modified from Clark and Downey 1992; Gale and Ward 2024).

Genus *Lacosteaster* Gale & Ward, 2024

Lacosteaster Gale & Ward, 2024: 9, figs 5–7.

Type species. *Lacosteaster lauerorum* Gale & Ward, 2024: 9, figs 5–7.

Diagnosis. As the type species by monotypy.

Lacosteaster lauerorum Gale & Ward, 2024

Figs 2–4

Lacosteaster lauerorum Gale & Ward, 2024: 9, figs 5–7.

Type material. The holotype LF 4905 was collected in the Calcaire de Ménerbes Formation and was deposited in the Lauer Foundation for Paleontology, Science and Education in Wheaton. It comes from an unknown quarry in the Lacoste village. It is almost complete and shows its actinal face (Fig. 4A).

Type locality. Lacoste, southeastern France.

Type strata. Calcaire de Ménerbes Formation, Late Burdigalian.

Material examined. Twelve specimens were studied. They were collected in the Calcaire de Ménerbes Formation and were deposited in the Musée de Confluences in Lyon. Eight of them come from the Soubeyran quarry in the Ménerbes village (MDC.20056151 to MDC.20056152, MDC.20062672 to MDC.20062677), two from an unknown quarry in the Ménerbes village (MDC.20056003, MDC.20056007) and two from an unknown locality (MDC.20056147, MDC.20056149) (Table 1).

Emended diagnosis. Species with a broad circular disc, narrow rounded interbranchial areas and eight to

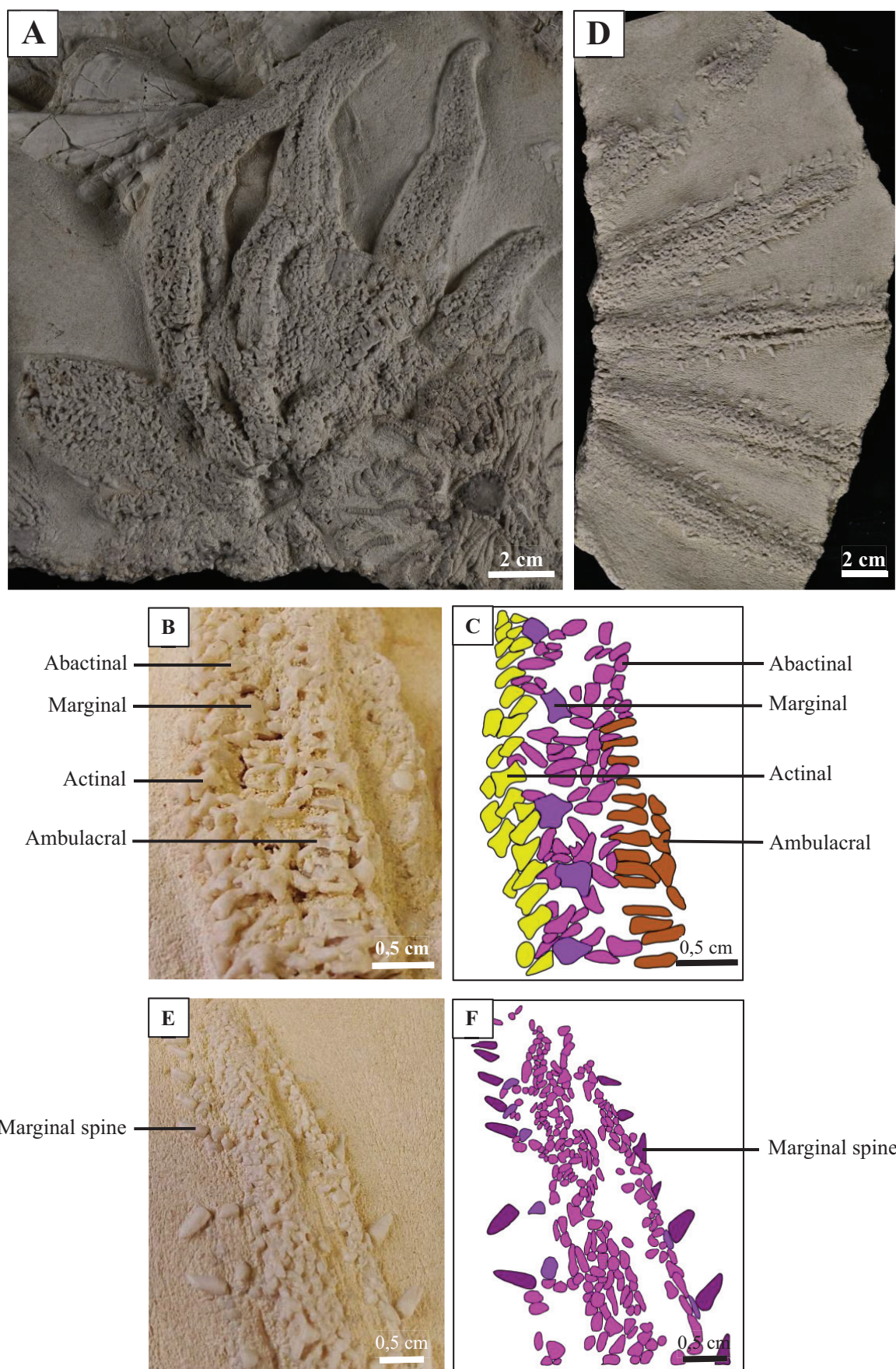


Figure 2. *Lacosteaster lauerorum* Gale & Ward, 2024. **A.** General view of the specimen MDC.20056151; **B.** Close-up of an arm, and **C.** Its interpretative scheme; **D.** General view of the specimen MDC.20062673; **E.** A close-up of an arm and **F.** Its interpretative scheme. **B, C, E, F:** distal position upwards.

twelve long tapering arms ($3.3 < R/r < 4.5$). Abactinals small, circular, ovoid or lobed; bearing spinelets; forming an irregular and dense mesh. Some abactinals enlarged and surmounted by a large spine. One discontinuous row of marginals twice as large as the abactinals, star-shaped, surmounted by a short, broad and conical spine. Marginals inconspicuous with every 3rd or 4th marginal enlarged. Up to four rows of actinals small; rectangular to ovoid, with a narrow center and wide ends; surmounted by a long, thin and straight spine and by spinelets; reaching the end of the arms. Adambulacrals short, broad, rectangular in actinal view or L-shaped in adradial view, surmounted by a long, thin and straight subambulacral spine as well as by four to six furrow spines organized in a longitudinal fringe. Ambulacrals with a straight base as well as a triangular and proximally projected head. Orals long, broad, surmounted by one large spine proximally and by an uncertain number of smaller spines distally to it (Gale and Ward 2024).

Description of the material examined. Four specimens display their abactinal face (Fig. 2), five their actinal face (Fig. 3), three both their abactinal and actinal faces (Table 1). No specimen is complete, eight are only represented by arms, four by both their disc and some arms.

The specimens studied are large ($r = 3$ to 5 cm and $R = 10$ to 17 cm). They have a broad circular disc, narrow rounded interbranchial areas and eight to eleven long tapering arms (Figs 2A, D, 3A).

Abactinals are small, up to 2 mm long, circular, ovoid or lobed and surmounted by spinelets. Some abactinals are enlarged, probably corresponding to discontinuous radial series, being twice as large as the others and bearing a large round spine. They form an irregular and dense mesh (Figs 2B, C, E, F, 4B–D). Madreporites are large, round, flat, with regular grooves and ridges. Two madreporites are visible on opposite sides of the disc of the specimen MDC.20056151 (Fig. 2A).

Marginals are twice as large as the abactinals, up to 4 mm long and star-shaped, with five lobes. They are rhombic, inconspicuous, similar in size to the actinals, with every 3rd or 4th marginal enlarged. They are surmounted by a short, up to 4 mm long, broad and conical spine. A single discontinuous row of marginals is recognizable and overlaps adjacent plates (Figs 2B–E, 4B, C).

Actinals are small, up to 1 mm long and rectangular to ovoid, with a narrow center and wide ends. They are surmounted by a long, thin and straight spine and by spinelets. Up to four rows of actinals are recognizable proximally, the number of rows decreasing distally and the last row reaching the end of the arms. They are organized in longitudinal and transversal series, alternating with the adambulacrals and overlapping each other (Figs 2B, C, 3B–F).

Adambulacrals are short, up to 1 mm long, broad, rectangular in actinal view and L-shaped in adradial view because of a distally oriented adradial extension. They are surmounted by one up to 2 mm long, thin and straight subambulacral spine (Fig. 3B–F). They are also surmounted by a fringe of up to three or four furrow spines preserved in the specimens MDC.20056147 and MDC.20062672.

Ambulacrals are long and thin. The base is short, slender and devoid of wings. The shaft is slightly longer and thinner than the base. The head is short, slender, triangular, projected proximally and has teeth along its entire length. The *actam* is narrower than the shaft and forms a triangle longer than wide. There are no furrows or crests. The first ambulacrals are shorter, broader and triangular (Fig. 3B–G).

Orals are up to 5 mm long and 2 mm broad. They are surmounted by an up to 5 mm long, thin and straight spine projecting towards the center of the mouth. Their irregular surface suggests that they were also surmounted by spinelets (Fig. 3D, E, G).

Remarks. The differences between the holotype described by Gale and Ward (2024) (Fig. 4A) and the specimens described here are few. Gale and Ward (2024) described a fringe of four to six furrow spines on the adambulacrals, when we only observed three to four furrow spines. These numbers are reasonably close when considering the natural variability, preservation and preparation biases and do not contradict the identification as *Lacosteaster lauerorum*.

Gale and Ward (2024) noted that *Lacosteaster lauerorum* resembles extant solasterids by the number and morphology of its arms but differs from them by the spination of its marginals, actinals and adambulacrals. Abactinals, which were not visible on the holotype and which are visible on the specimens studied here, provide new information. Like extant solasterids, they form an irregular mesh and are covered by spinelets. However, unlike extant solasterids, they are not paxilliform, and some are larger and surmounted by a large spine.

Occurrence. Late Burdigalian, Early Miocene, Ménerbes and Lacoste area, southeastern France.

Family Oreasteridae Fisher, 1908

Diagnosis. Family with a pentagonal to stellate body shape, five short tapering arms and rounded interbranchial areas. Abactinals forming a reticulated mesh with large pore areas. Radials forming regular series, often enlarged, cone-shaped, surmounted by a large spine and large granules. Marginals large, rectangular and arranged in two continuous rows. Intermarginals sometimes present. Actinals small, round, arranged in regular series and surmounted by large granules. Pedicellariae present, alveolar and leaving notches on the plates (modified from Döderlein 1936; Clark and Downey 1992).

Genus *Cruciformaster* Travers & Fau, gen. nov.

<https://zoobank.org/32A6AE5A-0A78-401B-8FAD-E755D73B7C7A>

Type species. *Cruciformaster pedicellarius* gen. nov. et sp. nov.

Etymology. In reference to the superomarginals of this genus that differentiate it from other oreasterid genera by being cruciform rather than rectangular.

Diagnosis. As the type species by monotypy.

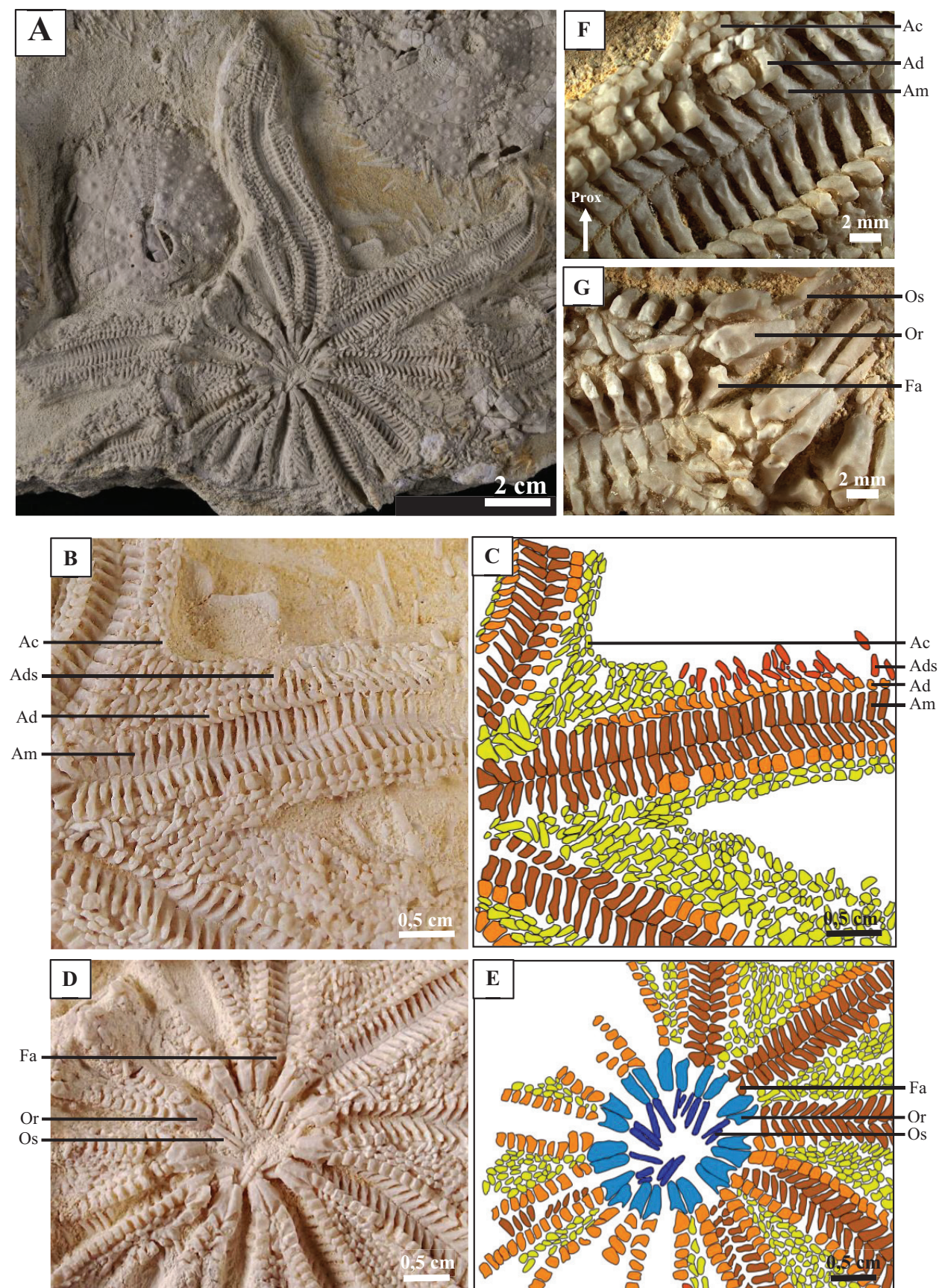


Figure 3. *Lacosteaster lauerorum* Gale & Ward, 2024. **A.** General view of the specimen MDC.20062677; **B.** A close-up of an arm and **C.** Its interpretative scheme; **D.** Close-up of the disc and **E.** Its interpretative scheme; **F.** Close up of an arm and **G.** Close-up on the disc. Ac (yellow): actinals, Ad (light orange): adambulacrals, Ads (dark orange): adambulacral spines, Am (brown): ambulacrals, Fa (brown): first ambulacrals, Or (light blue): orals and Os (dark blue): oral spines.

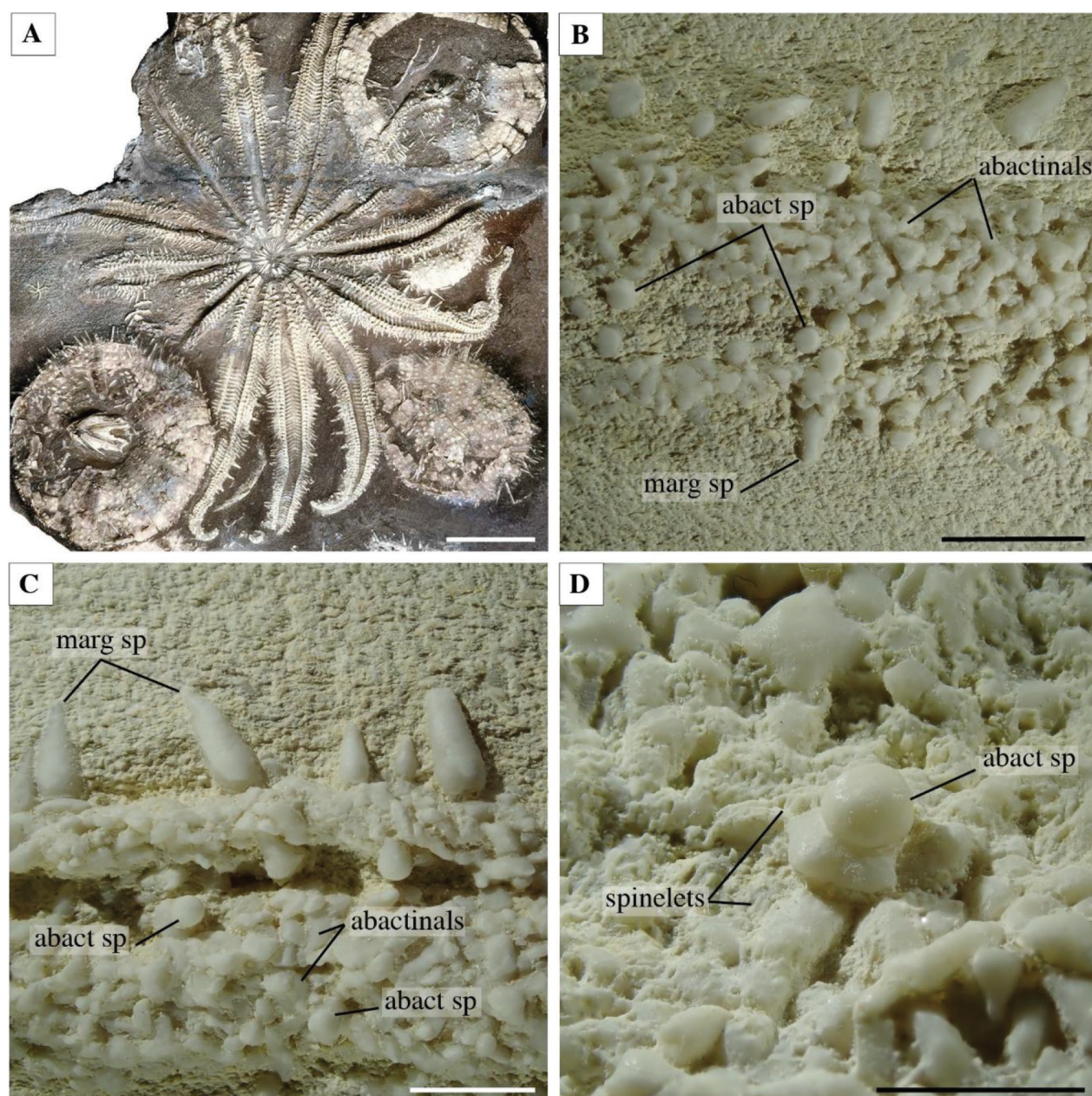


Figure 4. *Lacosteaster lauerorum* Gale & Ward, 2024. **A.** General view of the holotype LF 4905, modified from Gale and Ward (2024; Fig. 6). **B, C.** Details of the arms and spines of the specimen MDC.20062673; **D.** Details of the arm and spines of the specimen MDC.20056149. Abbreviations: abact sp: abactinal spine, marg sp: marginal spine. Scale bars: 5 cm (A); 1 cm (B); 5 mm (C, D).

***Cruciformaster pedicellarius* Travers & Fau, sp. nov.**

<https://zoobank.org/3B0A01C5-0AB3-4323-8E9C-A8C3F838CE18>

Figs 5, 6

Type material. Two individuals are present on the same slab. The largest one, showing its almost complete actinal face, is designated as the holotype MHNG-GEPI-87379a. The smallest one, showing part of one of its arms, is designated as the paratype MHNG GEPI-87379b. The slab was collected in the Calcaire de Ménerbes Formation. It was part of Nicolas Tourment private collection in Marseille and was deposited in the Muséum d'Histoire Naturelle in Geneva. It comes from an unknown quarry in the Ménerbes village (Table 1).

Type locality. Ménerbes, southeastern France.

Type strata. Calcaire de Ménerbes Formation, Late Burdigalian.

Etymology. In reference to the actinals and adambulacra of this species which have notches corresponding to the insertion of pedicellariae.

Diagnosis. Species with a broad pentagonal disc, wide rounded interbranchial areas and five short tapering arms ($R/r = 2.2$). Abactinals organized in a mesh formed of large cone-shaped abactinals bearing a large conical spine and of small ovoid abactinals connecting the latter. Superomarginals large and cruciform around the disc, gradually decreasing in size and becoming oval towards the arm tips. Inferomarginals

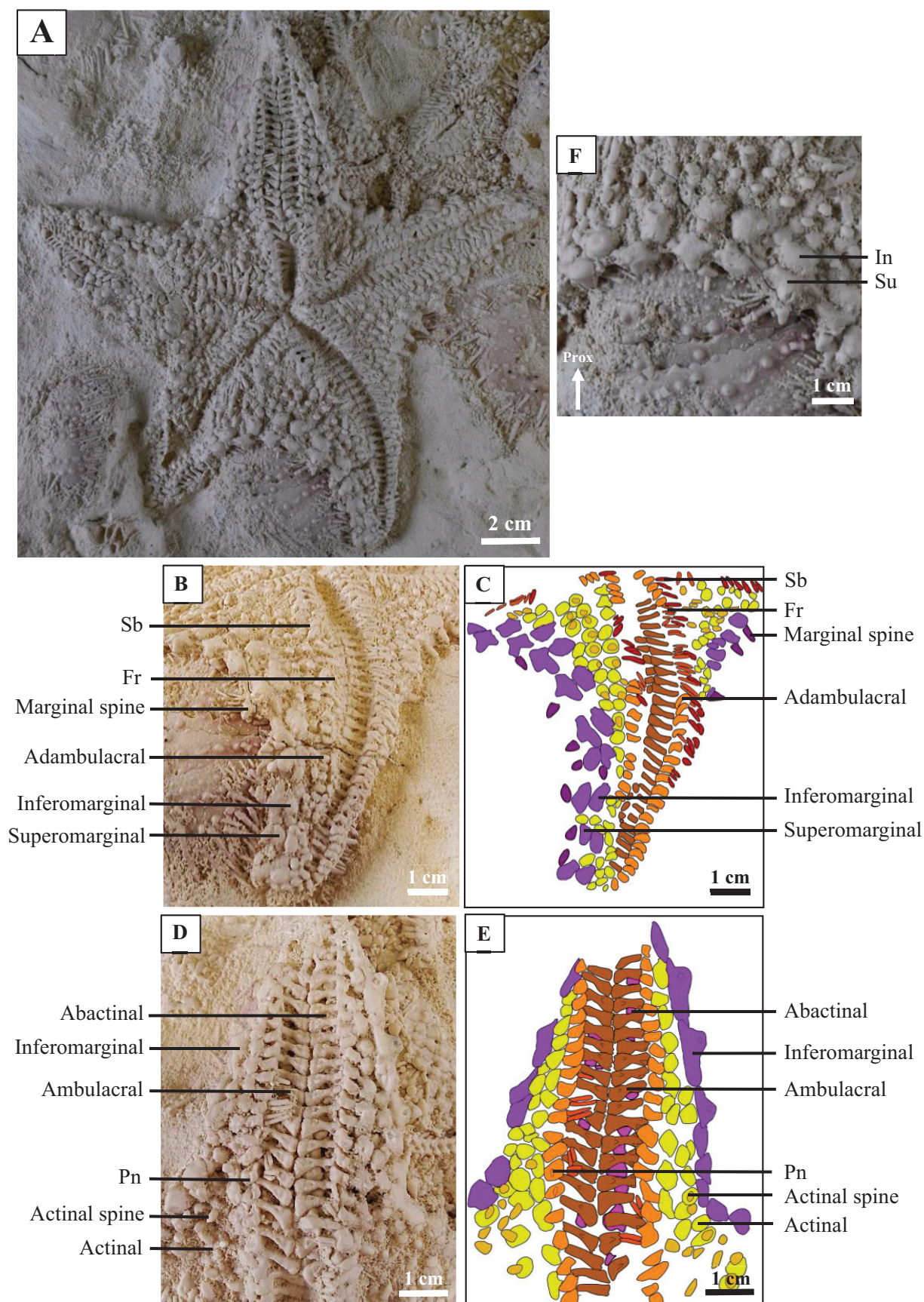


Figure 5. *Cruciformaster pedicellarius* gen. nov. et sp. nov. **A.** General view of the holotype MHNG-GEPI-87379a. with **B.** A close-up of an arm and **C.** Its interpretative scheme; **D.** A close-up of another arm and **E.** Its interpretative scheme; **F.** A close-up of an interbrachial area. Fr (dark orange): furrow spines, In: inferomarginals, Pn: pedicellariae notches, Sb (dark red): subambulacral spines and Su: superomarginals.

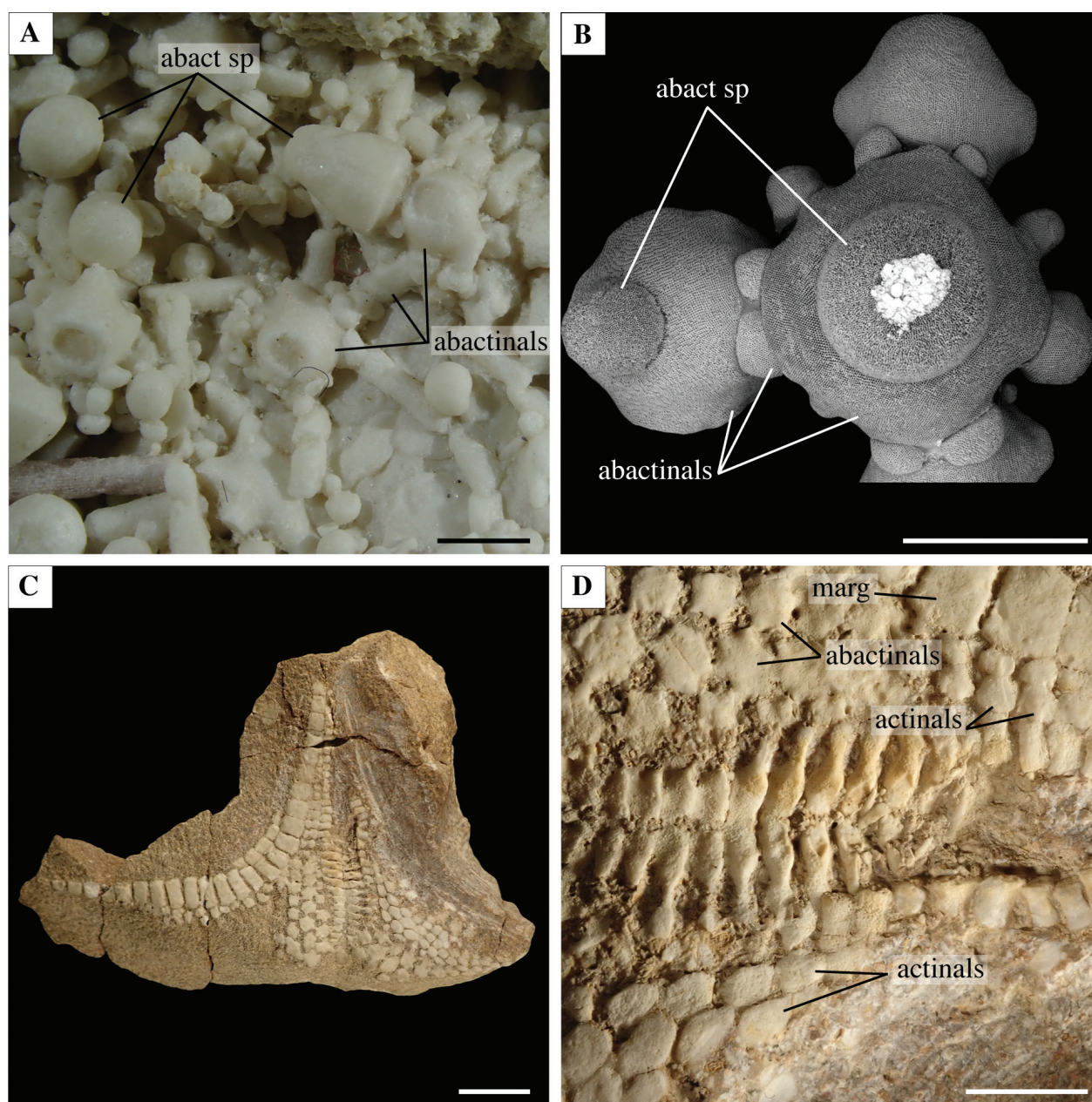


Figure 6. *Cruciformaster pedicellarius* gen. nov. et sp. nov. **A.** Close-up of the abactinals of the paratype MHNG-GEPI-87379b; **B.** Scanning electron microscope image of the abactinals of the extant specimen USNM 7511 of the extant species *Oreaster reticulatus*, note how larger spine bearing abactinals are connected together by smaller abactinals to form a mesh, just as in *Cruciformaster pedicellarius* gen. nov. et sp. nov.; **C.** General view of the fossil specimen USNM 240815 identified as *Goniodiscaster* (?) by Blake (1986) with **D.** A close-up showing the regular hexagonal shape of the abactinals. Abbreviations: abact sp: abactinal spine, marg: marginal. Scale bars: 2 mm (**A**, **B**); 2 cm (**C**); 1 cm (**D**).

large and lobed around the disc, gradually decreasing or increasing in size and becoming oval towards the arm tips. Marginals surmounted by a short, broad and conical spine. Up to three rows of small and round actinals, surmounted by a small and ovoid spine, reaching three quarters of the arms. Adambulacrals short, broad, rectangular in actinal view or L-shaped in adradial view, surmounted by a long and broad subambulacral spine and by two to three long and thin furrow spines. Ambulacrals with a winged base as well as a triangular and proximally projected head. Orals large, longer than high and triangular. Abactinals, marginals, actinals and

adambulacrals covered by large granules. Actinals and adambulacrals with notches corresponding to the insertion of alveolar bivalve pedicellariae.

Description. Two individuals are present on the same slab. The paratype, smaller, is in abactinal view and poorly preserved (Fig. 6A). The holotype, larger ($r = 4$ cm and $R = 9$ cm), is in actinal view and almost complete. It has a broad pentagonal disc, wide rounded interbrachial areas and five short tapering arms (Fig. 5A).

Primary abactinals are larger and cone-shaped, with a flattened base and an elevated top surmounted by a large conical spine. Secondary abactinals are smaller and

ovoid, forming a mesh by linking the primary abactinals. Abactinals are surmounted by large granules (Fig. 6A).

Superomarginals are large, up to 1 cm long and cruciform around the disc, gradually decreasing in size and becoming oval towards the arm tips. Inferomarginals are large, up to 1 cm long and lobed around the disc, gradually decreasing in size and becoming oval towards the arm tips. Marginals are surmounted by a short, up to 3 mm long, broad and conical spine as well as by large granules (Fig. 5B–F).

Actinals are small, up to 3 mm long and round. They are surmounted by a small, up to 1 mm long and ovoid spine as well as by large granules and notches left by alveolar bivalve pedicellariae. Up to three rows of actinals are recognizable proximally, their number decreasing distally and the last row reaching three quarters of arm length (Fig. 5B–F).

Adambulacra are short, up to 2 mm long, broad, rectangular in actinal view and L-shaped in adradial view. They are surmounted by two types of spines: on their actinal face, by a up to 4 mm long, broad, straight and blunt subambulacral spine and on their adradial face, by two to three up to 4 mm long, thin, arched and truncated furrow spines as well as by large granules and notches left by alveolar bivalve pedicellariae (Fig. 5B–E).

Ambulacra are short and broad. The base is short, broad and with symmetrical wings. The shaft is short and thin. The head is short, broad, triangular, projected proximally and has teeth along its entire length. The *actam* is as large as the shaft and forms a triangle longer than wide. There is a furrow but no crests (Fig. 5B–E).

Orals are up to 5 mm long, 2 mm wide, triangular and were most likely surmounted by spines and granules (Fig. 5A).

Remarks. Goniasterids and oreasterids are similar in morphology, but differences, notably in the shape of their abactinals, have been noted in the literature (Blake 1986). Most goniasterids have hexagonal-shaped, hexagonal and flattened abactinals arranged in a tessellated pattern, while oreasterids tend to have cone-shaped abactinals, with a circular to star-shaped flattened base and an elevated top (Fig. 6B). Some oreasterids, such as the genus *Culcita*, resemble goniasterids as juveniles, exhibiting densely tessellated abactinal plates and a relatively flat pentagonal-shaped body (e.g. Kano et al. 1991; Yiu and Mah 2024), but during growth, the abactinal skeleton becomes reduced and reorganized into a mesh-like pattern. Döderlein (1917) has reported in the oreasterids: “a tendency of certain dorsal plates to swell, to take on a cushion, hump or cone shape” (translated from German). *Cruciformaster pedicellarius* has cone-shaped abactinals, typical of the Oreasteridae family. It possesses cruciform-shaped marginals, contrary to other Oreasteridae genera. This justifies the establishment of a new genus and species.

The fossil record of the Oreasteridae family is poorly documented and uncertain, with only two known fossil occurrences whose taxonomic placements remain debated. Meneghini (1886) described the species *Goniodiscus ferrazii* from the Tertiary deposits of Italy. The specimen is relatively large ($R = 110$ mm, $r = 87$ mm) and displays a broadly pentagonal outline; however, as all arms are broken, the original body shape may have been more stellate in life.

The marginal ossicles are block-shaped, and the abactinal plates appear to exhibit a stellate arrangement. The genus *Goniodiscus* Müller & Troschel, 1842 is now regarded as a junior synonym of *Culcita* Agassiz, 1836, and species originally assigned to *Goniodiscus* have since been redistributed among 14 genera spanning the families Oreasteridae, Goniasteridae, Odontasteridae, Asterodiscidae, and the subfamily Ganeriinae (Asterinidae). Accordingly, the taxonomic affinities of *Goniodiscus ferrazii* remain uncertain and require formal redescription. Blake (1979, 1986) described the specimen USNM 240815 from the Eocene of Mexico corresponding to part of the disc and three arms (Fig. 6C). Blake (1986) attributed it to the genus *Goniodiscaster* Clark, 1909 due to the stellate shape of its abactinals (Fig. 6D). He also argued that the presence of multilocular and miliolid foraminifera in the matrix, typical of shallow and warm environments, indicates that this specimen shared the same ecology as extant oreasterids. However, the affinities of the genus *Goniodiscaster* have been greatly discussed in the literature. *Goniodiscaster* was initially assigned to the Goniasteridae by Clark (1909), but was later moved to the Oreasteridae by Döderlein (1936). Fisher (1919), Clark (1938) and Clark and Rowe (1971) followed Clark’s (1909) classification, whereas other authors (e.g. Spencer and Wright 1966; Clark 1993; Rowe and Gates 1995) adopted Döderlein’s (1936) broader concept of the Oreasteridae. More recently, Mah (2018) reaffirmed the position of *Goniodiscaster* in the Goniasteridae. Upon re-examination of the specimen USNM 240815, we found no differentiation among the abactinals that would suggest that they were organized in a mesh, nor were any conical abactinals present. These results do not contradict Blake’s (1986) identification of this specimen as *Goniodiscaster*, but rather confirm its affinity with the Goniasteridae.

Blake and Aronson (1998) described the specimen USNM 49018 from the Eocene of the Seymour Island corresponding to the tip of an arm. They argued that this specimen belongs to the Oreasteridae based on its enlarged protruding inferomarginals, on its domed irregular abactinals and on the possibility of the ambulacra to be closed to protect the tube feet. Blake and Aronson (1998) compared it to the genera *Anthena* Gray, 1840 and *Goniodiscaster* which used to be part of the Oreasteridae. *Anthena* and *Goniodiscaster* both have a flat rather than a domed body, and are now part of the Goniasteridae, suggesting that USNM 49018 should also be considered as a Goniasteridae. Therefore, *Cruciformaster pedicellarius* gen. nov. et sp. nov. is the first oreasterid properly described, with an unambiguous taxonomic treatment.

Occurrence. Late Burdigalian, Early Miocene, Ménerbes area, southeastern France.

Order Paxillosida Perrier, 1884

Family Astropectinidae Gray, 1840

Diagnosis. Family with five tapering arms. Abactinals small and paxilliform. Marginals large; block-like; surmounted by granules, spinelets and often spines on the inferomarginals; arranged in two continuous rows

and frequently separated by fascioles. Superambulacra developed. Orals generally large and triangular, sometimes constricted and bar-shaped. Odontophores concealed. Pedicellariae, when present, simple, spiniform and fasciculate. Tube feet tapering, with a narrow tip or knob (modified from Clark and Downey 1992; Chao 1999).

Genus *Astropecten* Gray, 1840

Diagnosis. Marginals block-like. Supermarginals smaller than the inferomarginals. Inferomarginals bearing spines which form a peripheral fringe. Intermarginals fascioles small, not angular and filled with spinules. Actinal interbrachial areas small. Adambulacral furrow margin angular and surmounted by three furrow spines. All plates except madreporite, superambulacra, ambulacra and odontophores bearing granules, spinelets or spines which are never webbed. Pedicellariae, rare, and simple, made of two to four modified spines (modified from Clark and Downey 1992; Chao 1999).

Astropecten sp.

Fig. 7

Material examined. The specimen MHNGr.PA.2624 was collected in the Calcaire de Ménerbes Formation and deposited in the Muséum d'Histoire Naturelle in Grenoble. It comes from an unknown quarry in the Lacoste village (Table 1).

Description. The specimen exhibits its abactinal face, with the disc, four complete and one partial arm. It is large ($r = 2.5$ cm and $R = 10$ cm), with a broad disc, wide angular interbrachial areas and five long narrow tapering arms (Fig. 7A).

Abactinals are small, up to 1 mm long and paxilliform (Fig. 7B–E). The madreporite is a 5 mm-long oval plate with a crenelated surface, and is located interradially close to the supermarginals (Fig. 7D, E).

Marginals are large, rectangular, up to 2 mm long and 6 mm high proximally but squared, up to 3 mm long and high distally. They are arranged in two continuous rows and separated by deep narrow fascioles proximally, but by more reduced fascioles distally. The surface of the supermarginals is irregular, which could indicate the presence of spines or be a preservation/preparation bias. Inferomarginals are surmounted by up to five spines, which increase in size distally and which are long, thin, curved, flattened, with a rounded base and acute tip. Inferomarginal spines form a peripheral fringe (Fig. 7B–E).

Ambulacra have a long, broad and straight base; a short and thin shaft; a short and broad head (Fig. 7D, E).

Remarks. There are currently 104 recognized species of extant *Astropecten* (Mah, 2025). The present specimen can be attributed to the *Astropecten* genus based on its broad disc, angular interbrachial areas and long arms; on

its block-like marginals with well-developed fascioles; on its inferomarginal spines projecting horizontally and forming a peripheral fringe (Koehler 1921; Clark and Downey 1992; Chao 1999). It lacks key features necessary for species-level identification.

Six extant *Astropecten* species have been reported in the Mediterranean Sea (Koehler 1921; Parenzan 1934; Costello et al. 2001): *Astropecten aranciaceus* (Linnaeus, 1758), *Astropecten bispinosus* (Otto, 1823), *Astropecten irregularis* (Pennant, 1777), *Astropecten jonstoni* (Delle Chiaje, 1827), *Astropecten platyacanthus* (Philippi, 1837) and *Astropecten spinulosus* (Philippi, 1837). The present specimen resembles fossil and extant specimens of *Astropecten irregularis*. It shares a similar size, R averaging 6 cm and reaching 10 cm, R/r ranging from 3.5 to 5. It lacks supermarginal spines as the subspecies *Astropecten irregularis pentacanthus* (Delle Chiaje, 1827) and has 4 to 6 inferomarginal spines (Koehler 1909; Koehler 1921; Pillon 2022). It differs from fossil and extant specimens of *Astropecten irregularis* by the absence of granules on the supermarginals. *Astropecten irregularis pentacanthus* is notably represented by fossils from the Pleistocene of Torrente Stirone and Fuime Taro, Italy (Fig. 8E) (Borghi et al. 2009).

Many *Astropecten* species have been found in Cenozoic sediments, although most are represented only by isolated skeletal elements, such as *Astropecten saucatsensis* Valette, 1924, from the Burdigalian of southwestern France. *Astropecten saucatsensis* differs from specimen MHNGr.PA.2624 in having prominent spine-attachment tubercles on the supermarginals. By contrast, only a few nearly complete fossils are sufficiently preserved to allow direct comparison with the present specimen (Zulliger 2009; Zulliger and Lessios 2010). *Astropecten montalionis* (Meneghini, 1852) from the Pliocene of Montañone, Italy (Fig. 8A; Jaselli and Collareta 2018) differs from the present specimen in having round interbrachial areas, longer and thinner arms; larger, more regular and better organized abactinals; smaller and as long as high marginals; shorter, broader and conical inferomarginal spines.

Astropecten bononiensis (Cavara, 1886) from the Pliocene of Mongardino, Italy (Fig. 8B; Cavara 1886) was erected because the specimen lacked sufficient characters to be related to any existing species. Its validity is questionable.

Astropecten bispinosus (Otto, 1823) from the Pliocene of Bra, Italy (Fig. 8C; Sacco 1893) differs from the present specimen in having a narrower disc, longer and more slender arms, and marginals that are smaller and approximately as high as they are long. The supermarginals of *A. bispinosus* also bear a prominent spine. *Astropecten linati* del Prato, 1896 closely resembles *A. bispinosus*, but is distinguished by its longer supermarginal and inferomarginal spines (Hess 1955; Jaselli and Collareta 2018).

Astropecten forbesi (Heller, 1858) from the Miocene of Margarethen, Austria (Fig. 8D; Heller 1858) differs from the present specimen in having a narrower disc, longer and thinner arms as well as smaller and as long as high marginals.

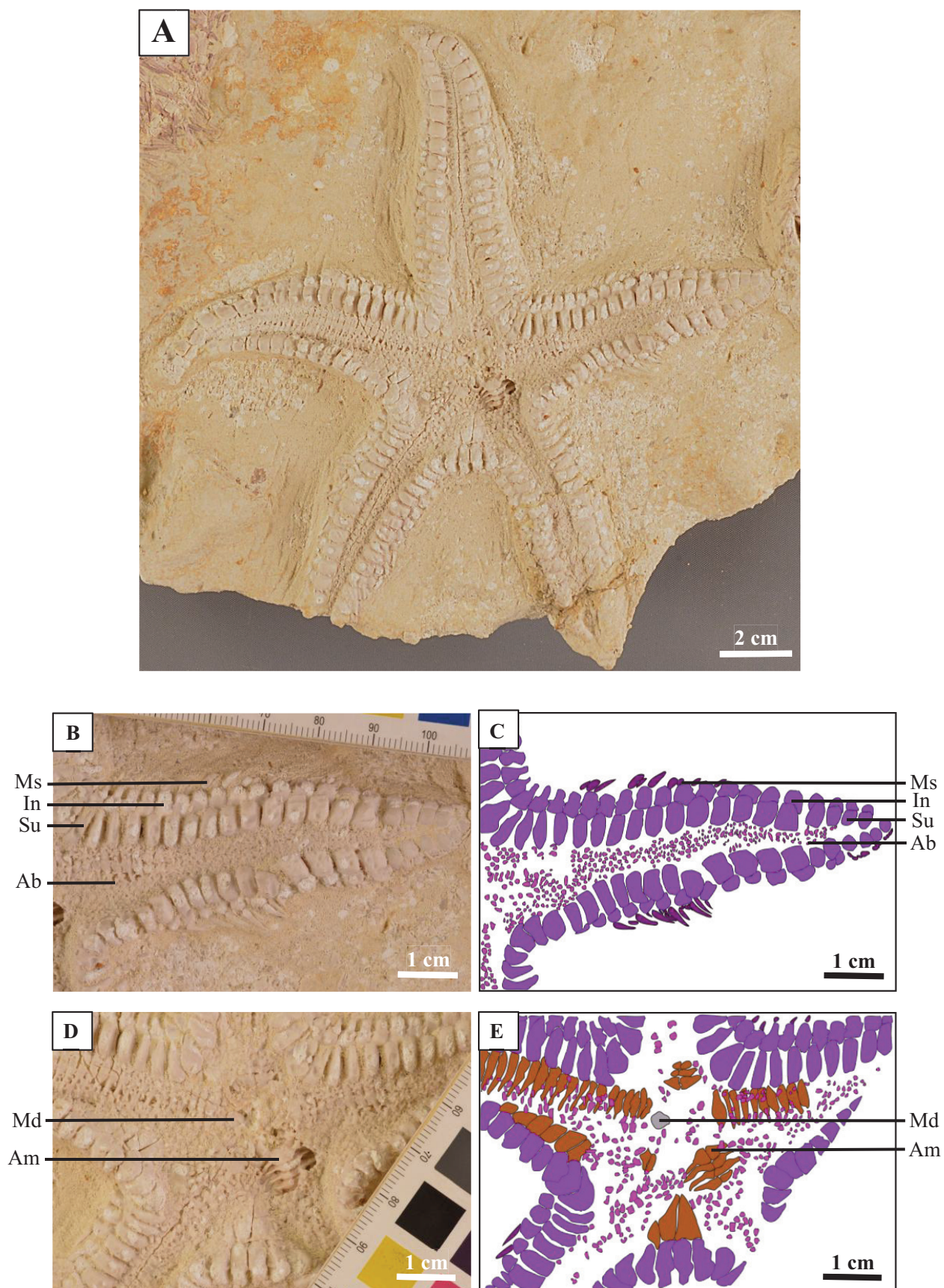


Figure 7. *Astropecten* sp. **A.** General view of the specimen MHNGr.PA.2624 with **B.** A close-up of an arm and **C.** Its interpretative scheme; **D.** A close-up of the disc and **E.** Its interpretative scheme. Ab (pink): abactinals, Am (brown): ambulacra, In (light purple): inferomarginals, Md (grey): madreporite, Ms (dark purple): marginal spines and Su (light purple): superomarginals.

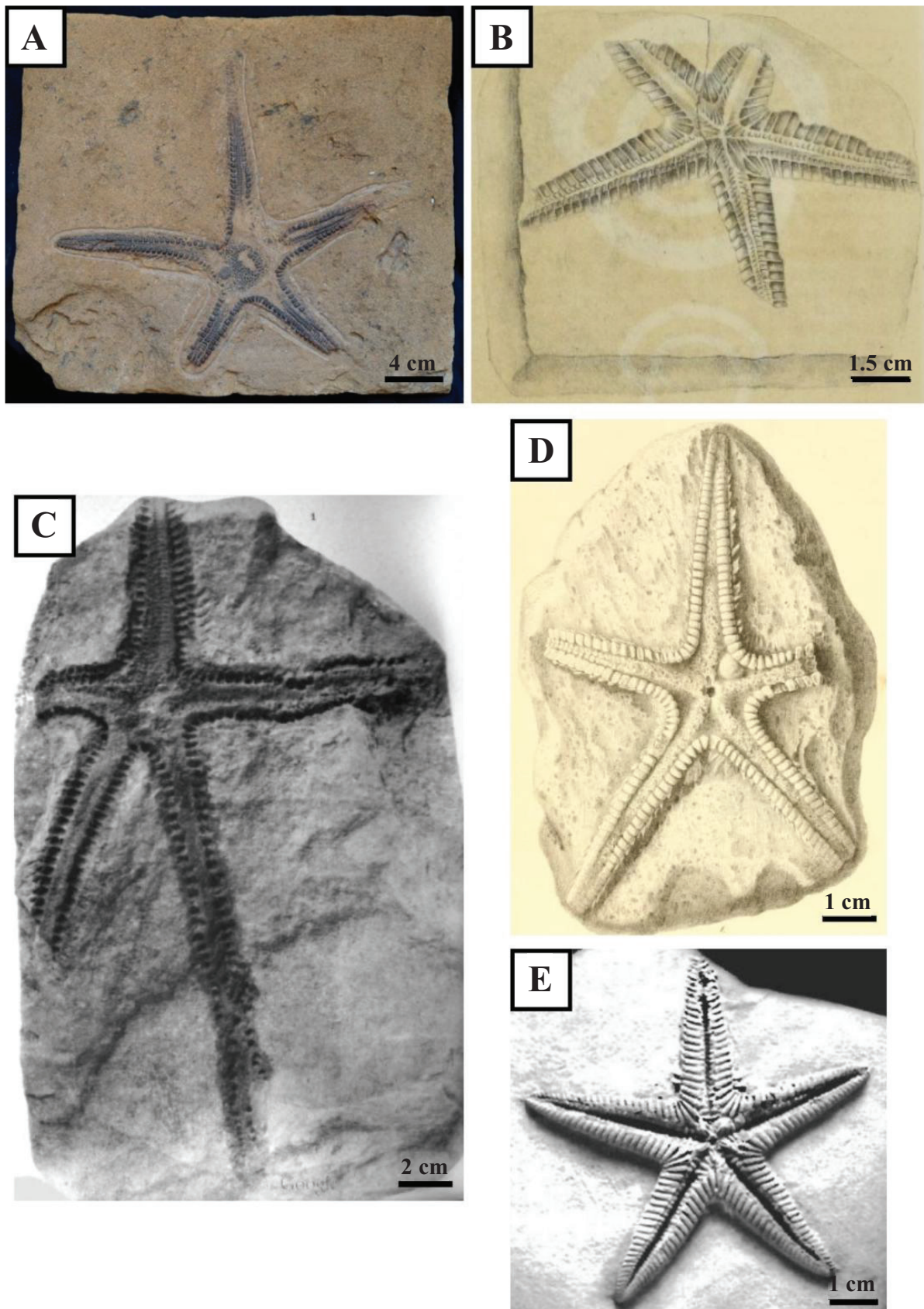


Figure 8. *Astropecten* fossils. **A.** General view of the holotype (MSNPI I-17605) of *Astropecten montalionis* (Meneghini, 1852) figured by Jaselli and Collareta (2018); **B.** Drawing of the holotype (UNIBO) of *Astropecten bononiensis* Cavara, 1886 figured by Cavara (1886); **C.** General view of a specimen (MCCB) of *Astropecten bispinosus* (Otto, 1823) figured by Sacco (1893); **D.** Drawing of the holotype (NHMW) of *Astropecten forbesi* (Heller, 1858) figured by Heller (1858); **E.** General view of a specimen (UNI-PR) of *Astropecten irregularis pentacanthus* (Delle Chiaje, 1827) figured by Borghi and Bajo Campos (2009).

Astropecten navodicensis Nosowska, 1997 differs from specimen MHNGr.PA.2624 in having the outer face of the superomarginals covered by very small tubercles and the inferomarginals bearing horse-shoe-shaped tubercles.

Superorder Spinulosacea Blake, 1987
Order Spinulosida Perrier, 1884

Family Echinasteridae Verrill, 1867

Diagnosis. Family with usually a small disc; normally five cylindrical or tapering arms, rounded in cross-section; angular interbranchial areas, acute when the arms are swollen proximally. Abactinals polygonal, oblong or round, imbricating to form an irregular mesh and bearing numerous spines. Papulae grouped in meshes. Marginals often inconspicuous. Intermarginals sometimes present. Actinals frequently few. Adambulacra relatively small with rarely more than three spines along the furrow margin. Orals small. Pedicellariae absent (modified from Hayashi 1940; Clark and Downey 1992).

Genus *Menerbesaster* Travers & Fau, gen. nov.

<https://zoobank.org/43DEB329-3DE1-467F-AA19-432AC2A63D89>

Type species. *Menerbesaster bongrainae* gen. nov. et sp. nov.

Etymology. Named after the village of Ménerbes where the specimen was found.

Diagnosis. As the type species by monotypy.

***Menerbesaster bongrainae* Travers & Fau, sp. nov.**

<https://zoobank.org/71BA7447-9C48-4DD4-AD1B-6387BB3EEF6C>

Fig. 9

Type material. The holotype MDC.20062679 was collected in the Calcaire de Ménerbes Formation and is deposited in the Musée des Confluences in Lyon. It comes from the Soubeyran quarry in the Ménerbes village (Table 1).

Type locality. Soubeyran quarry, Ménerbes, south-eastern France.

Type strata. Calcaire de Ménerbes Formation, Late Burdigalian.

Etymology. Dedicated to Madelaine Bongrain who published the first paleoecological study on the Miocene pectinid bivalve and echinoderm accumulations found in the Calcaire de Ménerbes Formation.

Diagnosis. Species with five arms ($R/r > 2.5$). Abactinals small, round, oblong or lobed, probably bearing spines and forming a regular mesh. Marginals inconspicuous and undifferentiated morphologically. Up to five rows of small, round and flat actinals, organized in longitudinal series and overlapping each other.

Ambulacra with a slightly winged base as well as a moderately triangular and proximally projected head. Third and second ambulacra compressed. First ambulacra larger and longer than high.

Description. The specimen exhibits its abactinal face, with the disc and five incomplete arms ($r = 1.5$ cm and $R > 3.7$ cm). Interbranchial areas are wide and angular. Interbranchial septa are reinforced by a high density of overlapping plates (Fig. 9A).

Abactinals are small, up to 4 mm long, round, oblong or lobed. The irregularity of their surface suggests that they were surmounted by spines. They form a regular mesh (Fig. 9B–G).

Marginals are not differentiated from abactinals and actinals. The series cannot be traced from the disc to the arm tips because of the incomplete condition of the five arms.

Actinals are small, up to 3 mm long, circular and flat. Up to five rows of actinals are recognizable proximally. They are arranged in longitudinal series and overlap each other (Fig. 9B, C, F, G).

Adambulacra are small and squared (Fig. 9F, G). Ambulacra are long and thin. The base is long, broad, with straight margins and thin wings. The shaft is short and thin. The head is short, broad, triangular, projected proximally and has teeth along its entire length (Fig. 9D–G). Third and second ambulacra are compressed. First ambulacra are larger, up to 3 mm long and 2 mm high (Fig. 9A).

Remarks. The abactinals arranged in a regular mesh and the inconspicuous marginals indicate that *Menerbesaster bongrainae* gen. nov. et sp. nov. belongs to the Echinasteridae (Hayashi 1940; Clark and Downey 1992; Mah and Blake 2012). *Menerbesaster bongrainae* gen. nov. et sp. nov. differs from *Echinaster*, *Henricia* Gray, 1840, *Aleutihenricia* Clark & Jewett, 2010 and *Odontohenricia* Rowe & Albertson, 1988 in the size, shape and number of its actinal series. It resembles *Rhopiella hirsuta* (Koehler, 1920) in that both possess large actinal interradial fields and robust interbranchial septa on the disc (Fisher 1940; Clark and McGown 1962). However, it differs from *Rhopiella hirsuta* by its abactinal mesh with smaller and more regularly arranged abactinals.

Echinaster jacobsoni is the only species of Echinasteridae known in the fossil record. It is represented by fossils from the Eocene of Denmark (Rasmussen 1972). It differs from *Menerbesaster bongrainae* gen. nov. et sp. nov. in having ambulacra with a shorter and broader base with more developed wings, a longer and thinner shaft, a shorter and broader head with more pronounced teeth. *Henricia venturana* Durham & Roberts, 1948 from the Cretaceous of California, USA was first described as an Echinasteridae, but is now considered as an indeterminate asteroid according to Gale and Jagt (2021).

Occurrence. Late Burdigalian, Early Miocene, Ménerbes area, southeastern France.

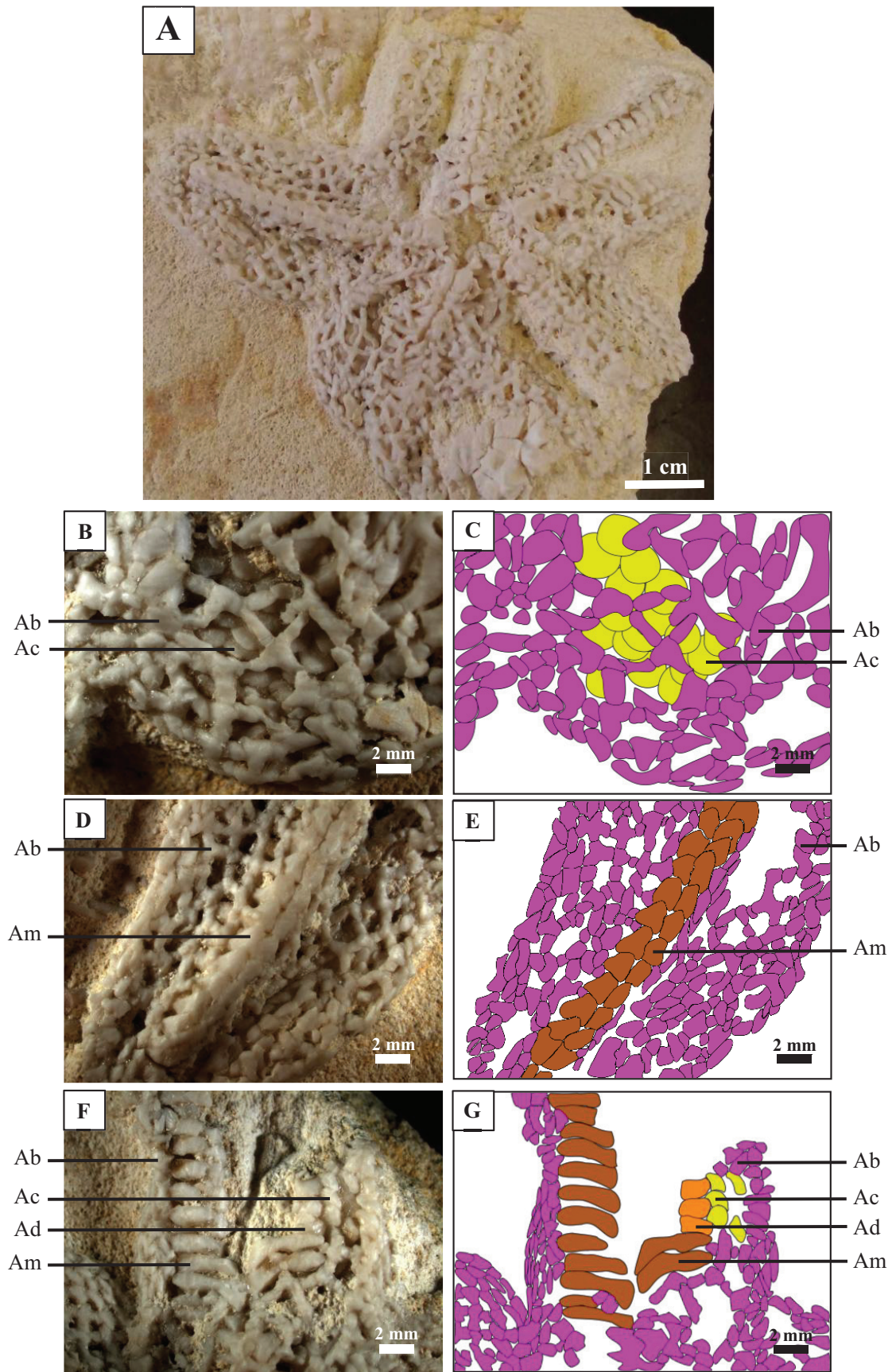


Figure 9. *Menerbesaster bongrainae* gen. nov. et sp. nov. **A.** General view of the holotype MDC.20055541 with **B.** A close-up of an interbrachial area and **C.** Its interpretative scheme; **D.** A close-up of an arm and **E.** Its interpretative scheme; **F.** A close-up of another arm and **G.** Its interpretative scheme. Ab (pink): abactinals, Ac (yellow): actinals, Ad (orange): adambulacrals and Am (brown): ambulacrals. **B–G:** proximal position upwards.

Additional remarks on paleoecology

According to Bongrain (2013), the Calcaire de Ménerbes fauna is composed of megathermal invertebrates, i.e. large and/or currently living in shallow water tropical zones, which is consistent with the thermal maximum reached during the Burdigalian-Langhian transition. Regular sea urchins inhabit the infralittoral zone; bivalves, the circalittoral zone and irregular sea urchins, both the infra- and circalittoral zones (Bongrain 2013). Extant species of the genus *Tripneustes* for example, are widespread and found in exclusively circumtropical very shallow environments (<75 m depth; Lawrence and Agatsuma 2007). Irregular sea urchins are endobenthic, living in soft sediments; while bivalves and regular sea urchins are epibenthic, dwelling on a variety of substrates (Bongrain 2013).

Extant oreasterids mostly inhabit warm and very shallow environments (i.e. 0 to 100 m deep), with only a few species occurring in mesophotic environment (Mah and Blake 2012; Mah 2023). The deepest recorded occurrence for this family is 275 meters (Mah 2023). In boreal regions, extant solasterids are mostly found at shallow (from 0 to 200 m) to upper bathyal (up to 1000 m) depths (Fisher 1911; Clark and Downey 1992). In tropical areas, solasterids occur primarily in deeper environments (>200 m; Mah and Fujita 2020). Extant astropectinids are predominantly distributed in cold waters, though they also occur in temperate and tropical regions (Mah and Blake 2012). Extant echinasterids occur in a wider range of habitats, in cold, temperate, and tropical environments (Mah and Blake 2012). Extant astropectinids are endobenthic and found in soft bottoms, while other families (Echinasteridae, Oreasteridae and Solasteridae) are epibenthic and found on various substrates (Blake 1990; Clark and Downey 1992; Mah and Blake 2012). The co-occurrence of these four families from the Burdigalian of the Apt basin is remarkable, as these families occupy ecologically distinct habitats and rarely overlap in their distribution. Comparable assemblages can be found today in the Caribbean Sea (Downey 1978; Alvarado 2011), although the only oreasterid species *Oreaster reticulatus* only occurs in shallow water (from 0 to 69 m; Clark and Downey 1992) and the solasterids occur in slightly deeper environments (e.g. *Solaster carribaeus* Verrill, 1915 occurs at depths ranging from 64 to 649 m deep; Downey 1978, Clark and Downey 1992). While Astropectinids and echinasterids are recorded from the Mediterranean Sea, oreasterids and solasterids are not present anymore (Koukouras et al. 2007; Mecho et al. 2014), highlighting the uniqueness of the described fauna.

Extant oreasterids and echinasterids are mainly deposit feeders and predators of small prey, whereas extant solasterids and astropectinids are mainly predators of large prey (Blake 1990; Clark and Downey 1992; Mah and Blake 2012). *Cruciformaster pedicellarius* gen. nov. et sp. nov. may have predated *Tripneustes planus* as *Oreaster reticulatus* does on *Tripneustes ventricosus* (Lamarck, 1816) today (Scheibling

2012). *Astropecten* sp. may have fed on juveniles of *Gigantopecten restitutus* given that in *Astropecten*, bivalves constitute one of the two main sources of food today (Baeta and Ramon 2013).

The assemblage of organisms that do not live in the same environments and at such high densities indicates that they were transported and concentrated. The exceptional preservation of the organisms - bivalves with their two valves still connected, sea urchins with their Aristotle's lantern and spines, comatuloids, asteroids and ophiuroids with their skeletal parts in articulation - indicates that they were transported during their lifetime or shortly after their death and buried rapidly (Bongrain 2013). The rapid burial is also supported by the position of the asteroids which have been preserved extended and parallel to the slabs. Since asteroids are capable of escaping thin layers of sediments, they tend to be folded on themselves when the burial is slow, which is not the case here.

Conclusions

Here we describe in detail the asteroid fauna from the Calcaire de Ménerbes Formation for the first time, including two new genera and species: *Cruciformaster pedicellarius* gen. nov. et sp. nov., *Menerbesaster bongrainae* gen. nov. et sp. nov., *Lacosteaster lauerorum* Gale & Ward, 2024 and *Astropecten* sp. Each taxon represents a different family, highlighting an exceptional diversity: Astropectinidae, Echinasteridae, Oreasteridae, and Solasteridae. *Cruciformaster pedicellarius* gen. nov. et sp. nov. is the first fossil species belonging to the Oreasteridae, while *Menerbesaster bongrainae* gen. nov. et sp. nov. and *Lacosteaster lauerorum* Gale & Ward, 2024 are the second fossil species belonging to the Echinasteridae and Solasteridae, respectively. Finally, similar assemblages have been discovered in the Jurassic and Cretaceous of western Europe, but the new assemblage described here is the first in the Miocene.

Acknowledgements

We thank Didier Berthet (Musée des Confluences in Lyon), François Vigouroux (Musée des Confluences in Lyon) and Claudie Durand (Muséum d'Histoire Naturelle in Grenoble) for giving us access to the collections. We are grateful to Nicolas Tourment for transferring the specimens from his collection to the MHNG to allow for formal description of the new species *Cruciformaster pedicellarius*. We thank Jérôme Nibbio (Serre Frères & Cie), Paul Mariotta (Carrières de Provence) and the Espace La Costa team for giving us access to the quarries. We thank Philippe Sorrel (Université de Claude Bernard Lyon 1) for stimulating discussion in the field. We thank Christopher Meyer and Christopher Mah for their help providing access to the USNM collections, and to Scott Whittaker from the Scientific Imaging Lab (National Museum of Natural History, Smithsonian Institution) for his assistance with SEM imaging. MF thanks Gene Hunt of

the Paleobiology Department, National Museum of Natural History, for serving as her fellowship sponsor. We thank Loïc Villier and an anonymous reviewer for their comments that helped improve the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

An AI language model (ChatGPT) was used to assist with English-language editing of parts of the manuscript.

Funding

AT was supported by the Laboratoire de Géologie de Lyon - Terre, Planètes, Environnement (LGL-TPE), through a funding by the Centre

National de Recherche Scientifique Auvergne-Rhône-Alpes (CNRS). MF received financial support from the Swiss National Science Foundation (grant No P500PN_206858).

Author contributions

AT and MF identified, described and illustrated the taxa. MR, PC and BL conceived and designed the project. PC organized a three-day field trip during which AT, MR and BL visited the quarries and private collections. PC and MF facilitated the acquisition of the MHNG specimens. All authors contributed to, or reviewed, drafts of the manuscript and approved the final version.

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Data availability

The specimens studied are housed in the Musée des Confluences (MDC), Lyon, France; in the Muséum d'Histoire Naturelle de Grenoble (MHNGr), Grenoble, France and in the Muséum d'Histoire Naturelle de Genève (MHNG), Geneva, Switzerland.

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