

Revision of the genus *Mariania* (Echinoidea) with the description of two new species from the Miocene of Italy

PAOLO STARA, ENRICO BORGHİ & ANDREAS KROH



New material from the Miocene of Italy allows revision of the spatangoid genus *Mariania* Airaghi, 1901 and proposal of an emended diagnosis. Particularly characteristic, previously overlooked features of the genus include the presence of well-developed phyllodes made up from short, almost equidimensional plates in oral ambulacra II, III and IV. Unlike in other Spatangoidea, where the adoral plates rapidly become elongated towards the margin, they stay short in *Mariania* and are not constricted halfway between the peristome and the margin. In addition, most species of *Mariania* possess a characteristic domal profile with steep sides and lack a raised keel in aboral interambulacrum 5. Their petals are wide, open distally and extend almost to the margin. The plastron is not indented behind the episternal plates and the labral plate extends to the second ambulacral plates. Fascioles are missing in all specimens examined. The combination of these morphological features enable the separation of *Mariania* from the genera *Macropneustes*, *Hypsopatagus* and *Spatangus*, to which members of the genus have been assigned by previous authors. Cladistic analysis carried out to unravel the uncertain systematic position of *Mariania* failed to find well-supported relationships, but firmly places *Mariania* within the Brissidina. Most previous family attributions could be, however, ruled out. Based on the available data a placement within Spatangoidea seems most likely, where it takes up an intermediate position between maretids, loveniids and spatangids. Three different species are identified within the studied sample: *Mariania marmorae*, the type species of the genus; *M. stefaninii* sp. nov. from the late Burdigalian–early Langhian of northern Italy; *M. comaschicariae* sp. nov. from the Burdigalian of Sardinia. These new species are distinguished from *M. marmorae* by their lower tests, shorter labral plates and shorter petals. *Mariania comaschicariae* sp. nov. differs from *M. stefaninii* sp. nov. by its lower test, more anterior apical disc and less numerous plates in the oral anterior paired ambulacra. Test morphology and parent rock sedimentology suggest that *Mariania* was an epifaunal echinoid, which lived in inner shelf environments, characterized by soft bottoms and a tropical climate. • Key words: Echinodermata, Spatangoidea, new species, phylogeny, Neogene, Mediterranean.

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Mariania Airaghi, 1901, is a rare echinoid, known only from the early and middle Miocene of the Mediterranean area (Fig. 1), which has no living representatives. The type species, *Macropneustes marmorae* Desor in Agassiz & Desor, 1847, originally recorded from the Burdigalian of Corsica, was transferred to the newly established genus *Mariania* by Airaghi in 1901. Other occurrences of *M. marmorae* were subsequently reported from the Miocene of northern Italy (Botto Micca 1896; Airaghi 1901; Manzoni 1881; Stefanini 1908, 1919), Sardinia (Cotteau

1897; Lambert 1909; Comaschi Caria 1963, 1972), and the Rhône Basin, in southeastern France (Lambert 1915, Philippe 1998).

The validity of the characters used by Airaghi when first proposing the genus was questioned soon after publication (Checchia Rispoli 1902; Lambert 1909, 1915). Notwithstanding more than a century of interest in this genus, its systematic position is still unclear and the separation from apparently closely related taxa such as *Spatangus* Gray, 1825, is still uncertain due to the lack of clear,

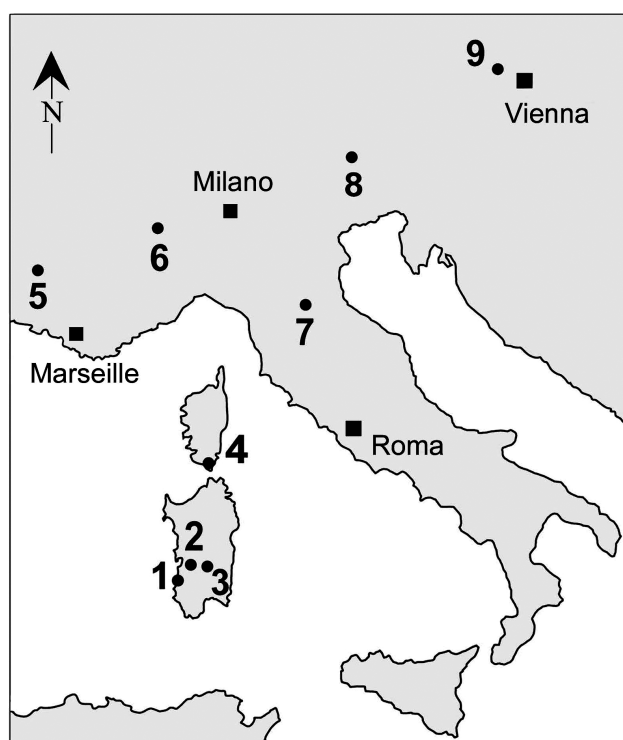


Figure 1. Location map of the records of *Mariania* from Europe. 1 – Funtanazza, near Guspini (Sardinia); 2 – Cameseda, near Ales (Sardinia); 3 – Baraci, near Isili (Sardinia); 4 – Bonifacio (Corsica); 5 – Montpezat near Gard, La Combe near Mus, Rhône Basin (France); 6 – Colli di Torino (Piedmont); 7 – Serra dei Guidoni, near Bologna (Emilia-Romagna); 8 – Forcella, Meduno, Mieli and Preplans (Friuli); 9 – Grübern, near Maissau (Austria).

distinctive characters. New material from five early and middle Miocene localities in northern Italy and Sardinia, as well as additional material housed in public institutions offers new data and made possible a full re-description including an assessment of the oral plating of the genus. Three different species could be distinguished among the new material, two of which are new.

Previous work

Macropneustes marmorae, the type species of *Mariania*, was not figured in the original description of Agassiz & Desor (1847) and the first illustration was provided by Cotteau (1877). Later it was transferred to *Hypsopatagus* by Botto Micca (1896), subsequently to *Spatangus* by Cotteau (1897) and finally was made the type of a new genus (*Mariania*) by Airaghi (1901). The diagnostic characters of the new genus were objects of discussion just after the publication of the Airaghi's work. In particular, Lambert (1909) affirmed that the distinctive characters stated by Airaghi, such as the petals, depressed and open distally, and the primary tubercles, disposed in the shape of a "V" on each

plate, were not always present in the specimens attributed to this genus, for example in the fossil material from Sardinia (Lambert 1909) and the Rhône Basin (Lambert 1915). Likewise, the presence or absence of fascioles was debated; Airaghi (1901) reported "fascioles non visible" and "fascioles absent" in different parts of his diagnosis. Cotteau (1877) affirmed that the fascioles were not present in well preserved specimens from Corsica. Stefanini (1908) thought to find traces of a subanal fasciole but, after Lambert's statement (1909) to the contrary, admitted that those traces were due to imperfect preservation of his specimens. Later on, Cottreau (1914) stated that he found a distinct subanal fasciole in a specimen of *M. marmorae*, but Lambert (1915) maintained that Cottreau's observation was based on a misidentified specimen, which in reality belonged to *Spatangus pustulosus* Wright, 1864. *Mariania* has been sometimes confused with that species, to which it shows considerable similarities and with which it co-occurs at some localities (Cottreau 1914, Philippe 1998). Indeed, Philippe (1998) treated *Mariania* as a subgenus of *Spatangus*, suggesting a progressive transformation of *S. pustulosus* into *Mariania*, with the occurrence of intermediate forms at the same site.

Not only the status of *Mariania* has been questioned, but also its systematic position has been much debated. Lambert (1909) associated it with the Asterostomatidae and, later (Lambert & Thiéry 1924), with the Megapneustinae. Mortensen (1950) affirmed that the structure of the apical system and the arrangement of the primary tubercles in *Mariania* rather indicated its affinity with the Palaeopneustinae, in particular with the genus *Megapneustes*. More recently, *Mariania* was attributed to the Brissidae by Fischer (1966) and to the Spatangidae by Philippe (1998). Currently it is tentatively included in the family Maretidae by Smith & Kroh (2011) and Kroh (2014).

In addition to *M. marmorae*, three other taxa have been assigned to this genus in earlier works. *Spatangus euglyphus* Laube, 1868, from the Miocene of Veneto (northern Italy), was transferred to *Mariania* by Stefanini (1919). A variety of this species, *Mariania euglypha brevistella*, was described by Venzo (1935) from the same area. *Spatangus deyidieri* Cotteau, 1897, from the Burdigalian of the Rhône Basin (France) and Austria has been assigned to *Mariania* by Lambert (1915) and Kroh (2005), respectively.

Material and methods

Phylogenetic analysis

To elucidate the systematic position of *Mariania*, phylogenetic analyses using the matrices of Stockley *et al.* (2005)

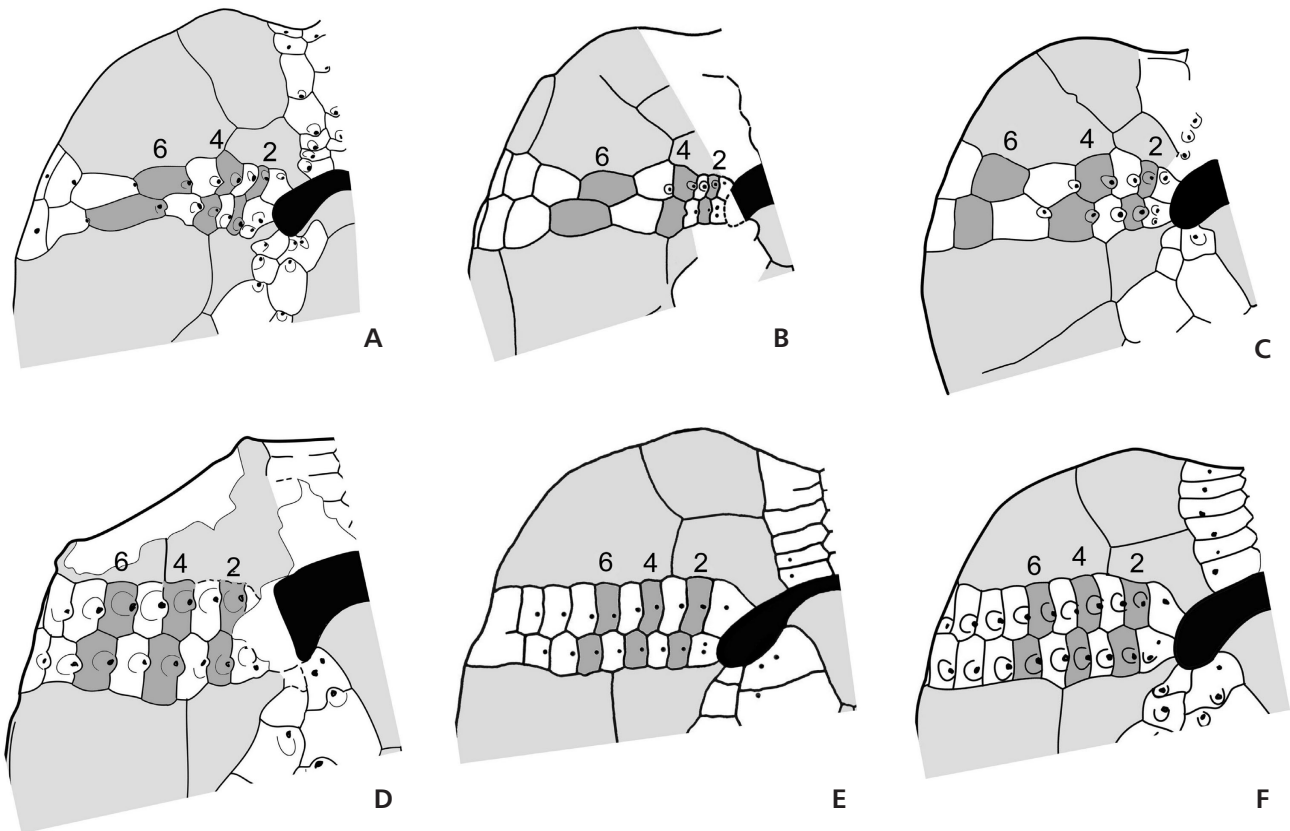


Figure 2. Comparative schemes of the anterior ambulacra with plates 2, 4 and 6 highlighted (dark grey). • A – *Spatangus purpureus* Müller, 1776 (partially modified from Smith & Kroh 2011). • B – *Spatangus pustulosus* Wright, 1864, Malta (Gatt Collection, E1087). • C – *Spatangus thieri*, Funtanazza (Comaschi Caria collection, MDLCA 7054/00191278 1). • D – *Mariania marmorae*, Funtanazza (MAC PL1524). • E – *Mariania stefaninii* sp. nov., Serra dei Guidoni (IGF 101716). • F – *Mariania comaschicariae* sp. nov., Baraci (MDLCA 23534). Interambulacra shaded (light grey). Schemes not in scale, they are all reported with the same ambulacrum length.

and Kroh & Smith (2010) have been carried out. From the latter only members of the Spatangoida clade, plus two holasteroids as outgroup taxa, were used; on account of its ethmolythic apical disc and amphisternous plastron, *Mariania* clearly is a member of the Spatangoida. In addition to the four species of *Mariania* recognized herein, the two sole species of *Plethotaenia*, another related form, were added to the Kroh & Smith matrix. Of the original 306 characters, only 88 were phylogenetically informative for the taxon set analysed herein and the analysis was thus restricted to these characters in order to save computation time (Appendix 1). Like in the original analysis, characters with clear ontogenetic progression were treated as ordered (A4, A6, B44, B45, D29). One of these (D29) has six different states in the present dataset and was thus downweighted in order not to give undue emphasis to that single character. In contrast to the former, the full matrix of Stockley *et al.* (2005) was used, the only change here being the addition of *Mariania*. As in Stockley *et al.*, three characters (6, 46, 77) were treated as ordered and another three (8–10) were given a weight of 0.33; all other characters were treated as unordered and of equal weight. In addition, for both datasets,

explorative analyses treating all characters as unordered and of equal weight were run.

Heuristic analyses were carried out in PAUP* version 4.0b10 (Swofford 2005), with 1,000 random repetition cycles and in TNT (Goloboff *et al.* 2008) using New Technology Search. Bootstrap percentages are based on 100,000 fast (simple addition without branch swapping) heuristic searches in PAUP*, respectively 1000 replicates with New Technology Search in TNT. Since TNT does not support fractional weighting, analyses employing downweighted characters in PAUP* were run with the other characters upweighted by a correction factor of three (Stockley *et al.* matrix) and six (Kroh & Smith matrix), respectively.

Material

Twenty-three new, more or less complete specimens of *Mariania* could be located for the present study, 9 of them from the early Miocene of Sardinia, 3 from the Burdigalian of Friuli and 11 from the late Burdigalian–early Langhian

Table 1. Length of the plates in the oral ambulacrum II: range and mean value. Last column: the relation between plates 6 and plates 2 is expressed as the ratio between $(a.2 + b.2)/2$ and $(a.6 + b.6)/2$. All data expressed as %AL (length of the ambulacrum measured along the suture between the two columns).

Species	pl. 2a, 2b		pl. 4a, 4b		pl. 6a, 6b		ratio pl.6/pl.2
	range	mean	range	mean	range	mean	
<i>Spatangus purpureus</i>	0.56–0.67	0.61	0.74–0.81	0.77	2.26–3.21	2.73	4.47
<i>Spatangus pustulosus</i>	0.46	–	0.81–0.88	0.84	2.43	–	5.28
<i>Spatangus thieryi</i>	0.53–0.74	0.63	1.09	–	2.19–2.4	2.29	3.63
<i>Mariania marmorae</i>	0.99	–	1.23	–	1.23–1.38	1.30	1.31
<i>Mariania deyderi</i>	0.95–0.99	0.97	1.36–1.46	1.41	2.10	–	2.16
<i>Mariania stefaninii</i>	0.71–0.75	0.73	0.89	–	0.89	–	1.22
<i>Mariania comaschicariae</i>	1.03–1.18	1.10	0.99	–	1.08	–	0.98

Table 2. Biometric data of the different species of *Mariania* (including data from Philippe 1998 and Kroh 2005 for *M. deyderi*). %TL = percentage of test length.

	<i>Mariania marmorae</i> Desor, 1847 (n = 4)		<i>M. deyderi</i> Cotteau, 1897 (n = 8)		<i>M. stefaninii</i> sp. nov. (n = 4)		<i>M. comaschicariae</i> sp. nov. (n = 8)	
	range (mm)	mean (%TL)	range (mm)	mean (%TL)	range (mm)	mean (%TL)	range (mm)	mean (%TL)
TL	37–54		35.3–74		48–56		45–59	
TW		110		96		97		101
TH		59		35		48		37
L1		4.5		–		7		5
L2		20		24		25		20
L3		20		14		13		14
L4		43		35		45		44
L5		24		19		25		24
L6		24		23.5		23		29
L7		58		47		50		53
L8		41.5		42		49		41
L9		65		–		48		49
L10		20		–		14		16
L11		63		–		46		51
L12		21.5		–		15		16
L13		25		11		21		18

of Emilia, northern Italy. Only a single specimen (from Emilia) still bears part of its spine cover. Seven of the Sardinian specimens were collected by one of the authors (PS); two of these are deposited at the Museo di Geologia e Paleontologia Domenico Lovisato, University of Cagliari, and the remaining five are deposited at the Museo di Storia Naturale “Aquilegia” of Masullas. The other two, belonging to *Mariania marmorae*, are kept in the Museo di Geologia e Paleontologia Domenico Lovisato, Dipartimento di Geologia; one of them was figured by Comaschi Caria (1972, pl. 47, fig. 1.3). The fossil material from Emilia and Friuli belongs to the Manzoni and Stefanini collections, housed at the Museo di Storia Naturale, Sezione di Geologia e Paleontologia, University of Firenze. The specimens of *Mariania* described by Airaghi (1901), at that time hosted at the Museo Regionale di Scienze Naturali of Torino, were lost in 1943 (personal communication, D. Ormez-

zano, January 2015). The oral plating of *M. marmorae* was prepared by Andrew B. Smith and completed by one of us (PS), and is based on a specimen in the palaeontological collections of the University of Lyon, France (specimen EM 12134, see Smith & Kroh 2011). Data on *Spatangus euglyphus* is based on five complete specimens from the early Miocene of Veneto (Vicenza Province, northern Italy): a possible syntype from Santa Libera di Malo in the collection of the Natural History Museum in Vienna (specimen NHMW 2015/0122/0001), two from Altavilla (Museo Civico Dal Lago of Valdagno) and two from Schio (IGF collection). A complete test of *Spatangus pustulosus* from Malta (Gatt Collection, E1087) and 13 specimens of *Spatangus thieryi* (Lambert, 1909) (MDLCA 7054/00191278 1–5, 10022/00190591 1–2, 10141/00192985 1–3, MAC PL1601–3) were utilized for comparison.

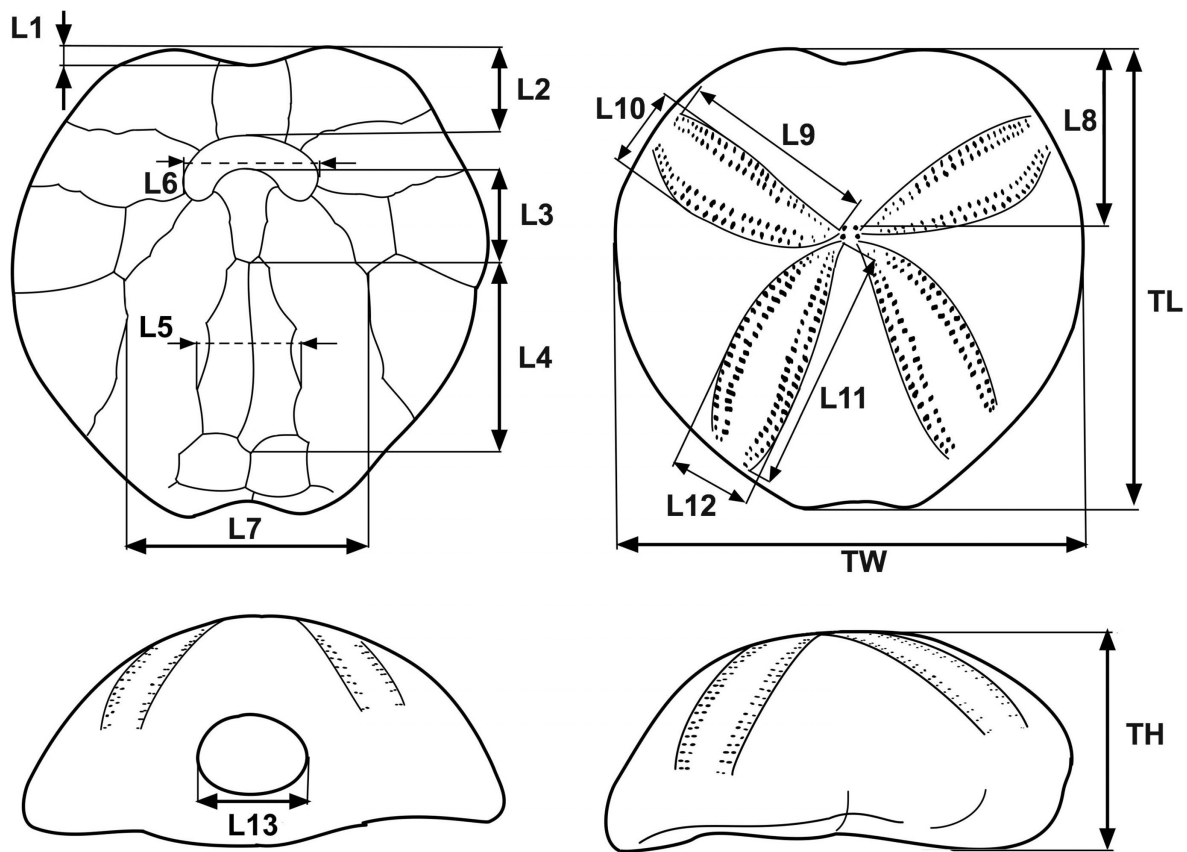


Figure 3. *Mariania* Airaghi, 1901, morphometric measures taken in the examined specimens. Measures of L9 and L11 were taken along the test surface.

A new measure – PLR or plates length ratio – is here introduced to define the dimensional variation of the plates forming the columns of the oral ambulacra II and IV, from the peristome towards the test margin. The most significant feature to compare species of *Mariania* and *Spatangus* was found to be the ratio between the length of the plates 2 and 6 in each column (Fig. 2, Table 1). PLR is expressed as the ratio between $(a.2 + b.2)/2$ and $(a.6 + b.6)/2$.

The results of a univariate biometric analysis, based on the measures taken from 14 specimens (Fig. 3), are reported in Table 2. The measures of the test length are in mm and the other dimensional parameters are expressed as a percentage of test length.

Numbering in plate drawings follows Lovén's (1874) system and interambulacra are shaded in grey. Systematic palaeontology follows Kroh & Smith (2010) and geographic coordinates are provided in WGS84.

Abbreviations. – AL – length of oral ambulacrum II; CI – consistency index; L1 – depth of the frontal sinus; L2 – distance from the anterior border of peristome to the anterior test margin; L3 – length of the labral plate; L4 – length of the sternum; L5 – width of the sternum; L6 – width of the peristome; L7 – width of the plastron plus the peri-plastral area made of the two posterior ambulacra; L8 – distance

from the apical disc to the anterior test margin; L9 – length of the anterior petals; L10 – width of the anterior petals; L11 – length of the posterior petals; L12 – width of the posterior petals; L13 – width of the periproct; MPTs – most parsimonious trees; RCI – rescaled consistency index; RI – retention index; TH – test height; TL – test length; TW – test width.

Institutional abbreviations. – IGF – Museo di Storia Naturale, Sezione di Geologia e Paleontologia, University of Firenze, Italy; MAC – Museo di Storia Naturale “Aquilegia” of Masullas, Italy; MDL – Museo Civico Dal Lago of Valdarno, Italy; NHMW – Natural History Museum Vienna, Department of Geology & Palaeontology, Austria; MDLCA – Museo di Geologia e Paleontologia Domenico Lovisato, Cagliari University, Italy.

Geological setting

Three localities bearing *Mariania* have been examined in Sardinia; Calada Bianca near Funtanazza (Arbus, Cagliari Province), Baraci near Isili (Cagliari Province) and Came-seda near Ales (Oristano Province). The beds harbouring the echinoids at Baraci belong to the Nurallao Formation,

informally defined in Barca *et al.* (2005), which consists of two members: the Duidduru member, comprising coarse-grained clastics from transitional (deltaic) environments, and the overlying marine deposits of the Arenarie di Serralunga (proposed by Sowerbutts & Underhill 1998).

The sequence cropping out at Funtanazza (39° 36' 27.57" N, 8° 27' 58.91" E) represents the distal-most marine facies of the Fossa di Funtanazza Basin (Cherchi 1974, Assorgia *et al.* 1997). The section exposed just in front of the sea-side is *ca* 25 m thick and consists of yellowish-grey, fine-grained biocalcarenites, intercalated with biohermal limestones and volcanoclastic tuffites, which were deposited in a circalittoral setting (according to Assorgia *et al.* 1997, Annino *et al.* 2000), during the late Aquitanian. The assemblage is dominated by the bivalve *Aequipecten northamptoni* (Michelotti, 1839), and subordinate spatangoids and bryozoans. Deeper water deposits are indicated by the occurrence of abundant scaphopods (*Dentalium* sp.) and solitary corals. *Mariania marmorae* is present at the base of the exposed section, just 0 to 2 m above the sea level, associated with *Spatangus thieri*, schizasterids and other spatangoids. Although the echinoids are usually well preserved, they are deprived of spines and most of them are damaged or incomplete, and randomly oriented, suggesting a moderate transport; according to our observations, we interpret this facies to originate from a sublittoral setting.

At Baraci (39° 45' 01.66" N, 9° 10' 05.66" E) a 30 m thick sequence belonging to the Nurallao Formation crops out along the lower part of the hill (480–510 m a.s.l.) located 5 km E-SE of the village (Stara *et al.* 2012). It consists of biogenic calcarenites and sandstones interbedded with marlstones belonging to the Arenarie di Serralunga. A grey marly arenite, apparently poor in macrofossils, is well visible just at the base of the hill, extending laterally for *ca* 300 m. Immediately below this layer there is a fossiliferous bed (504 m a.s.l.), rich in echinoids, consisting of a grey, fine-grained, calcareous arenite. The holotype of *Mariania comaschicariae* sp. nov. was collected from this bed, which belongs to the upper part of the Arenarie di Serralunga, dated to the late Aquitanian-early Burdigalian. The rich echinoid assemblage includes spatangoids, schizasterids and echinolampadids, mainly represented by the genera *Spatangus*, *Aliaster*, *Ova*, *Pericosmus*, *Hypsoclypus* and *Faorina* (see Stara *et al.* 2012, Stara & Borghi 2012).

Mariania comaschicariae sp. nov. is present also in the Aquitanian (Casula *et al.* 2001, Cherchi *et al.* 2008) marly sedimentary rocks of Cameseda (39° 46' 35.34" N, 8° 48' 05.73" E), near Ales. It co-occurs with a rich echinoid assemblage mainly consisting of *Spatangus thieri*, *S. sardicus* Lambert, 1909 and other spatangoids (Lambert 1909, Comaschi Caria 1972). Additionally, specimens belonging to *Faorina*, *Pericosmus*, *Schizaster*, and

Aliaster have also been collected (by PS). Fossils are commonly abraded and fragmented, likely indicating transport.

The specimens from Serra dei Guidoni (Province of Bologna, northern Italy, 44° 14' 20.71" N, 10° 58' 19.01" E) were collected from the Pantano Formation, which belongs to the Bismantova Group (Amorosi *et al.* 1993). In the study area the Pantano Formation was deposited during the late Burdigalian–early Langhian. It consists of the Sasoguidano Member and the overlying Montecuccolo Member (Fregni & Panini 1995). Although the exact locality that yielded *Mariania* was not reported by Manzoni (1881) and Stefanini (1908), a number of echinoids, including *Echinolampas* and a few incomplete specimens of *Mariania*, were collected (by EB) from coarse-grained biocalcarenites located just at the base of the Montecuccolo Member. Amorosi (1991) interpreted the lower part of the Montecuccolo Member as a subtidal setting, with sedimentation ruled by migration of megaripples and sandwaves. The echinoids usually lack spines and are randomly oriented, thus suggesting transport, though reduced energy conditions allowed these thin-shelled spatangoids to be uncommonly preserved as complete tests.

The specimens of *Mariania* reported by Stefanini (1919) from Friuli (northern Italy) were collected from the Burdigalian Marna di Bolago unit, informally defined in Massari *et al.* (1986). This unit overlays the Aquitanian Arenarie di Preplans and marks the beginning of a transgressive phase which ends at the top of the overlying late Burdigalian Arenarie di San Gregorio unit (Massari *et al.* 1986). The total thickness of the Marna di Bolago unit is 60 m. At the base there is a transgressive glauco-arenitic deposit (some 5 m thick) with abundant bivalves and fish teeth, overlaid by calcareous marlstones. The palaeo-environment is interpreted as an outer shelf deposit grading into more proximal conditions indicating a pro-delta towards the top (Zanferrari *et al.* 2008). The Marna di Bolago corresponds to the levels 31–36 of the “Molasse a *Pecten*” described by Stefanini (1917), thus including the levels bearing *Mariania* (beds 34–35, “Strato a echinidi e relativa arenaria glauconiosa”; Stefanini 1919, p. 143). Indeed, rare specimens of *Mariania* were reported by Zenari (1929) from the marly sedimentary rocks of this unit, associated with pectinids.

Spatangus euglyphus is present in the Arenarie di Sant’Urbano unit, cropping out in Veneto (northern Italy), above all in the province of Vicenza. The late Oligocene basal part of the unit is overlaid by Aquitanian coralline limestones and then by well-cemented arenites with a shallow water fauna mainly consisting of pectinids and astriclypeid echinoids (De Angeli & Beschin 2012). The Arenarie di Sant’Urbano yielded specimens of *S. euglyphus* at Valmarana, Monteviale and Santa Libera di Malo, indicated as type localities by Laube (1868), and from Altavilla, Creazzo and Schio (Stefanini 1919).

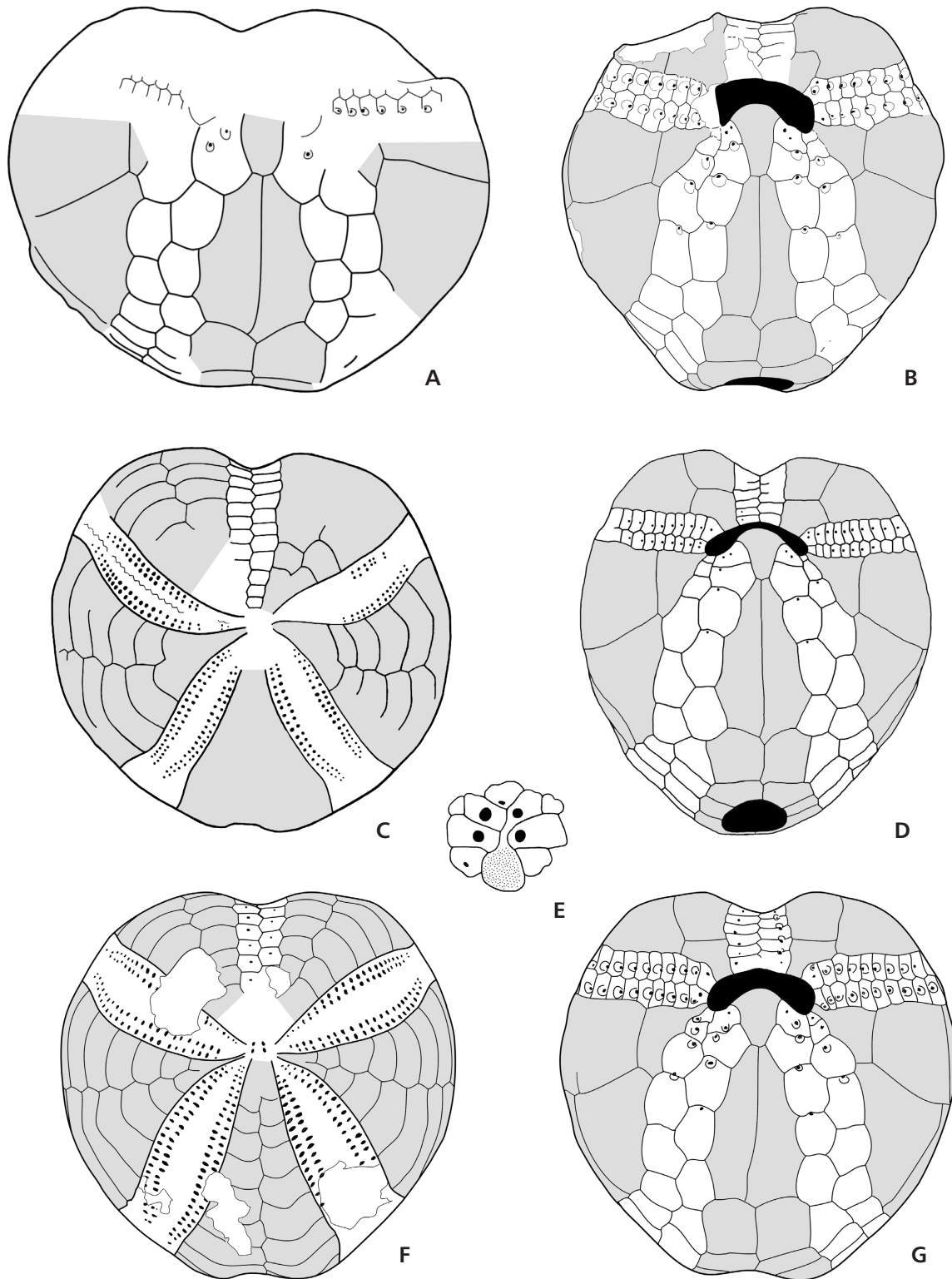


Figure 4. *Mariania* Airaghi, 1901, schemes of the plating structure. Interambulacra shaded. Schemes not to scale; they are all reported with the same test length. • A, B – *Mariania marmorae* (Desor in Agassiz & Desor, 1847), A – oral view of a specimen (EM 12134, from Corsica), highlighting the suture line of the demi-ambulacrum II, with short and almost equally-sized plates (partially modified from Smith & Kroh 2011); B – oral plating scheme of the specimen MAC PL1524, Funtanazza (Sardinia). • C, D – *Mariania stefaninii* sp. nov., Serra dei Guidoni (northern Italy); C – aboral plating of the holotype (IGF 101719); D – oral plating of IGF 101716. • E–G – *Mariania comaschicariae* sp. nov., Baraci (Sardinia); E – apical system of MAC PLSN; F – aboral plating in the holotype (MDLCA 23533); G – oral plating of MDLCA 23534.

Results

Morphology of *Mariania*

The uncertainty about the diagnostic characters of *Mariania* largely was a result of the poor preservation of the specimen described by Cotteau (1877), who provided the first illustration of *M. marmorae*. Cotteau's specimen is antero-posteriorly compressed and lacks a large part of the oral face. As a consequence, the sole published oral plating (Smith *in* Smith & Kroh 2011) is incomplete. Despite the poor preservation in the anterior part and loss of plates, the perradial sutures in ambulacra II and IV indicate the occurrence of a series of rather numerous (at least 7–8) short ambulacral plates (Fig. 4A), which do not almost increase in length towards the test margin. This observation is corroborated by more complete specimens entirely consistent with the specimens figured by Cotteau (1877) that were newly collected from the lower Miocene succession of Funtanazza. The complete oral plate drawing derived from one of these specimens (Fig. 4B) confirms the occurrence of a series made of short, almost equidimensional plates. The phyllodes extend almost to the ambitus and consist of well-developed unipores with a large periporal area. Five to six similar shaped plates, bearing single pores, are present also in the adoral ambulacrum III. The mean value of PLR is close to 1 (Table 1).

The studied specimens showing these characters share further morphological features: a characteristic turtle-shaped test profile; absence of a strongly raised keel in aboral interambulacrum 5; low and almost vertical posterior face, steep sides (Figs 7C, I, 9F, I); rather sharp margin; a weak frontal sinus deepening only near the anterior test margin (Fig. 7A, G). The oral face is flat or sunken (Figs 7G, 9C, D, I), with a sunken groove connecting the peristome to the anterior margin. The oral paired ambulacra are almost flush or slightly sunken; often the depression extends to the test margin. The apical disc is ethmolytic, with four gonopores (Fig. 4E); the anterior pores are closer together than the posterior ones. Genital plate 2 is slightly extended to the rear of the posterior ocular plates. The petals are long and broad, more or less open distally, and flush (Fig. 10A) or slightly depressed (Fig. 9H). The interporiferous zones are broad, their width being 2 to 3 times that of a single poriferous zone. The petals II and IV diverge strongly (120° – 130°), slightly bending anteriorly and extending almost to the margin. Pores within the petals are weakly conjugate. Interambulacra 1 and 4 are amphiplacous. The labral plate extends to mid-way down the second adjacent ambulacral plate 2. A dense, heterogeneous tuberculation, made of perforate and crenulate primary tubercles, is scattered across the whole aboral surface (Fig. 7A, C). The periproct is wide and transverse, located in the upper part of the low posterior

face, and bordered by the plates 5.a.4 to 5.a.8 and 5.b.4 to 5.b.8 (Fig. 5A–C). Enlarged subanal pore-pairs are not present.

Not a single trace of fasciole bands could be found in any of the well-preserved specimens examined. Although Comaschi Caria (1972) claimed to have found a subanal fasciole in a specimen from Funtanazza (Sardinia, pl. 47, fig. 2), we were unable to verify this observation. Comaschi Caria's specimen, still preserved in the MDLCA collection (10082–00191886, Fig. 7A), turned out to be strongly damaged posteriorly, precluding detection of a subanal fasciole. The absence of a subanal fasciole in *Mariania* is further corroborated by the shape of the episternal plates, which are not indented to the rear by the adjacent ambulacral plates, and by the pattern of the tuberculation, in comparison with other spatangoids of similar size which feature subanal fascioles.

Specimens from the Miocene of Sardinia and Emilia, although sharing the main distinctive characters of *Mariania*, differ from the type species in having lower tests, shorter labral plates, and shorter and narrower petals. Additionally, they have a higher number of plates in the oral ambulacra II–IV. Among these there are further differences between the specimens coming from Sardinia and those from Emilia, indicating the presence of two new, yet undescribed species of *Mariania*.

Systematic placement of *Mariania*

The type species of the genus *Mariania*, *M. marmorae*, has been attributed to three other genera in earlier studies: *Macropneustes* (Desor *in* Agassiz & Desor 1847), *Hypsopatagus* (Botto Micca 1896) and *Spatangus* (Cotteau 1897). All these genera differ from *Mariania* in having well developed fascioles, shorter phyllodes and elongated plates outside the phyllodes in adoral ambulacra II and IV. *Macropneustes*, in addition, differs by its narrower interporiferous zones in the petals. *Hypsopatagus* has a longer labral plate extending to the fourth ambulacral plate and a strong constriction of interambulacrum 5 behind the episternal plates. *Megapneustes* has more open petals and aboral primary tubercles aligned in distinct rows inside the peripetalous fasciole.

Hitherto, *Spatangus* was considered as the most closely related genus (Philippe 1998), and species such as *Spatangus pustulosus* from Malta (Fig. 2B) and *S. thieryi* from Sardinia (Fig. 2C), have been repeatedly confused with *Mariania*, with which they commonly co-occur (Lambert 1909, Cottreau 1914, Comaschi Caria 1963, Philippe 1998). In *S. purpureus* Müller, 1776, the type species of *Spatangus*, the phyllodes are much less extensive and the plates in the oral ambulacra II–III–IV become distinctly longer halfway from the peristome towards the test margin

(PLR up to 6, Fig. 2A); this is true (see Table 1) also for the examined specimens attributable to *S. pustulosus* and *S. thieryi*. Furthermore, in both *S. purpureus* and *S. pustulosus* the oral ambulacra narrow midway towards the margin, which is not the case with *Mariania*. In addition, in *Spatangus* primary tubercles are restricted to a small part of the aboral surface, whereas they occur all over the aboral surface in *Mariania*. Lastly, the labral plate of *S. purpureus* is much shorter than in *Mariania*, extending only to the first ambulacral plate.

Cladistic analysis. – Heuristic analysis in PAUP* using the original character type and weighting scheme of Kroh & Smith (2010) resulted in six MPTs of 376.72 steps length (CI = 0.327, RI = 0.631). Tree topology is the same in all six trees, which differ only in branching order within the *Mariania* clade and placement of *Periaster* either as sister-taxon to Schizasteridae or to Schizasteridae + Prenasteridae. The trees diverge from the topology presented by Kroh & Smith (2010, fig. 2B) by the different branching order within crown-group spatangoids. Namely, aeropsids are not resolved as sister to micrasterids and the branching order of Spatangioidea is reversed. As in the original analysis, Bootstrap support for most of these nodes is virtually non-existent, therefore these differences are not discussed in any more detail. *Mariania* species are resolved as monophylum (with moderate Bootstrap support) within crown-group Brissidina and appear as sister-group to a clade containing Spatangidae (*Spatangus*, *Plethotaenia*), brissids and some stem-group Spatangioidea (*Megapneustes*, *Macropneustes*). Loveniidae and Maretiidae form the next relatives of the whole group; none of these nodes, however, shows significant support.

Analysis treating all characters as unordered and of equal weight similarly failed to generate a well-supported tree and resulted in 70 MPTs of 379 steps length (CI = 0.335, RI = 0.629), the strict consensus of which fails to resolve branching order within the suborder Brissidina at all. *Mariania* is again included in the latter group. A further analysis was run after reweighting characters by their RCI based on the first analysis. It resulted in three MPTs of 78.39 steps length (CI = 0.496, RI = 0.744, Fig. 6A). The topology is almost identical to the one in Kroh & Smith (Fig. 3B), with the exception that palaeopneustinids are recovered as a monophylum. *Mariania* is resolved as sister taxon to Loveniidae in this analysis, again without significant support.

Analysis in TNT recovers almost exactly the same topology, with the exception that the branching order of *Spatangus* and *Plethotaenia* has been reversed. Like in PAUP* very few clades show significant bootstrap support. Using implied weighting (K = 3.000) with equal prior weights results in two most parsimonious trees, largely identical to the previous analysis, but resolving *Mariania*

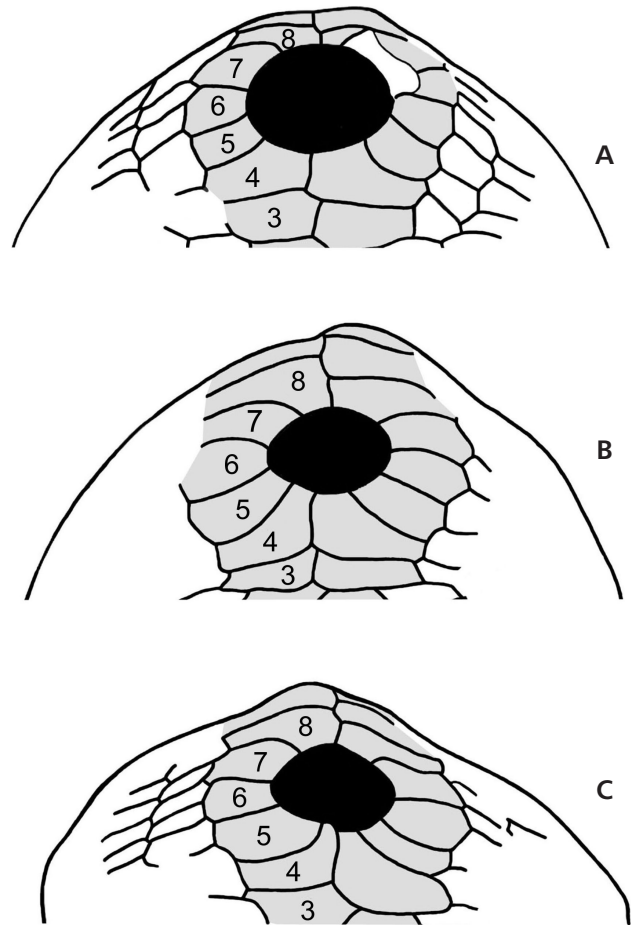


Figure 5. Schemes of the plates surrounding the periproct. • A – *Mariania marmorata* (MAC PL1524). • B – *Mariania stefaninii* (IGF 101716). • C – *Mariania comaschicariae* (MDLCA 23534). Interambulacra shaded, drawings not to scale.

as sister-group to loveniids in one tree and loveniids + eupatangids + maretiids + eurypatagids in the other.

Heuristic analysis of the much larger matrix of Stockley *et al.* (2005) in PAUP* required extremely long computing time and thus the number of repetition cycles had to be reduced to 25. Using the original character type and weighting scheme of Stockley *et al.* (2005), the analysis resulted in 328 MPTs of 529.979 steps length (CI = 0.209, RI = 0.658) with a tree topology similar to that of Stockley *et al.* (2005, fig. 2), but with some differences of exact branching order. *Mariania* is resolved as sister taxon to *Archaeopneustes* within a clade containing also *Spatagobrius* and *Scrippsechinus*, and which is the sister group to Maretiidae + Loveniidae + Spatangidae. None of the relevant nodes shows any Bootstrap support. A renewed analysis (100 repetition cycles) after reweighting the characters by their RCI found 30 MPTs (length = 65.89, CI = 0.367, RI = 0.802, Fig. 6B) and resolved *Mariania* as sister to *Archaeopneustes* as a basal clade of the Brissidina, again without bootstrap support. Replaying the analyses

under a weighting scheme where all characters were assigned equal weights fared even worse and largely fails to resolve relations within the Brissidina, though a sister-group-relationship of *Mariania* as sister to *Archaeopneustes* was found too, which in the following reweighted (by RCI) analysis again resolved as a basal clade within the Brissidina.

In TNT the matrix of Stockley *et al.* (2005) resulted in four MPTs of 531.3 steps length (using their original weighting scheme). The strict consensus has strong similarities to that found after reweighting by Stockley *et al.*, but shows considerable differences within the Brissidina. Like in PAUP* *Mariania* is rooted in a clade together with *Archaeopneustes*, *Scrippsechinus* and *Spatagobrissus* that is resolved as derived Brissidina, and sister-group to taxa traditionally placed into loveniids and maretiids. Spatangidae, in contrast to the original tree and the analysis in PAUP*, were resolved as members of an early Brissidina offshoot that also contains *Brissus*, *Brissopsis* and other *bona fide* brissids. Bootstrap support for most of these clades, including those containing *Mariania* was well below 50%.

Analysis under equal character weights resulted in the same pattern and returned seven MPTs of 567 steps length. The strict consensus of these contains a large polytomy involving most Brissidina genera. Within this polytomy only a few smaller clades were resolved, typically those that show some bootstrap support in other analyses. *Mariania* was again grouped with *Archaeopneustes*, but without bootstrap support. Re-analysis using implied weighting ($K = 3.000$) resulted in a single most parsimonious tree that corresponded well to the tree found by Stockley *et al.* (2005, fig. 2). In this tree, *Mariania* + *Archaeopneustes* are resolved as most basal offshoot of the Brissidina.

One of the major problems in reconstructing relationships within Brissidina is the common occurrence of secondary loss of fascioles in adults. A similar phenomenon is shown by pedicellariae, which show common secondary loss in echinoids (Coppard *et al.* 2012). Unfortunately, for many atelostomates, particularly the fossil ones, no information on fasciole presence in juveniles is available, wherefore this impediment cannot be easily overcome. Analyses of the Kroh & Smith (2010) matrix under exclusion of fasciole characters results in a largely unresolved tree, but always finds a clade comprising spatangids, loveniids, maretiids and *Mariania*. Strangely, an analysis of the Stockley *et al.* (2005) matrix fails to generate reproducible results in TNT and results in very different tree topologies depending on the value of the random seed.

Historical placement. – Past authors have placed *Mariania* in various families. Lambert (1909, p. 102) attributed it to the “sub”family Asterostomatidae within his “Protospatangues” [*Protospatangus* is now considered a synonym of

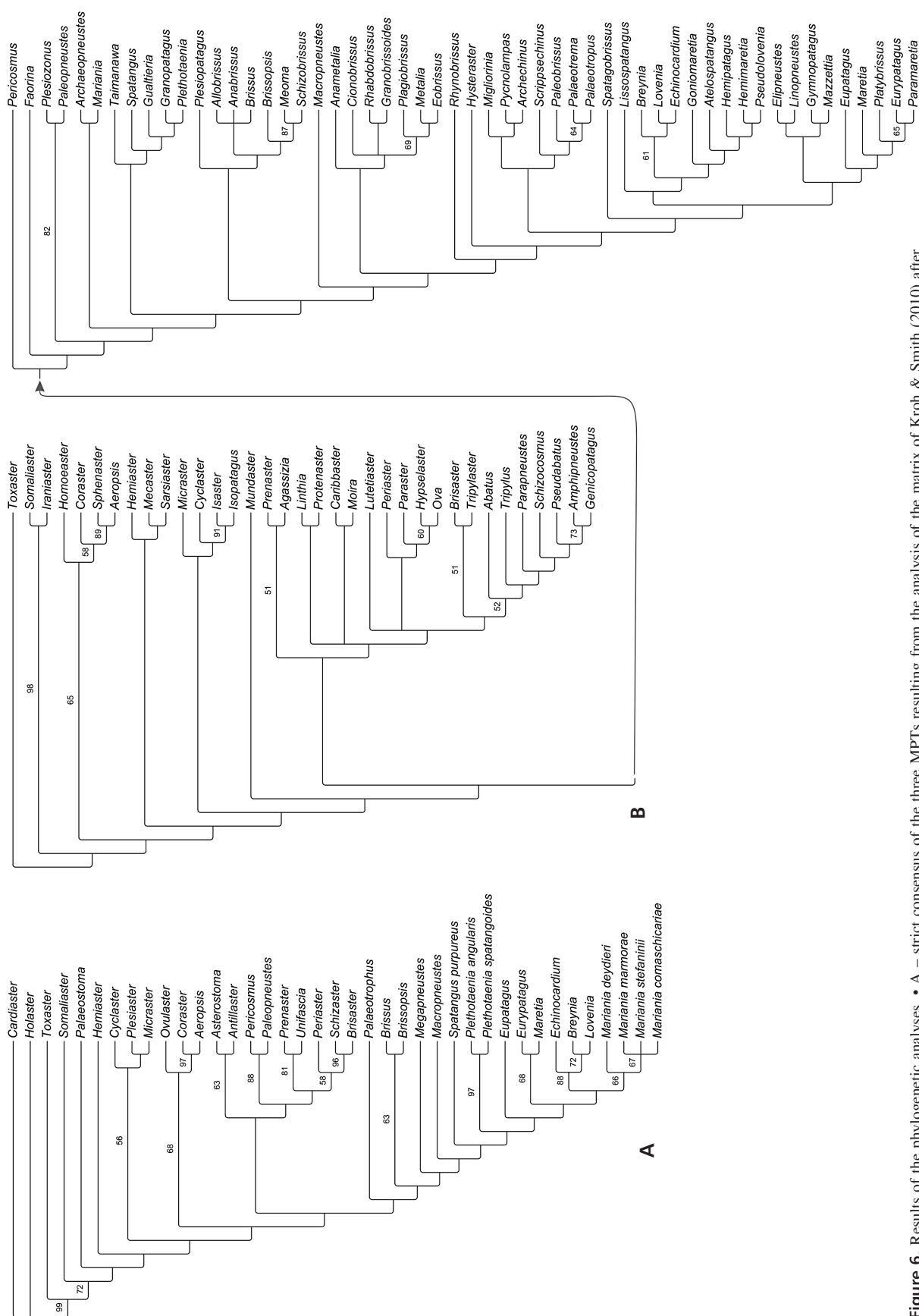
Spatangus (see Smith & Kroh 2011)]. Later, Lambert & Thiéry (1924, p. 444) transferred it to their “tribe” Megapneustinae within Asterostomatidae. Mortensen (1950, p. 284) suggested that *Mariania* should be placed “incertae sedis under the Palæopneustidae [sic]”. Fischer (1966) put *Mariania* in the Brissidae and Smith & Kroh (2011) included it in the Maretiidae.

Placement within Asterostomatidae, which has been confirmed as polyphyletic by Stockley *et al.* (2005), is clearly not a viable option. Taxa attributed to that family in the past share a subcentral peristome, lack of anterior sulcus and commonly a thick-shelled test, none of which is true for *Mariania*. *Mariania* does, however, show similarities with the sister-group of Asterostomatidae, the Antillasteridae. With these *Mariania* shares the wide petals, equally developed poriferous zones, labrum extending to ambulacral plate 2, lack of fascioles in adults and well-developed phyllodes. Unfortunately, antillasterids are likewise of uncertain systematic position, being variably resolved as basal Brissidina or as basal Paleopneustina in the analyses. However, while the analyses always found as sister-group relationship between *Antillaster* and *Asterostoma*, they never found a relationship to *Mariania*, wherefore the observed similarities are interpreted as superficial in nature here.

Likewise, Mortensen’s (1950) attribution of *Mariania* to Paleopneustidae likewise is not supported by the available data. Both datasets analysed above recover Paleopneustina and Brissidina as separate clades within the Spatangoida, and *Mariania* is consistently attributed to the latter. Mortensen’s decision was based in part on Lambert’s observation that *Mariania* seems to be related to *Megapneustes*, which he considered to be “fairly certain” a paleopneustid. Few of the genera attributed to paleopneustids by Mortensen, however, are retained in the family today (Smith & Kroh 2011), which appears to represent a small clade basal to prenasterids and schizasterids (Stockley *et al.* 2005, Kroh & Smith 2010). Paleopneustidae are characterized by the lack of a frontal groove, long labral plate extending to third or fourth ambulacral plate and – where known – marginal and/or peripetalous fascioles, at least in juveniles. None of this fits well with *Mariania*.

Likewise, a placement within the Brissidae as proposed by Fischer (1966, U591) seems not well supported. As currently defined they are characterized by a wide, but very short labral plate not extending beyond the first adjacent ambulacral plate, narrow, straight sided and usually sunken petals. Both a peripetalous and subanal fasciole are developed in most members of the family (Smith & Kroh 2011). *Mariania* does not fit with any of these characteristics.

The inclusion within Maretiidae, as suggested by Smith & Kroh (2011), is also problematic. Commonly, members



of this group show a reduction of the adapical pore pairs in the anterior zone of the anterior petals. Most forms also show short sternal plates and a marked constriction of interambulacrum 5 behind the episternal plates. In addition, a subanal fasciole is typically developed. Again, *Mariania* does not share these characters.

Of all the affinities proposed so far, the attribution to Megapneustidae by Lambert & Thiéry (1924) seems to fit best, judging by the morphological comparison to the type genus. Like *Mariania*, it shows heterogeneous aboral tuberculation without sunken areoles, presence of a frontal notch, equally developed poriferous zones in the anterior petals, high profile and lack of an indentation behind the episternal plates. Unfortunately, megapneustids are poorly known, as is their relation to the similar macropneustids (Smith & Kroh 2011, therefore, treat them as a single group). Based on their type genera the two families are resolved as either basal to the Brissidina (Stockley *et al.* 2005) or basal to the Spatangoidea (Kroh & Smith 2010). Surprisingly, *Mariania* fails to group with either type-genus in the analyses carried out here, probably owing to the fasciole characters – both *Macropneustes* and *Megapneustes* show subanal and peripetalous fascioles, while *Mariania* seems to lack any fascioles (possibly secondarily lost).

Systematic palaeontology

Order Spatangoida L. Agassiz, 1840
Suborder Brissidina Kroh & Smith, 2010
Superfamily Spatangoidea Gray, 1825
Family incertae familiae

Genus *Mariania* Airaghi, 1901

[= *Airaghia* Lambert, 1910, p. 3 (*nom. van.*)]

Type species. – *Macropneustes marmorae* Desor in Agassiz & Desor, 1847, p. 9 (115), by original designation (Airaghi 1901, p. 211).

Species included. – *M. marmorae* (Desor in Agassiz & Desor, 1847), Aquitanian of Sardinia and Burdigalian of Corsica. *M. deyderi* (Cotteau, 1897), Burdigalian, Rhône Basin (France) and Northern Alpine Foreland Basin (Austria). *M. stefaninii* sp. nov., late Burdigalian–early Langhian of Emilia, Burdigalian of Friuli, Italy. *M. co-*

maschicariae sp. nov., Aquitanian–Burdigalian of Sardinia.

Emended diagnosis. – Cordiform spatangoid echinoid with ethmolytic apical disc, four gonopores, broad petals extending to the margin, equally developed poriferous zones in petals, heterogeneous tuberculation aborally, areoles of aboral tubercles not sunken, labrum extending to second ambulacral plate, plastron fully tuberculate and not indented behind episternal plates, well-developed phyllodes with low and sub-equal plates extending to margin and absence of fascioles in adult specimens.

Mariania marmorae (Desor in Agassiz & Desor, 1847)

Figures 2D, 4A, B, 5A, 7A–I

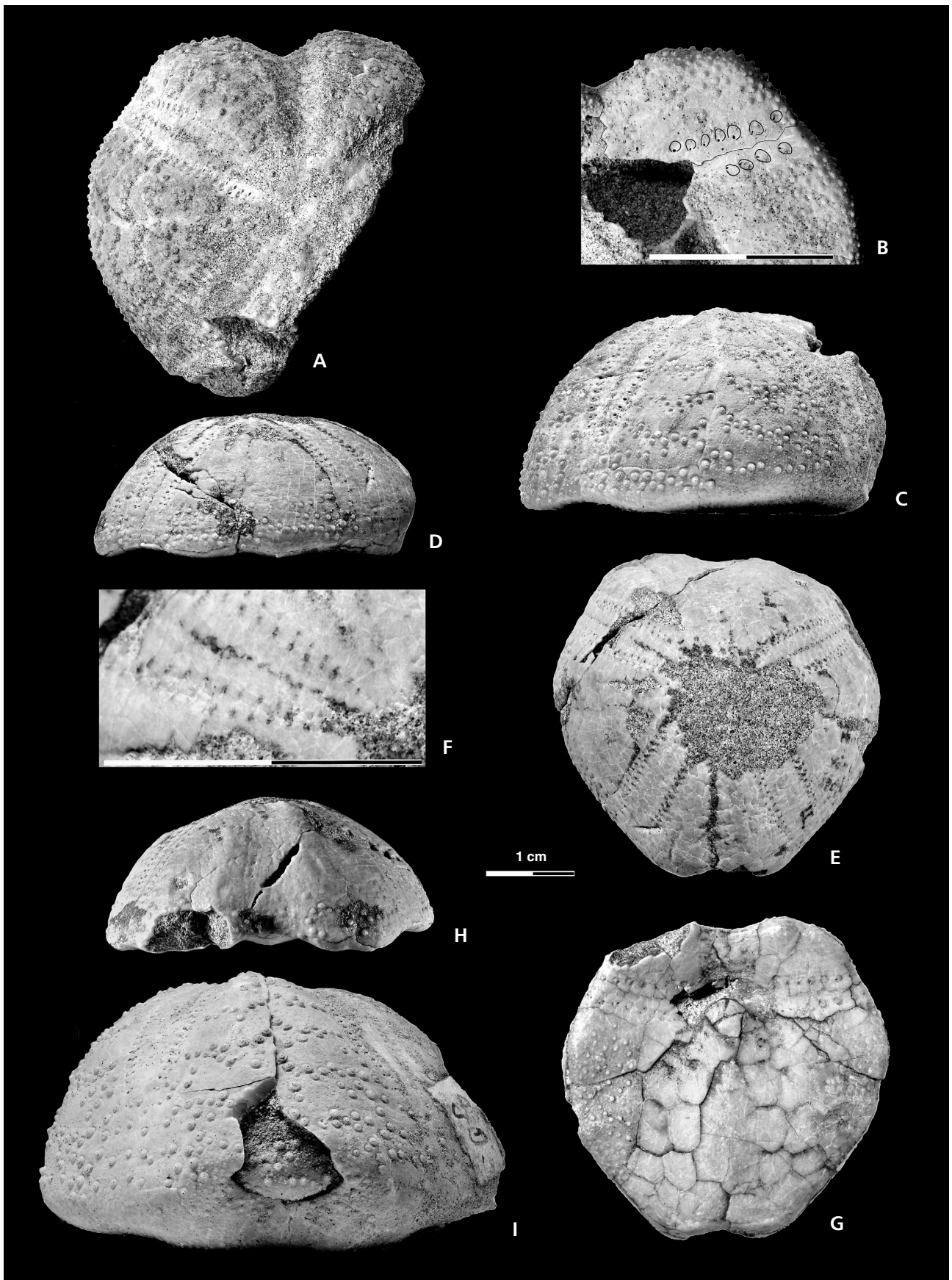
- 1847 *Macropneustes Marmorae* Desor in Agassiz & Desor, p. 9 (115).
- 1877 *Macropneustes Marmorae* Desor, 1847. – Cotteau, pp. 320–322, pl. 15, figs 1, 2.
- 1897 *Spatangus marmorae* (Desor, 1847). – Cotteau, pp. 7–10, pl. 4.
- 1909 *Mariania (Macropneustes) marmorae* (Desor, 1847). – Lambert, p. 103, pl. 9, fig. 6, pl. 11, fig. 7.
- 1963 *Spatangus marmorae* (Desor, 1847). – Comaschi Caria, pp. 23–24, pl. 3, fig. 4.
- 1972 *Spatangus marmorae* (Desor, 1847). – Comaschi Caria, pp. 62–63, pl. 47, fig. 1.3.
- ? 1998 *Spatangus (Mariania) marmorae* (Desor, 1847). – Philippe, p. 219, pl. 25, fig. 7.

Type material. – Repository of Desor's syntypes unknown. Cotteau's (1877) re-description was based on the specimen R92 (École des Mines, Locard collection), which may or may not have been part of Desor's original material.

Material studied. – Three specimens from the late Aquitanian of Funtanazza, Sardinia (MDLCA 10082/00191886 and 10083/00191886, MAC PL1524), one specimen from the Burdigalian of Corsica (University of Lyon EM 12134, based on photographs).

Diagnosis. – A species of *Mariania* with particularly high test (50–63% TL), domed profile, weak sulcus between peristome and margin, and long labral plate (18–19% TL, 1.5 times longer than wide).

Figure 7. *Mariania marmorae* (Desor in Agassiz & Desor, 1847), Funtanazza (Sardinia). • A–C – specimen MDLCA 10082/00191886; A – aboral view; B – partial oral view of the anterior ambulacrum IV, highlighting the unipores with enlarged periporal areas; C – left lateral view. • D–H – specimen MAC PL1524; D – left lateral view showing the typical turtle-shaped profile; E – aboral view; F – enlarged view of anterior aboral ambulacrum; G, H – oral and anterior views, respectively. • I – posterior view of MDLCA 10083/00191886. All scale bar equal 1 cm.



Description. – Small-sized test (TL = 37–54 mm in the studied sample), almost as long as wide, with heart-shaped outline that is slightly truncated posteriorly (Figs 4A, B, 7E, G). Anterior sulcus wide and shallow (L1 = 3.5–5.5% TL; Fig. 7A, E). Profile domed, with steep sides (Fig. 7C, D, H, I), maximum height lies around the apical disc and reaches 63% TL. Posterior face low and slightly undercut. Oral face flat to slightly concave, depressed anterior of peristome (Fig. 7G).

Apical disc: Anterior of the centre (L8 = 41.5% TL), ethmolytic, with four gonopores, the posterior pair of which are further apart than the anterior ones.

Ambulacra: Ambulacrum III non-petaloid, with minute, undifferentiated pores. Adorally ambulacrum III forms a shallow groove between peristome and margin. Paired ambulacra petaloid, with wide, straight to slightly bowed petals, extending almost to margin in plan view. Poriferous zones equally developed (Fig. 7F), with 18–20 elongate isopores per column. Interporiferous zones up to three times as wide as a single poriferous zone at widest point. Anterior paired petals form an obtuse angle of 120°–130°, the posteriors an acute angle of 60°–70°. Adorally well-developed phyllodes are present. Those of ambulacra II and IV extend almost to the margin and consist of up to 15 low plates (mean PLR = 1.3), bearing large unipores with broad periporal area. Oral ambulacra I and V form broad, naked periplastral areas (Figs 4A, B, 7G). Enlarged subanal pores are absent.

Interambulacra: Aborally the interambulacra are slightly inflated between the petals. All interambulacra amphiplacous, basicoronal plates of paired ambulacra typically extending to fourth adjacent ambulacral plates. Plastron slightly inflated, adjunct, with labral plate extending to second adjacent ambulacral plates. Labrum tapering to the rear, wedge-shaped and moderately long (1.5 times longer than wide). Sternal plates narrow and long, extending to the fifth ambulacral plates. Plastron not indented behind first pair of episternal plates.

Tuberculation: Aboral tuberculation heterogeneous, with large, perforate, crenulate primary tubercles spread across whole aboral surface except for interporiferous zones of petals (Fig. 7A, C, I). Tubercles crowded along adapical plate margins, forming irregular chevron-shaped clusters. Secondary and miliary tuberculation dense. Adoral tuberculation slightly more regular, with interambulacra covered by moderately closely spaced, primary tubercles (Fig. 7G). Plastron fully tuberculate. No fascioles.

Peristome: broad (mean L6 = 24% TL) and rather close to the anterior test margin (L2 about 20% TL).

Periproct: transverse and wide (Fig. 7I), framed by five plates on either side (5.a.4 to 5.b.8, Fig. 5A).

Remarks. – Most of the morphological characters used here to distinguish between *M. marmorae* and the two new species of *Mariania* were not reported in the descriptions provided by Botto Micca (1896), Airaghi (1901), Lambert (1909), Stefanini (1919) and Philippe (1998). A re-examination of the fossil material attributed to *M. marmorae* in these papers is necessary to confirm their identification at the specific level. Material attributed to *M. marmorae* by Stefanini (1919), examined at IGF, is here transferred to a new species, *M. stefaninii* sp. nov., on account of its lower test, more central apical disc, shorter labral plate and narrower petals. Specimens studied by Airaghi (1901) seem different from *M. marmorae*, as highlighted by Lambert (1915), and appear similar to *M. stefaninii* sp. nov. Unfortunately, the specimens from Piedmont were lost in 1943 (personal communication, D. Ormezzano, January 2015).

Distribution. – Miocene, late Aquitanian of Sardinia (Lambert 1909; Comaschi Caria 1963, 1972), Burdigalian of Corsica (Cotteau 1877).

Mariania deyrieri (Cotteau, 1897)

Figure 8A–E

- 1897 *Spatangus Deyrieri* Cotteau, pp. 185–187, pl. 10, figs 2–4, pl. 11, figs 1–6.
- 1914 *Spatangus Deyrieri* Cotteau, 1897. – Cottreau, p. 76.
- 1915 *Mariania Deyrieri* (Cotteau, 1897) (*Spatangus*). – Lambert, pp. 205–206.
- 1998 *Spatangus (Mariania) deyrieri* Cotteau, 1897. – Philippe, pp. 216–219, pl. 25, figs 4–6.
- 2005 *Mariania deyrieri* (Cotteau, 1897). – Kroh, pp. 186–187, fig. 91, pl. 80, fig. 1a–e.

Type material. – Two syntypes described and figured in Cotteau (1897, pp. 21–23, pl. 10, Muséum Requien, Avignon, France, MR 3 000 211), from the Burdigalian of Reillanne, Alpes-de-Haute-Provence, France (Philippe 1998).

Material studied. – One specimen from the Lower Burdigalian of Grübern (Zogelsdorf Formation), near Maissau, Austria (NHMW 1998z0048/0102).

Diagnosis. – A species of *Mariania* with low profile (28–34% TL), relatively tall phyllodal plates (highest value of PLR in *Mariania*), short and narrow sternum, and periproct bordered by plates 5.a/b.5 adorally.

Description. – Small-sized test (TL = 37–54 mm), broadly

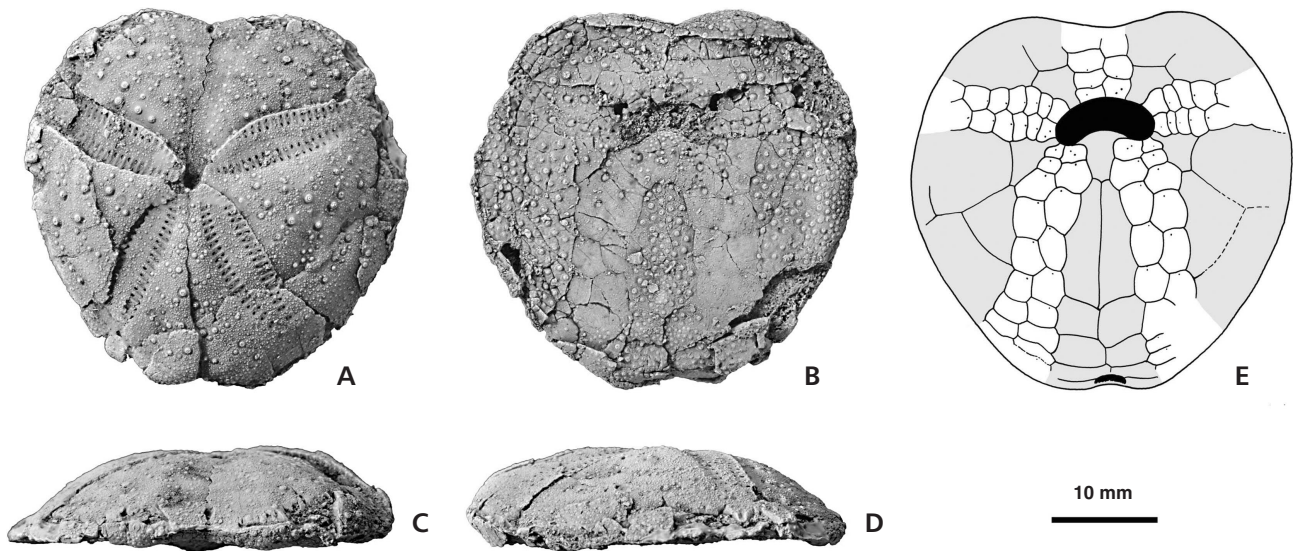


Figure 8. *Mariania deyrieri* (Cotteau, 1897) from Grübern, Austria (NHMW 1998z0048/0102). • A–D – aboral, oral, anterior and right lateral views, respectively. • E – oral plating. Specimens coated with ammonium chloride, interambulacra shaded, poorly visible sutures stippled.

heart-shaped with transversely truncated posterior margin and broad, but shallow, frontal sinus. Profile low, with a low, obliquely truncated posterior end. The maximum height rarely exceeds 35% TL and lies around the apical disc. Oral side flat with slightly inflated plastron.

Apical disc: slightly anterior of the centre (L8 = 42% TL).

Ambulacra: ambulacrum III non-petaloid, with only secondary and miliary tubercles. Paired ambulacra petaloid, only slightly closing distally. The interporiferous zones are up to one and a half times as wide as a single poriferous zone, and bear only secondary and miliary tubercles. On the oral surface, anterior paired ambulacra with plates slightly lengthening (mean PLR = 2.1), bearing large uni-pores with broad periporal area.

Interambulacra: in plan view four to five plates can be seen in interambulacra 1 and 4 adorally. Basicoronal plates of paired interambulacra typically extend to third adjacent ambulacral plates. Plastron narrow, not indented posteriorly and only slightly inflated. Labrum, elongate hexagonal, widest midways, extending to midway of second adjacent ambulacral plates.

Tuberculation: aboral tuberculation heterogeneous, with large, perforate, crenulate primary tubercles occurring on adapical plate margins. Primary tubercles present in all interambulacra, but missing from interporiferous zones of the petals. Secondary and miliary tuberculation dense. Adorally plastron and paired interambulacra fully tuberculate, while ambulacra are naked. No fascioles.

Peristome: rather close to the anterior test margin (L2 about 24% TL).

Periproct: transverse, lying on the overhanging posterior end of the test, framed by plates 5.a/b.5 adorally.

Remarks. – Unlike the other *Mariania* species, *M. deyrieri* has relatively tall phyllodal plates (PLR = 2.1) halfway between the peristome and margin in ambulacra II and IV. Yet, all other characters agree well with the features exhibited by the type species and placement in *Mariania* is confirmed here. Additional features distinguishing *M. deyrieri* from the other species are the shorter (mean L4 = 34% TL instead of 43–45%) and narrower sternum, more posterior peristome, smaller periproct and lower test (< 35% TL) (Table 2).

Distribution. – Miocene, Burdigalian of the Rhône Basin, France (Cotteau 1897, Lambert 1915, Philippe 1998), Early Burdigalian of Austria (Kroh 2005).

***Mariania stefaninii* sp. nov.**

Figures 2E, 4C, D, 5B, 9A–I

- 1881 *Mariania marmorae* (Desor, 1847). – Manzoni, p. 104.
- ? 1896 *Hypsospatangus Marmorae* (Desor, 1847). – Botto Micca, pp. 366–367.
- ? 1901 *Mariania marmorae* (Desor, 1847). – Airaghi, pp. 211–212, pl. 27, fig. 5p.
- 1908 *Mariania marmorae* (Desor, 1847). – Stefanini, p. 105, pl. 16, fig. 1.

1919 *Mariania marmorae* (Desor, 1847). – Stefanini, p. 143, pl. 14, fig. 8.

Type material. – Holotype: IGF 101719, a complete specimen. Paratypes: three complete specimens (IGF 101716, 101717 and 101718) and seven almost complete specimens (IGF 102169–102175), all from the type locality, one of them (IGF 101717) retaining some primary spines on the aboral surface. Forty-seven test fragments from the type locality.

Type locality. – Serra dei Guidoni, near Bologna, northern Italy.

Type stratum. – Upper Burdigalian to lower Langhian Pantano Formation, base of the Montecuccolo member.

Additional material. – Three specimens (IGF 102166–102168) from Friuli (northern Italy); one of them, from Meduno, is complete and was figured by Stefanini (1919, pl. 14, fig. 8). The other two are almost complete, but deformed tests (Forcella and Preplans). Additionally, there are 23 test fragments: 9 from Forcella, 8 from Preplans, 3 from Meduno and 3 from Meli.

Etymology. – In honour of the palaeontologist Giuseppe Stefanini.

Diagnosis. – A species of *Mariania* with moderately high profile (mean 48% TL), comparatively narrow petals, not quite reaching the ambitus in plan view, deep groove connecting the peristome and anterior margin, strongly projecting, triangular labral plate and numerous low phylloidal plates (10–12 per column) in ambulacra II and IV.

Description. – Small-sized test (mean TL = 52 mm), almost as long as wide (mean TW = 97% TL), with cordate outline (Fig. 9G). Profile domal (mean TH = 48% TL) with steep sides. Ambitus low with rather sharp margin (Fig. 9C–E). Wide, but shallow, anterior sulcus (mean L1 = 7% TL). Oral face flattened or distinctly concave (Fig. 9C, G).

Apical disc: subcentral (mean L8 = 49% TL, Fig. 9A, F), ethmolytic, with four gonopores.

Ambulacra: ambulacrum III non-petaloid, with minute undifferentiated pores only. Above the ambitus ambulacrum III is only weakly depressed, forming a comparatively

shallow frontal notch. Below the ambitus it forms a strongly depressed groove between peristome and margin (Fig. 9C, E). Paired ambulacra petaloid, slightly depressed aborally. Petals straight (posterior ones) to slightly bowed (anterior ones) and open distally. Anterior ones wide (mean L10 = 14% TL) and long, extending to 2–3 plates from the margin. Posterior ones only a little wider (mean L12 = 15% TL). The anterior paired petals form an obtuse angle of 110°–120°, the posterior ones an acute angle of 60°–70°. On the oral side ambulacra II and IV are distinctly depressed (Fig. 9D, E, I), with numerous (10–12 per column) low (mean PLR = 1.2) phylloidal plates extending to the ambitus (Fig. 9B). The periplastral plates of ambulacra I and V are slightly swollen.

Interambulacra: slightly inflated aborally between petals. Adorally all interambulacra are amphisternous. Basicoronal plates of paired interambulacra extend to fourth adjacent ambulacral plates, except along adradial suture to ambulacra II and IV, where they extend to the fifth or sixth plates. Plastron only slightly inflated, with triangular labral plate tapering to the rear. It extends to the second adjacent ambulacral plates and is only very slightly longer than wide (1 : 0.95). Sternal plates long and slender (mean L4 = 45% TL, mean L5 = 25% TL). Plastron not indented behind episternal plates (Figs 4D, 9C, G).

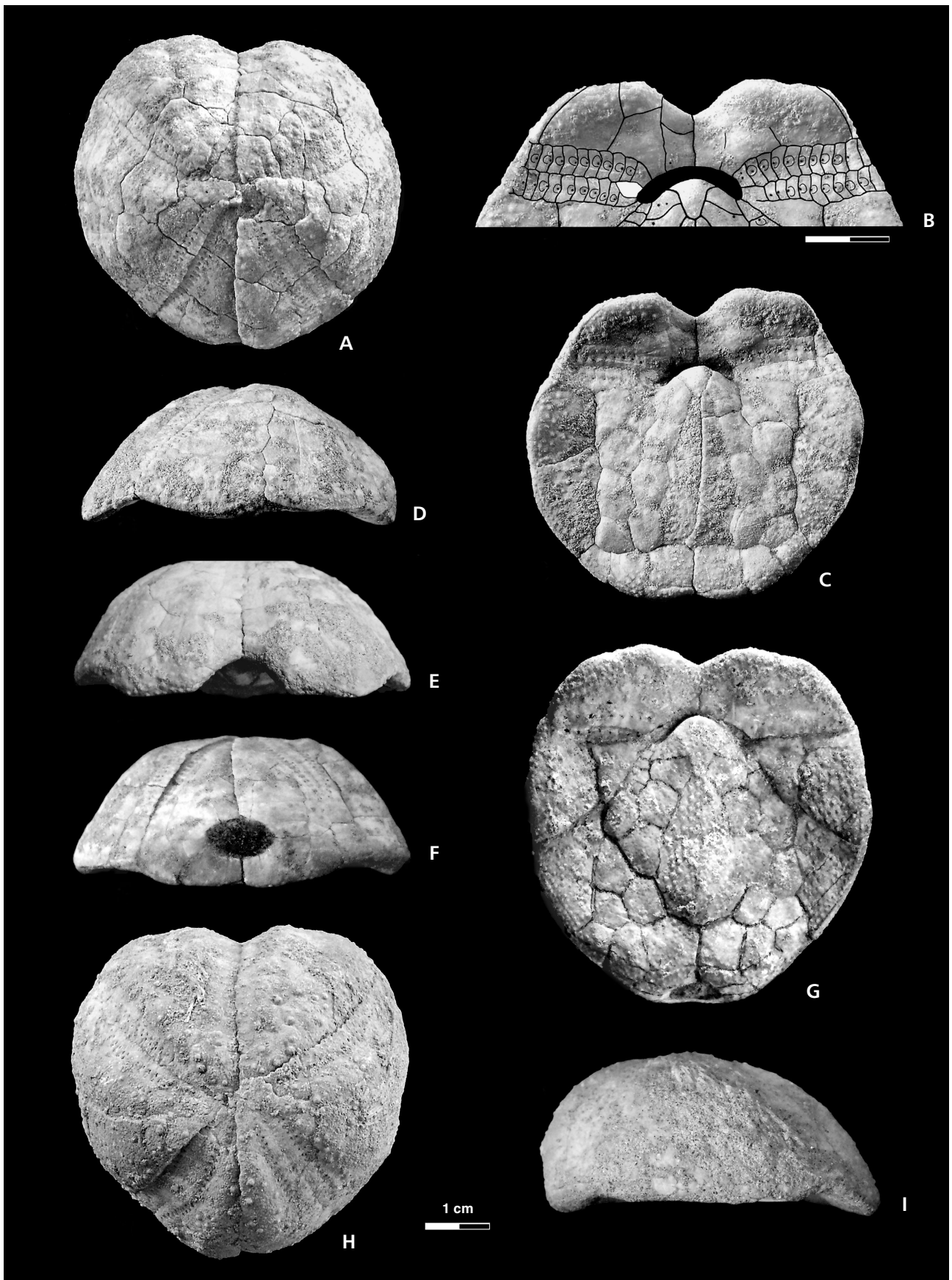
Tuberculation: aboral tuberculation heterogeneous, with large, perforate, crenulate primary tubercles irregularly scattered across whole aboral surface except for interporiferous zones. The largest tubercles are crowded along the adapical sutures, forming small clusters along the adradial (interambulacra 2 + 3) or interradian (interambulacra 1, 4, and 5) sutures. Adorally all interambulacra (including plastron) fully tuberculate, while the ambulacra are devoid of large tubercles. No fascioles.

Peristome: wide, crescent-shaped and overhung by the strongly projecting labral plate, almost obscuring the peristome in oral view.

Periproct: transverse, large (mean L13 = 21% TL, Fig. 9F), bounded by plates 5.a/b.4 adorally (Fig. 5 B).

Spines: a few primary spines, retained in the aboral interambulacrum 1, are short (spine length 8–12 mm), cylindrical and almost straight, with a smooth shaft and a hollow central cavity.

Figure 9. *Mariania stefaninii* sp. nov., Serra dei Guidoni (northern Italy). • A–E – holotype (IGF 101719); A – aboral view; B – close up of the anterior ambulacra; C–E – oral, left lateral and anterior views, respectively. • F – posterior view of IGF 101718. • G – oral view of IGF 101716. • H, I – respectively aboral and right lateral views of IGF 101718. Scale bars equal 1 cm.



Remarks. – *Mariania stefaninii* differs from all other species of the genus by its high number of phyllodal plates in ambulacra II and IV, the strongly projecting labral plate and the deep groove connecting the peristome and the anterior margin. From *M. marmorae* it differs, in addition, by its lower test, more central apical system, shorter labral and narrower petals. From *M. deyderi* it can additionally be distinguished by its higher test, longer sternal plates, different periproct position (in relation to plate number). It differs from *M. comaschicariae* also by its narrower petals, higher test and more concave oral face.

Distribution. – Miocene, late Burdigalian–early Langhian of Emilia (northern Italy), Burdigalian of Friuli (Stefanini 1919), possibly also in the Miocene of Piedmont (Airaghi 1901).

***Mariania comaschicariae* sp. nov.**

Figures 2F, 4E–G, 5C, 10A–H

Type material. – Holotype: MDLCA 23533. Paratypes: four specimens from the type locality (MDLCA 23534, MAC PL1548, MAC PL1617, MAC PL1650), and one specimen from Ales (MAC PL1849).

Type locality. – Isili, Sardinia, Italy.

Type stratum. – Arenarie di Serralonga, Nurallao Formation (Aquitanian to early Burdigalian).

Etymology. – Dedicated to the palaeontologist Ida Comaschi Caria.

Diagnosis. – A species of *Mariania* with low test (mean 37% TL), wide and long petals (extending to margin in aboral view), weak sulcus between peristome and margin, and short labral plate (14% TL, 1.15 times longer than wide).

Description. – Small-sized test (mean TL = 48 mm), almost as long as wide, with cordate outline (Fig. 10A, B, E). Profile domal and low (Fig. 10G), with steep sides and low ambitus (Fig. 10F–H). Shallow and rather wide anterior sulcus (mean L1 = 5% TL). Posterior face vertically truncated, not overhanging. Oral side flattened, distinctly depressed before peristome.

Apical disc: four gonopores, ethmolytic (Figs 4E, 10C), located anterior of centre (mean L8 = 41% TL).

Ambulacra: anterior ambulacrum non-petaloid, with minute partitioned isopores only, flush at apex, becoming increasingly sunken towards peristome, but forming only a shallow frontal notch. Paired ambulacra petaloid and slightly sunken aborally. Petals open distally, very wide and long (mean L9 = 49% TL, mean L11 = 51% TL), extending to margin in aboral view (Fig. 10A). The anterior paired petals form an angle of about 120°, the posterior ones an angle of 60°–70°. The interporiferous zones are at least 2 to 2.5 times as wide as a single poriferous zone. Adorally, ambulacra II and IV are depressed, with 8–10 low (mean PLR = 0.9) phyllodal plates per column. Oral ambulacra I and V form a broad periplastral area (L7 = 53% TL).

Interambulacra: basicoronal plates of anterior interambulacra extending to third ambulacral plates, those of the lateral ambulacra to the fourth or fifth ambulacral plates. Plastron barely inflated, with short (*ca* 14% TL, 1.15 times longer than wide), wedge-shaped labral plate extending to second adjacent ambulacral plates (Fig. 10B, E). Sternal plates long and narrow, slightly indented to the rear by the ambulacral plates 5. Plastron not constricted behind episternal plates.

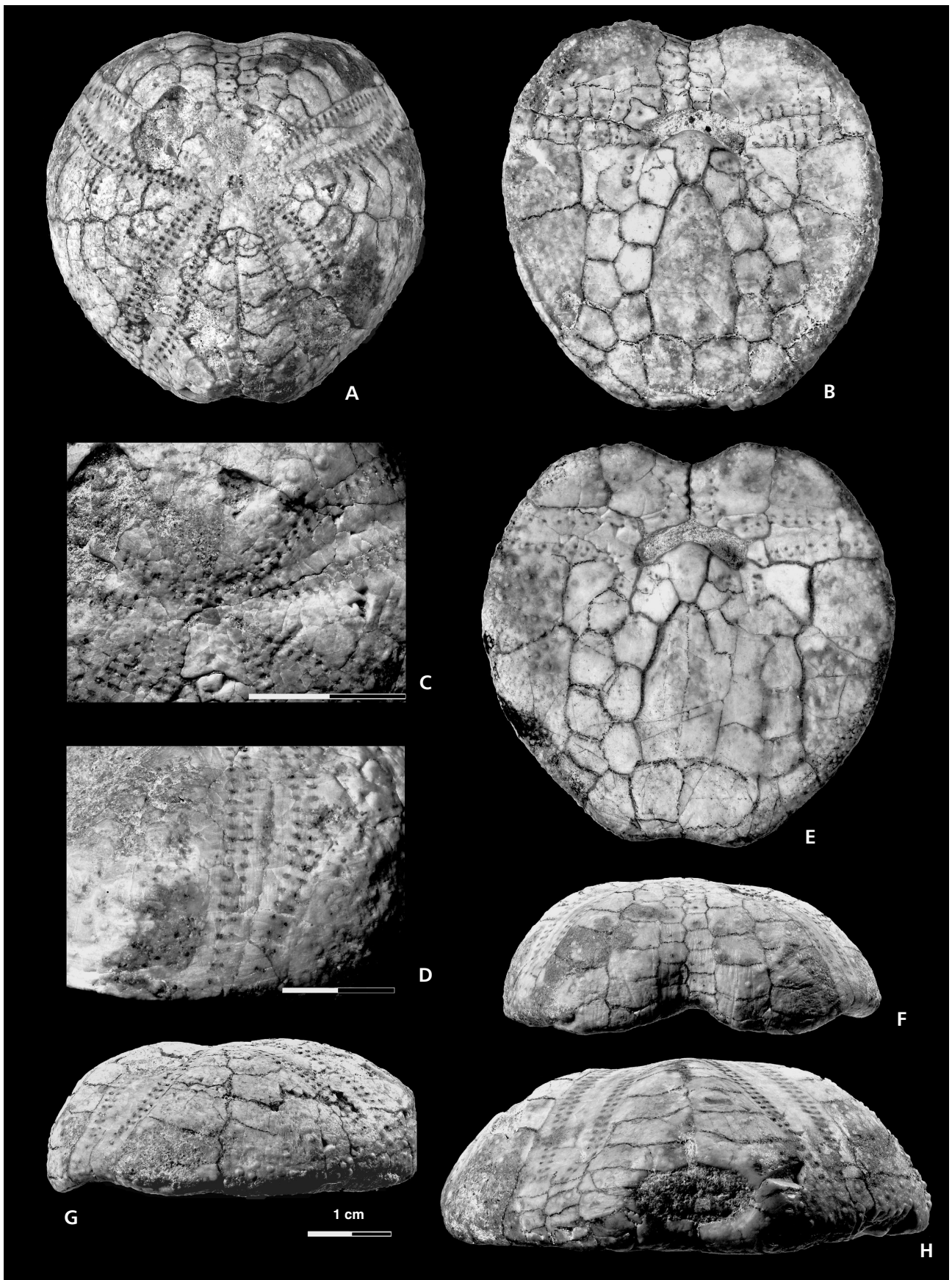
Tuberculation: primary tubercles are found in all the aboral interambulacra, from the apex to the margin, where they are closely spaced. Adorally, tuberculation consists of closely spaced primary tubercles, covering the whole interambulacral area with the exception of the labrum and the ambulacra. No fascioles.

Peristome: wide and rather close to the anterior test margin, partially overhung by projecting labrum (Fig. 10B, E).

Periproct: transverse (Fig. 10H), rather large (L13 = 18% TL), bounded by plates 5.a/b.4 adorally.

Remarks. – This species is closest to *M. marmorae*, from which it differs by the much lower test (mean TH = 37% TL vs 59% in *M. marmorae*), much shorter labral plate (mean L3 = 14% TL instead of up to 20%), shorter petals (mean L9 = 49% TL vs 65% TL, and L11 = 51% TL vs 63% TL) and the slightly higher number of phyllodal plates (up to 10 vs 7–8). From *M. stefaninii* sp. nov. it differs by having

Figure 10. *Mariania comaschicariae* sp. nov., Isili (Sardinia). • A – aboral view of the holotype (MDLCA 23533). • B–D – specimen MDLCA 23534; B – oral view; C – close up of the apical zone, with progressively reduced pore pairs in the anterior ambulacra; D – magnification of the distal part of petal III reaching the ambitus. • E – oral view of MAC PL1516. • F, G – respectively, anterior and left lateral view of MDLCA 23533. • H – posterior view of MAC PL1650. All scale bars equal 1 cm.



a lower test (TH = 37% TL vs 48% in *M. stefaninii*), more anterior apical disc, less overhung peristome, and much shallower groove between peristome and margin. From *M. deyderi* it can be easily differentiated by its larger petal width, labrum shape (wedge-shaped vs. elongate hexagonal), phyllodal plate shape (PLR 0.9 vs 2.1 halfway between peristome and margin), longer sternal plates and different periproct position (in relation to plating).

Distribution. – Aquitanian of Ales and Burdigalian of Isili (Sardinia).

Family Spatangidae Gray, 1825

Genus *Spatangus* Gray, 1825

Type species. – *Spatangus purpureus* Müller, 1776, p. 236.

Spatangus euglyphus Laube, 1868

Figure 11A–F

1868 *Spatangus euglyphus* Laube, pp. 35–36, pl. 6, fig. 5, 5a–c.

1919 *Mariania euglypha* (Laube, 1868). – Stefanini, pp. 142–143, pl. 15, fig. 6a, b.

Type material. – The material on which Laube based his description derived mainly from the collection of the geological cabinet (today: Department for Geodynamics and Sedimentology) of the University of Vienna. In addition, he also studied some specimens from the Natural History Museum Vienna and illustrated a few specimens from the Museo Civico of Vicenza. Unfortunately, no specimens of *S. euglyphus* are preserved in the University of Vienna collection and the illustrated syntype appears to be lost. A possible syntype of *S. euglyphus* from Santa Libera di Malo was found in the collection of the Natural History Museum Vienna (NHMW 2015/0122/0001). While not explicitly labelled as *S. euglyphus*, the specimen comes from a part of the collection that was available to Laube and was already part of the collection at that time. It is thus likely that it was among the material studied by Laube.

Additional material examined. – Four complete specimens from the early Miocene of Veneto (Vicenza Province, northern Italy): two from Altavilla (Museo Civico Dal Lago of Valdagno), two from Schio (IGF collection).

Remarks. – *Spatangus euglyphus* was transferred to *Mariania* by Stefanini (1919). In addition, a variety of this species, *Mariania euglypha brevistella*, was later described by Venzo (1935) from the same area, differing only in having shorter petals. In the illustrations provided by Laube (1868,

pl. 6, fig. 5b), Stefanini (1919, pl. 15, fig. 6a) and Venzo (1935, pl. 17, fig. 29a, b), the phyllodes are short and the plates in the oral ambulacra II and IV clearly lengthen towards the margin (mean PLR = 4). This is corroborated by the material examined (Fig. 11A–F). In addition, the test is less inflated, with the lateral sides inclined at an angle of ca 45°. The labrum is not well visible in any specimen examined, but based on the position of the suture between the sternal plates, which reaches almost to the peristome, it must be short, barely as long as wide. Aboral primary tubercles are less abundant than in the other species assigned to *Mariania*, being largely confined to the area of the petalodium, where they cluster along interrational sutures in interambulacra 1, 4 and 5, as well as the posterior columns of interambulacra 2 and 3. The petals are comparatively short (extending c. two thirds to margin in aboral view), narrow (interporiferous zones only slightly wider than single poriferous zone) and closing distally. The petals in *S. euglyphus brevistellatus* (Venzo, 1935) n. comb. are even shorter (Venzo 1935, pl. 17, fig. 29a). Whether or not a subspecific status is warranted for the short-petal form cannot be evaluated based on the meagre material available at present (Venzo's taxon was based on a single deformed specimen and no morphometric study has yet been carried out to evaluate the variation of this feature in *S. euglyphus*). In addition to the generally smaller petalodium in these two forms, the anterior poriferous zones of ambulacra II and IV the adapical pores are rudimentary, which is not the case in species of *Mariania*. Based on all these differences and the fact that Laube specifically mentions the presence of a subanal fasciole, it appears that these two taxa fit much better into the genus *Spatangus* than in *Mariania*.

Occurrence. – Arenarie di Sant'Urbano unit, early Miocene of Veneto (northern Italy).

Palaeoecological remarks

The elevate test of *Mariania* with flat, even concave, oral face, likely points to an epibenthic echinoid. Also, the absence of fascioles and of specialized funnel-building tube-feet, indicated by the occurrence of small pore-pairs in the frontal ambulacrum, as well as the absence of enlarged pores in the subanal region, corroborates this hypothesis (compare with Smith 1980). Species of *Mariania* probably passed bottom material made of organic matter and sediments, into their mouth. The large peripodia with pronounced ridges indicate the presence of well-developed penicillate tube feet in the phyllodes, which performed this function.

At Funtanazza (Calada Bianca), *Mariania marmorae* was associated with fragmented spatangoids and *Spatangus thieryi*. A similar echinoid assemblage is pres-

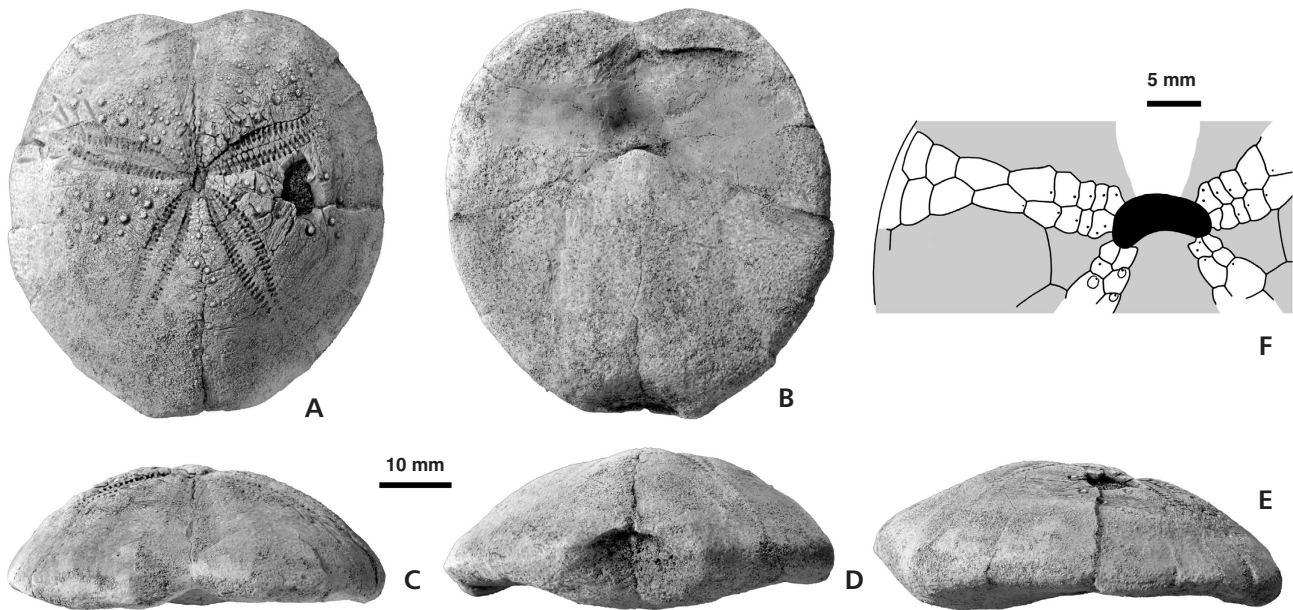


Figure 11. *Spatangus euglyphus* Laube, 1868, possible syntype from Santa Libera di Malo, Italy (NHMW 2015/0122/0001). • A–E – aboral, oral, anterior, posterior and right lateral views respectively. • F – plating of adoral ambulacra. Specimens coated with ammonium chloride, interambulacra shaded, sutures that were not visible are omitted.

ent also at Isili (Baraci), with the occurrence of *Hypsoclypus*, *Pericosmus* and *Faorina* (Stara et al. 2012). At Ales the echinoid assemblage consists of abundant *Faorina*, *Schizaster*, *Aliaster* other spatangoids and rare *Mariania comaschicariae*. The specimens are commonly abraded and fragmented, likely indicating a moderate transport. A shallow water setting, somewhat deeper than sublittoral, with sandy-silt bottom is assumed for these localities. About Funtanazza we suggest a sublittoral setting in sandy bottom.

At Serra dei Guidoni the sedimentary rocks at the base of the Montecuccolo Member were interpreted as deposited in a shallow inner shelf, likely a subtidal setting (Amorosi 1991). Nevertheless, Manzoni (1881) and Stefanini (1908) described a rich echinoid fauna of tropical affinity from this locality, consisting also of forms, which occur in slightly deeper settings today, e.g., *Faorina* (see Lane et al. 2000, Stara & Borghi 2012). Also, the co-occurrence of the brachiopods *Gryphus rovasendianus* (Seguenza, 1866) and *Terebratula sinuosa* (Brocchi, 1814) suggests that the depositional setting was indeed slightly deeper, likely in the circalittoral (Gaetani & Saccà 1984, Bertolaso et al. 2009), but new observations suggest a sublittoral setting.

Biogeography

According to the present state of knowledge *Mariania* is a short-lived genus evolved in the northern basins of the

West-Proto-Mediterranean Atlantic Region, that is, the modern Western Mediterranean Basin (see Harzhauser et al. 2002) precisely the Balearic Basin, at the onset of the Miocene. Most species are restricted to parts of that region: Sardinia + Corsica (*M. comaschicariae*, *M. marmarae*) and northern Italy (*M. stefaninii*). Only *M. deydieri* is slightly more widespread, occurring both in the Rhône Basin and the westernmost fringes of the Central Paratethys. It is one of the species that immigrated in the late Aquitanian or early Burdigalian from the Mediterranean Region (namely the French Rhône Basin) via the Molasse Trough to the Paratethys. Other examples of migration to the Paratethys are *Arbacina catenata*, *Clypeaster latirostris*, *Hemipatagus ocellatus*, *Parascutella paulensis* and *Psammechinus dubius dubius* (see Kroh & Harzhauser 1999; Kroh & Menkveld-Gfeller 2006, fig. 9; Kroh 2007). After the early Middle Miocene *Mariania* vanishes from the fossil record.

Conclusions

Newly recovered fossil material from the early and middle Miocene of Italy, namely Emilia, Friuli and Sardinia, enables us to provide an emended diagnosis for the poorly known genus *Mariania* and to distinguish it from related forms within the Spatangoidae. Previously undescribed key diagnostic features of this genus are the structure of the antero-lateral phyllodes, made up of a series of low plates extending almost to the test margin. This feature allows

clear separation from *Spatangus*, so far considered as the closest related genus (Philippe 1998), and in particular from the species *Spatangus pustulosus* (2b), *S. euglyphus* and *S. thieryi*, which have been repeatedly confused with *Mariania*, with which they are sometimes associated. All of these species have much shorter phyllodes than *Mariania*, since they end halfway between the peristome and the margin. The distal plates of the phyllodes in these forms are distinctly elongate, being usually half as wide as tall.

Within *Mariania*, we were able to distinguish four different groups, two of which (*M. stefaninii* sp. nov. and *M. comaschicariae* sp. nov.) represent new species. They are distinguished from the type species by a combination of metric and architectural features, including test height, petal width, apical disc position, labrum size and shape, number of phyllodal plates and periproct position.

Systematic placement of *Mariania*, however, remains problematic. Cladistic analysis using the extensive datasets of Stockley *et al.* (2005) and Kroh & Smith (2010), as well as various restricted and modified versions, failed to conclusively resolve the position of *Mariania*, although it is always included within the Brissidina. Two positions reoccurred in several analyses: an inclusion within crown Brissidina (Fig. 6A) closely related to spatangids, loveniids and maretiiids; and a basal position within Brissidina and related to *Archaeopneustes* (Fig. 6B).

Association of *Mariania* with *Archaeopneustes* results from the presence of large aboral tubercles, lack of fascioles, well-developed phyllodes and lack of indentation behind the episternal plates in both genera. Unfortunately, the placement of *Archaeopneustes* itself is unclear – it is one of the taxa earlier placed into the Asterostomatina by Fischer (1966), which was shown to be clearly polyphyletic by Stockley *et al.* (2005). Given the profound differences in plastron structure, petals and general shape, neither this sister-group relationship nor the basal position within Brissidina seem to be correct. Instead, we propose that *Mariania* is a crown-group member of Spatangoidea. For fully resolving its placement additional data on ontogenetic development of fascioles both in *Mariania* and several other atelostomates is needed.

Functional morphology of the corona of *Mariania* supported by actualistic comparison, sedimentary settings and associated taxa indicate that *Mariania* was an epibenthic browser, on shallow sand bottoms, preferring an inner shelf environment characterized by warm-temperate to tropical climate.

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