

Revision of the genus *Heterobrissus* (Echinoidea), with a new species from Sardinia, and redefinition of *Heterobrissus niasicus* (Döderlein, 1901) in *Echinopneustes* n. gen.

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ABSTRACT

Morphological characters previously unknown in *Heterobrissus montesi* Manzoni et Mazzetti, 1878, the type-species of the genus *Heterobrissus* Manzoni et Mazzetti, 1878, such as the oral plate structure and the position of the periproct, are herein described based on topo-typic material from the Middle Miocene of the Northern Apennines (Italy). Similar, well preserved specimens from the Early Miocene of Sardinia are attributed to *Heterobrissus lubellii* n. sp., which differs from *H. montesi* by its longer and wider petals and the peristome farther from the anterior margin of the test. The new available data confirm also that the genus *Archaeopneustes* Gregory, 1892 is junior synonym with *Heterobrissus*. Unreported specimens from the Late Oligocene of Alicante (Spain) enable to illustrate the plastron structure and other so far unknown features in *Pygospatangus salvae* Cotteau, 1890, the type species of the genus *Pygospatangus* Cotteau, 1890, and indicates that *Pygospatangus* is a junior synonym with *Heterobrissus*. *Heterobrissus salvae* differs from *H. montesi* mainly by its thicker shell and longer plates in the proximal part of the oral ambulacra I and V. The Recent species *Heterobrissus niasicus* (Döderlein, 1901), *H. erinaceus* Baker et Rowe, 1990 and *H. gigas* Baker et Rowe, 1990, from the Indo-Pacific, are herein transferred to *Echinopneustes* n. gen. *Echinopneustes* differs from *Heterobrissus* mainly by the labrum extending only to the adjoining ambulacral plate 2, not to plate 3 as in *Heterobrissus*, by the periproct being marginal, not inframarginal as in *Heterobrissus*, and bounded by the fifth plates in the interambulacrum 5, not by the fourth. The distribution of *Heterobrissus*, so far known from the Burdigalian of Sardinia, the Langhian of Northern Italy and the Serravallian of Cyprus, is extended to the Late Oligocene of Spain and to the Recent, with *H. hystrix* (Agassiz, 1880), today living in the Caribbean area. The functional morphology of the test, supported by actualistic comparison and by data taken from sedimentary settings and the associated taxa, indicates that *Heterobrissus* was an epibenthic feeder, preferring muddy outer shelf environments with tropical climate.

KEY WORDS

Echinoidea; *Heterobrissus*; Oligo-Miocene; Mediterranean; *Echinopneustes* n. gen.

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INTRODUCTION

Heterobrissus montesi Manzoni et Mazzetti, 1878, the type-species of the genus *Heterobrissus*

Manzoni & Mazzetti, 1878, was described on the basis of a single poorly preserved specimen from the Langhian Pantano Formation of Montese, near Modena (Northern Italy). This species was subse-

quently recorded in the same Formation from a number of other localities in the Northern Apennines (Manzoni, 1879, 1880; Mazzetti, 1881; Stefanini, 1908), and from the Early Burdigalian Nurallao formation of Isili, Sardinia (Stara et al., 2012). *Heterobrissus formai* Airaghi, 1901 and *H. cypriotes* Currie, 1935 were instituted on the basis of fossil material from the Langhian of Piedmont (Northern Italy) and the Serravallian of Cyprus, respectively. *Heterobrissus cypriotes* was subsequently considered as a junior synonym with the type-species by Smith & Gale (2009). Four Recent species are currently attributed (Baker & Rowe, 1990; Smith & Kroh, 2011) to the genus *Heterobrissus*: *H. niasicus* (Doderlein, 1901), *H. hemingi* (Anderson in Alcock, 1902), *H. gigas* Baker et Rowe, 1990 and *H. erinaceus* Baker et Rowe, 1990; all of them inhabit deep muddy bottoms in the Indo-Pacific. The genus *Archaeopneustes* Gregory, 1892 was originally distinguished from *Heterobrissus* by the position of the periproct and by the extension of the labrum (Mortensen, 1950), characters which prior to this study were unclear in *H. montesi*, due to the poor preservation of the available fossil material. According to Smith & Kroh (2011) and Kroh & Mooi (2019), *Archaeopneustes hystrix* (Agassiz, 1880), today living in the Caribbean area, could belong to *Heterobrissus*. Also *Pygospatangus* Cotteau, 1890, from the ?Eocene and the Late Oligocene of Spain, is considered as a possible junior synonym with *Heterobrissus* by Smith & Kroh (2011).

The uncertainty about the relationships existing between these genera was a result of the poor preservation of the holotype of *H. montesi*, which missed the oral face (Manzoni & Mazzetti, 1878, p. 354-355, fig. 2), and of the other specimens from the type-area subsequently described by Manzoni (1879, 1880) and Stefanini (1908). Also, the preservation of the holotype of *Pygospatangus salvae* is too poor (Cotteau, 1890, p. 17-18, pl. 14, fig. 1-3) to make any detail about the apical disc, the structure of the plastron, the peristome and tuberculation, so that the true affinities of this taxon cannot, so far, be determined (Smith & Kroh, 2011).

The aim of this paper was to complete the description of the diagnostic characters of the genus *Heterobrissus*, based on the re-examination of the original fossil material studied by Manzoni (1879, 1890) and Stefanini (1908) and on the study of unreported topotypic specimens from Emilia-Roma-

gna and of well preserved specimens recently collected from the Early Miocene of Sardinia. The relationships between *Heterobrissus* and the closely related genera have been discussed using unreported specimens from the Oligocene of Alicante (Spain) and Recent specimens of *H. niasicus*, with emphasis on the oral plate structure, a morphological character of major relevance in the systematic of spatangoids.

MATERIAL AND METHODS

Study area

The newly reported material of *H. montesi* was collected in the Langhian Pantano Formation from 6 different localities of the Emilia-Romagna Region (Northern Apennines; Fig. 1): Montese (the type-locality), Pescale, Zocca and Guiglia (Province of Modena), Monte Valestra (Reggio Emilia) and Jano near Sasso Marconi (Bologna). The holotype, a poorly preserved specimen, is missing at the Museo di Paleobiologia, University of Modena (MPUM), where the Mazzetti's collection is housed. Specimen numbers prefixed IGF are housed at the Museo di Storia Naturale, Sezione di Geologia e Paleontologia, University of Firenze. They consist of 12 specimens studied by Stefanini (1908) and 5 specimens collected by one of the authors (E.B.). None of the specimens figured in Manzoni (1979) has been traced at the IGF; two specimens illustrated in Stefanini (1908: pl. 14 figs. 4a,b, missing the oral face, and pl. 14, fig. 5, missing the aboral face) are available to study. The oral plating scheme has been taken from IGF.100335 (Jano) and IGF.101266.

Thirty-seven specimens of *Heterobrissus* collected by one of the authors (P.S.) from the Early Miocene of Sardinia (Arbus, Isili, Nureci and Genoni) were examined at the Museo di Storia Naturale "Aquila" of Masullas (MAC) and at the Museo di Paleontologia e Geologia Domenico Lovisato, University of Cagliari (MDLCA); thirty of them from the Early Burdigalian of the Nurallao formation of Isili (MDLCA.23788, MDLCA.23789, MDLCA.23790, MDLCA.23792, MAC.PL1509, PL1847, PL1860-70, PL2097, PL2165-73), four from the Burdigalian-Early Langhian Marne di Gesturi formation of the Nureci-Genoni area (MAC.PL2871-3, MDLCA.23791),

two from the same formation of Genoni (MAC.PL2095-6), one (MAC.PL2163) from the Late Oligocene-Early Aquitanian of Calada Bianca, near Funtanazza.

The holotype of *H. formai* Airaghi, 1901 is wanting at the Museo Regionale di Storia Naturale of Torino (MTPL); the observations reported by Stefanini (1908), who examined that specimen, have been utilised in the discussion.

The holotype of *Pygospatangus salvae* is housed at the Muséum National d'Histoire Na-

turelle, Paris (MNHN, repository code R62327). Ten specimens from the Oligocene (Late Chattian) of Xorret de Catí and Sierra de Monteagudo, near Novelda, Alicante (Spain), were examined in five private Spanish collections: Leonardo Hernandez (LH.01, 04), Clifford Saint Clair (CP.01-03) and Jose Carlos Saldaña (JS.01-02) from Alicante, Carlos Garcia (CG.01-02) from Madrid and Manuel Adel Alegre (MA.01) from Vinaròs. One of these specimens (CG.02) retains a number of primary spines.

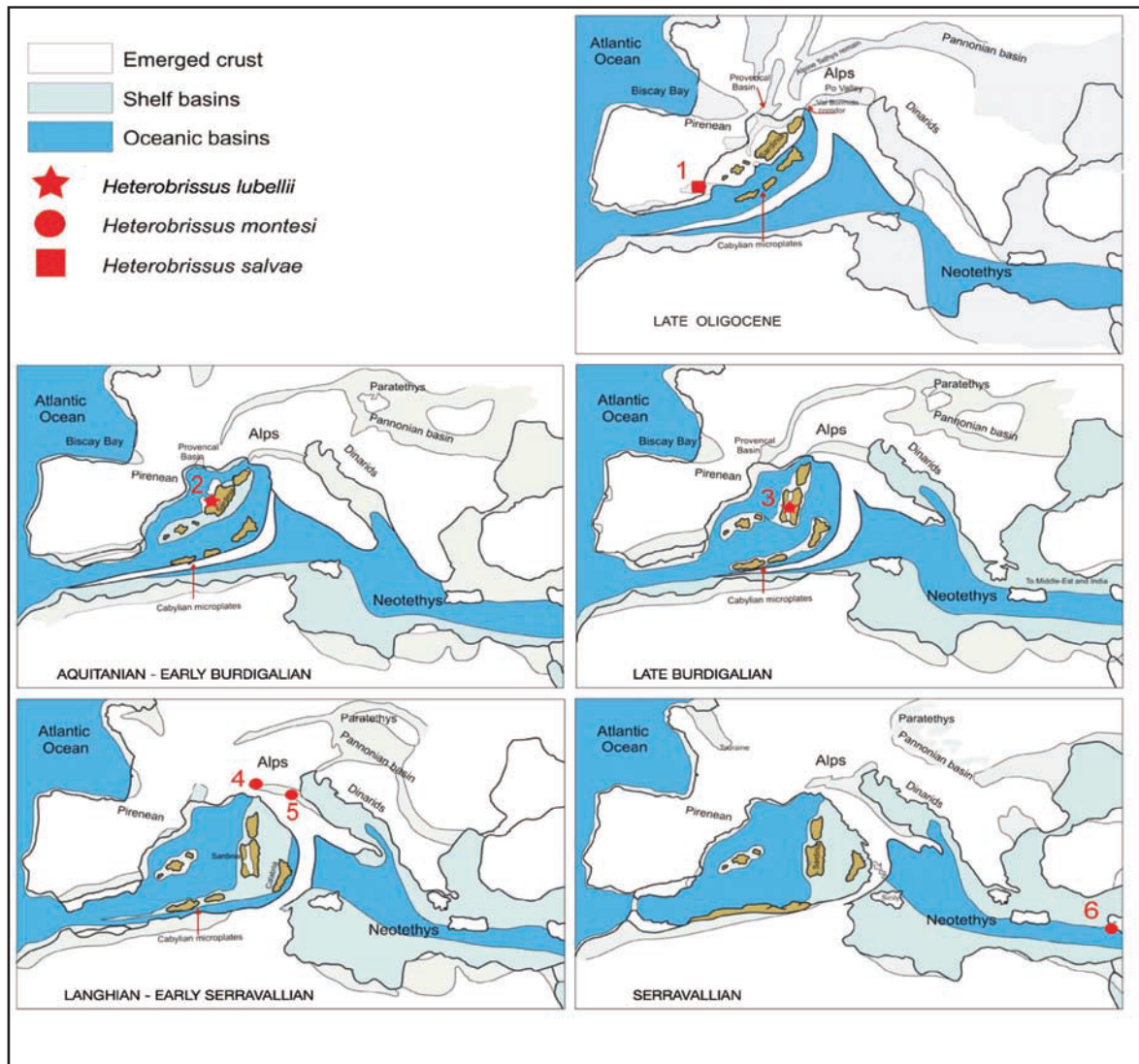


Figure 1. Location map of the *Heterobrissus*-bearing localities (partially modified from Rosenbaum et al., 2002 and Stara & Rizzo, 2013). 1: Alicante (Spain), Oligocene; 2: Funtanazza (Sardinia), Late Oligocene-Early Aquitanian; 3: Isili and Nureci (Sardinia), Burdigalian; 4: Pino Torinese (Piedmont), Langhian; 5: Guiglia, Montese, Monte Valestra, Pescale, Rocca Malatina, Jano and Zocca (Emilia-Romagna), Langhian; 6: Alessa near Limosol (Cyprus), Serravallian.

Six Recent specimens of *H. niasicus* from the Southern China Sea and the Philippines (MAC IVM203, 291-293, 446-448) and one of *Archaeopneustes hystrix* from Florida (Museum of Comparative Zoology, Harvard University, MCZ ECH-7813) were utilised in the discussion.

Systematic palaeontology follows Smith & Kroh (2011) and Kroh & Mooi (2019).

ABBREVIATIONS (used in Fig. 2, Tables 1–3). Fm = Formation (formalised); L1 = periproct height; L2 = periproct width; L3 = distance between the lower margin of the periproct and the test base;

L4 = anterior paired petal length (measure from the apical system to the last plate bearing pores); L5 = anterior paired petal width (measured at mid-length); L6 = posterior paired petal length; L7 = posterior paired petal width; L8 = distance between the frontal genital pores and the posterior test margin; L9 = distance between the tip of the labrum and the anterior test margin; L10 = labrum length; L11 = sternal plates length. TL, TW, TH = respectively, length, width and height of the test.

CONVENTIONS: in the Tables 1–3, TL is reported in mm, the other data are expressed as % of

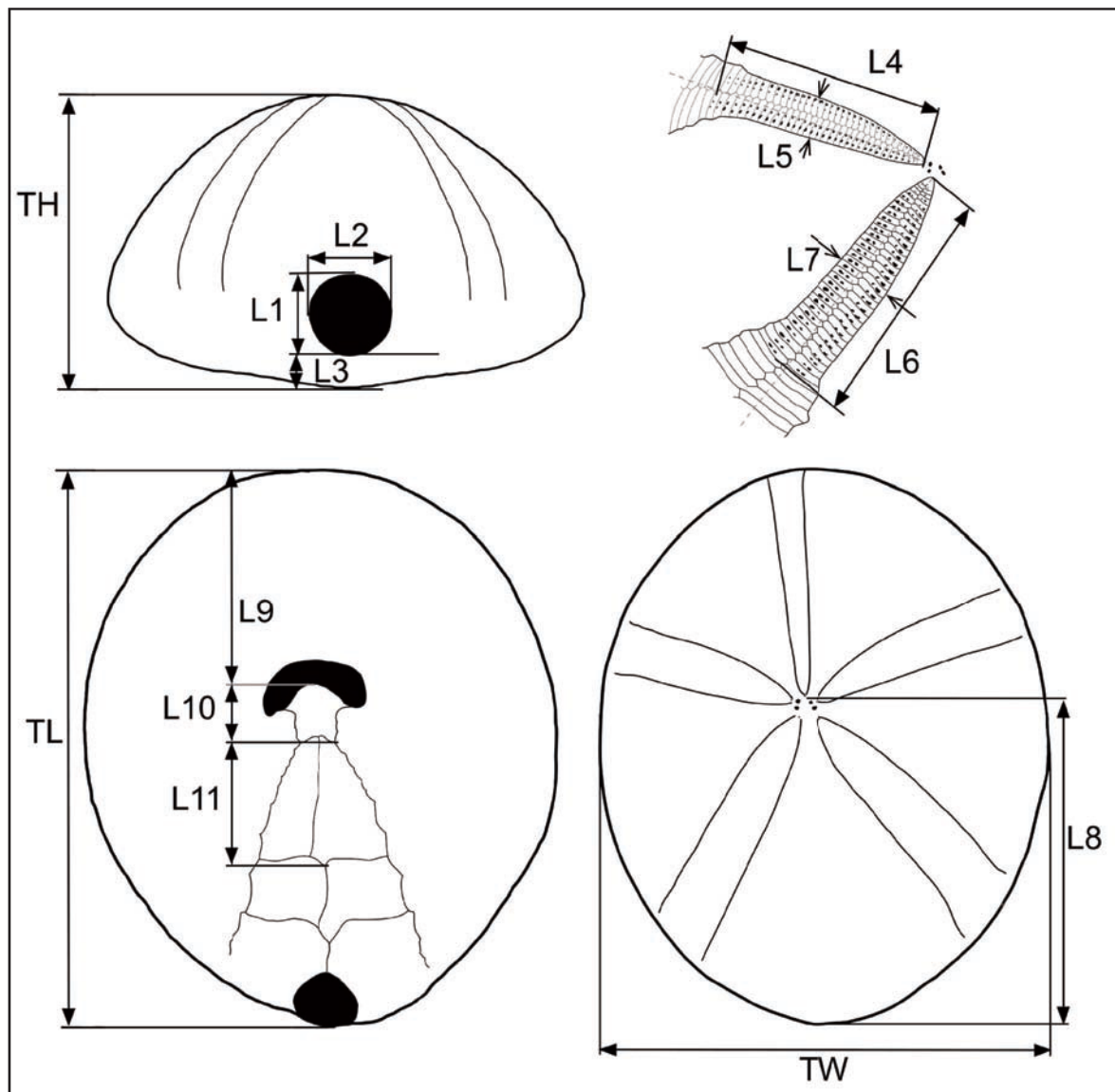


Figure 2. Scheme of the biometric measurements taken from the studied specimens.

<i>Heterobrissus montesi</i>	TL	TW	TH	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11
IGF 101266	116	80				0						33	10.5	25
IGF 101267	102	86.5		10	8	0						28.5	11	22.5
IGF 100345	104	74				0	42.5	10	47	11	56			
IGF 100346	101	77				0	46	10	50	12				
IGF 101268	90	96.5				0								
IGF.100335	86			11.5	11.5	0								
Stefanini (1908) pl. 14, fig. 4	98	90	40				46	10.5	51	12	55			
Stefanini (1908) pl. 14, fig. 5	102	79.5		9	7.5							36.5		
Stefanini (1908) specimen II	123	83.5	40.5			0					56	31		
Stefanini (1908) specimen III	108	85									56.5			
Stefanini (1908) specimen IV	99	89									54.5			
Mean values	102.5	84	40.5	10	9	0	45	10	49.5	11.5	55.5	32.5	11	24
<i>Heterobrissus lubellii</i> sp. nov.	TL	TW	TH	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11
MDLCA 23788	112	77	57	14	12	0	52	13.5	55	17	54	38	11	25
MDLCA 23789	109	84	51				49.5	12	60.5	14	60	38	9.5	22.5
MDLCA 23790	105	92	45			0	55	13	63	14	55	37		
MDLCA 23791	117	90	49	19	12	0		13	56	15	53	36	10	22
MAC PL1504	94	76.5	48	9	7.5	0	53	14	60	16	66	37		
MAC PL1505	103	92	49.5	15.5	14.5	0	45.5	13	66	14.5	53	37	11	
MAC PL1506	108	83	50	16	12.5	0	51	12	54	15	45	35	11	
MAC PL1508	115	80	38	11	11	0	48	12	56	16	53	35	8	25
MAC PL1860	121	77	48	11	9	0	49.5	11	54.5	12	56			
MAC PL1861	115	83	45	12	10	0	49	13	56.5	15	61			25
MAC PL1862	104	90	55			0	55	13	56	13	53	34	9	
MAC PL1864	103	69	47				45	13.5	51	13.5	57	37	11	23
MAC PL1872	110.5	91	47				54	12	61.5	14	61			
MAC PL1873	127	83	32					10		14	53			
MAC PL2095	125	82	36			0	43	11	56	13	65	38.5	11.5	20
MAC PL2096	110		55			0	47	13	55					
MAC PL2097	96	88.5	49	13.5	12.5	0					63	38	10	21
MAC PL2163	91	88	34			0	41	10	52	12	58	37	9	
Mean values	109	84	46	13.5	11	0	49	12.5	57	14	57	37	10	23
<i>Heterobrissus salvae</i>	TL	TW	TH	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11
Holotype MNHN.F.R62327	84	84.5	56	16.5	15.5	5								
LH.01	80	85.5	46			0	45.5	10	46.5	11	62	32.5	10	
LH.04	72	87.5	51				48		51					
CP.01	75	85					46	9	49	10.5				
CP.02	80	80	54	16.5	14.5	2	47.5	9.5	50	10		34		
CP.03	55	85					48.5	9.5	52	11		34	10.5	26
JS.01	75	82	46.5	13.5	16	1	44	10.5	46	11.5	61	32	11.5	27
CG.01	62	86.5		17.5	16	3		10		11	66	31	9	30
MA.01	69	80										34	11.5	26
Mean values	72.5	84	50.5	16	15.5	2	46.5	10	49	11	63	33	10.5	27.5

Table 1. Species of the genus *Heterobrissus* Manzoni et Mazzetti, 1878. Measures of TL in mm, the other biometric data expressed as % of TL.

species	TL	TW	TH	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11
<i>Heterobrissus montesi</i>	102.5	84	40.5	10	9	0	45	10	49.5	11.5	55.5	32.5	11	24
<i>Heterobrissus lubellii</i> sp. nov.	109	84	46	13.5	11	0	49	12.5	57	14	57	37	10	23
<i>Heterobrissus salvae</i>	72.5	84	50.5	16	15.5	2	46.5	10	49	11	63	33	10.5	27.5
<i>Heterobrissus hystrix</i>	127	82	50.5	12.5	13.5	6	-	8	-	9.5	54.5	35	10.5	23
2														
<i>Echinopneustes niasicus</i>	TL	TW	TH	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11
MAC IVM291	121	77.5	53	14	12.5	11	45	10	48.5	7.5	61	43	9.5	22
MAC IVM292	124	80	46	14	12.5	9	43	7.5	46	9	57	44	9.5	23.5
MAC IVM293	105.5	79.5	51	14	12.5	6	50.5	11.5	57	12	51.5	44	10.5	
MAC IVM446	137	80	51	15	11.5	8	46.5	9	46	9.5	53	40	10	21
MAC IVM447	114	80	55	14	14.5	6.5	51.5	11.5	56	11.5	55	42	9	20
MAC IVM448	93	77.5	56	13	13	12	47.5	10	48.5	12	55	43	10.5	21.5
Mean values	116	79	52	14	13	9	47.5	10	50.5	10.5	55.5	42.5	10	21.5
3														

Table 2. Species of the genus *Heterobrissus* Manzoni et Mazzetti, 1878. Mean biometric values in the studied samples. Measures of TL in mm, the other biometric data expressed as % of TL. Table 3. *Echinopneustes niasicus* (Doderlein, 1901), Recent. Indo-Pacific. Measures of TL in mm, the other biometric data expressed as % of TL.

TL. In the plating schemes, the plates are numbered according to Lovén's system (Lovén, 1874), the interambulacral zones are shaded grey, ambulacra unshaded.

Finding localities

The Bismantova Group (Northern Apennines) consists of the Pantano Fm and the Cigarello Fm (Amorosi et al., 1993). The Pantano Fm deposited during the Late Burdigalian-Langhian (Bettelli et al., 1989; Panini et al., 2005). The upper limit with the overlying Cigarello Fm is dated to the Langhian, within the *Praeorbulina glomerosa* zone and the lower part of the *Orbulina suturalis-Globorotalia peripheroronda* zone (Amorosi et al., 1996). Most of the specimens of *Heterobrissus* described in Manzoni (1880) and Stefanini (1908) were collected from siltstones overlying the Calvenzano Member at Jano and San Leo, near Sasso Marconi (Bologna). They belong to the upper part of the Pantano Fm that in that area has been dated to the Langhian and represents the deposition in an outer shelf setting (Panini et al., 2005). Also at Monte

Valestra (Reggio Emilia province) the most frequent lithology consists of grey sandy siltstones, alternating with stratified arenites. The echinoids, commonly deprived of spines and randomly oriented, are rather frequent within the graded arenite, representing low-energy resedimentation events from shallower settings. *Heterobrissus* is commonly associated with *Mazettia pareti* (Manzoni, 1879) and *Toxopatagus italicus* (Manzoni & Mazzetti, 1878) (see Borghi, 2012, 2013 and Stara & Borghi, 2012, for an overview).

The main *Heterobrissus*-bearing deposits examined in Sardinia belong to the Nurallao formation, which is represented at the base by the Duiddure member, made of coarse clasts from transitional (deltaic) environments, and of the overlying marine deposits of the Arenarie di Serralonga member, dated to the Aquitanian-Early Burdigalian (Sowerbutts & Underhill, 1998). At Isili (Cagliari province), four specimens attributed to *H. montesi* were recorded from the upper part (Early Burdigalian) of the Arenarie di Serralonga (Stara et al., 2012); 26 additional specimens have been recently collected from this locality by one of the authors

(P.S.). At Isili, *Heterobrissus* was collected from two different outcrops, located near Baraci and Nuraghe Longu; the second outcrop is stratigraphically lower. At Baraci, *Heterobrissus* is associated with *Sardospatangus*, *Opissaster* sp., *Ova ?karreri* (Laube, 1869); *Ova* sp., *Amusium* sp., *Faorina maullui* Stara et Borghi, 2012; at Nuraghe Longu, with *Sardospatangus*, *Opissaster* sp., *Ova ?karreri*; *Ova* sp., *Mariania comaschicariae* Stara, Borghi et Kroh, 2016; *Faorina orbignyi* (Cotteau, 1877), *Schizobrissus* sp. and *Clypeaster* sp. *Heterobrissus* is present in Sardinia also at Funtanazza, in a Late Oligocene to Late Aquitanian deposit (Annino et al., 2000), belonging to the unit E described in Assorgia et al. (1992), precisely in the Calada Bianca sub area (Late Oligocene to Early Aquitanian) described in Mancosu & Nebelsick (2016), and at Nureci and Genoni, in the Burdigalian-Early Langhian Marne di Gesturi formation (Assorgia et al., 1995).

The holotype of *Pygospatangus salvae* Cotteau (1890) was originally reported from the Eocene of Callosa (Alicante Province, Spain). However, this attribution is doubtful since all subsequent citations of this species were Oligocene in age (López & Sillero, 2006; Smith & Kroh, 2011). Also the specimens under study from Monteagudo, near Novelda (Alicante, Spain), were collected from sediments dated by micropaleontological analyses (Azema et al., 1969) to the Late Oligocene (Chatian), possibly also to the Early Aquitanian. The sediments, consisting of limestones alternating with marls, belong to the transgressive phase occurred at the Oligocene-Miocene boundary (Mapa Geológico de España, 1:50000, sheets 848 and 871).

RESULTS

The study of the fossil material of *H. montesi* from the type-area enables to describe previously unknown morphological features in the type-species, thus completing the list of the diagnostic characters in the type-species of the genus *Heterobrissus*. The specimens examined from the Early Miocene of Sardinia share the distinctive features listed in the following and, since they are better preserved on average, some illustrations are taken from them.

- Test ovate in outline with convex anterior and weakly pointed posterior (Fig. 3).

- Shell rather thin aborally; the plastron and the ambitus are more robust, with a maximum thickness of about 2–3 mm in correspondence of the sternal plates and around the periproct.

- Posterior face short and undercut, sometimes almost facing downwards (Figs. 9, 14).

- The apical system is ethmolytic, with four gonopores, the anterior pores placed closer to one another than the posterior pair. It corresponds to the scheme provided by Mortensen (1950, fig. 147) for *Archaeopneustes hystrix*.

- Frontal ambulacrum flush over the aboral surface, becoming slightly depressed only as it approaches the peristome; the pores are double in the upper part of the ambulacrum, farther down they are reduced to a narrow slit (Fig. 12).

- No occluded plates are present at the end of the paired petals (Fig. 10).

- Pores in the outer columns drop-shaped and larger than those in the inner columns (Fig. 11).

- Adorally, the ambulacra are strongly developed into conspicuous phyllodes (Figs. 8, 13): there are 7–8 unipores with a large periporal area in each column of the ambulacrum III, 10–12 in the lateral ambulacra II and IV (Fig. 13).

- The labral plate extends to half-way along the third plate in the adjacent ambulacral columns (Figs. 13, 19).

- Sternal, episternal and post episternal plates almost symmetrical, opposite rather than alternate and not indented by the ambulacral plates. The sternals extend to the adjoining ambulacral plates 9–10. Plates 5.a.4 and 5.b.4 are “L” shaped (Figs. 4, 13, 19).

- The structure of the plates in the oral interambulacra 1, 2, 3, 4 is amphiplacous. (Figs. 4, 13).

- Periproct inframarginal to almost oral (Figs. 4, 9, 14), framed by the plates 5.a.4, 5.b.4 to 5.a.7, 5.b.7 (Figs. 4, 13, 19).

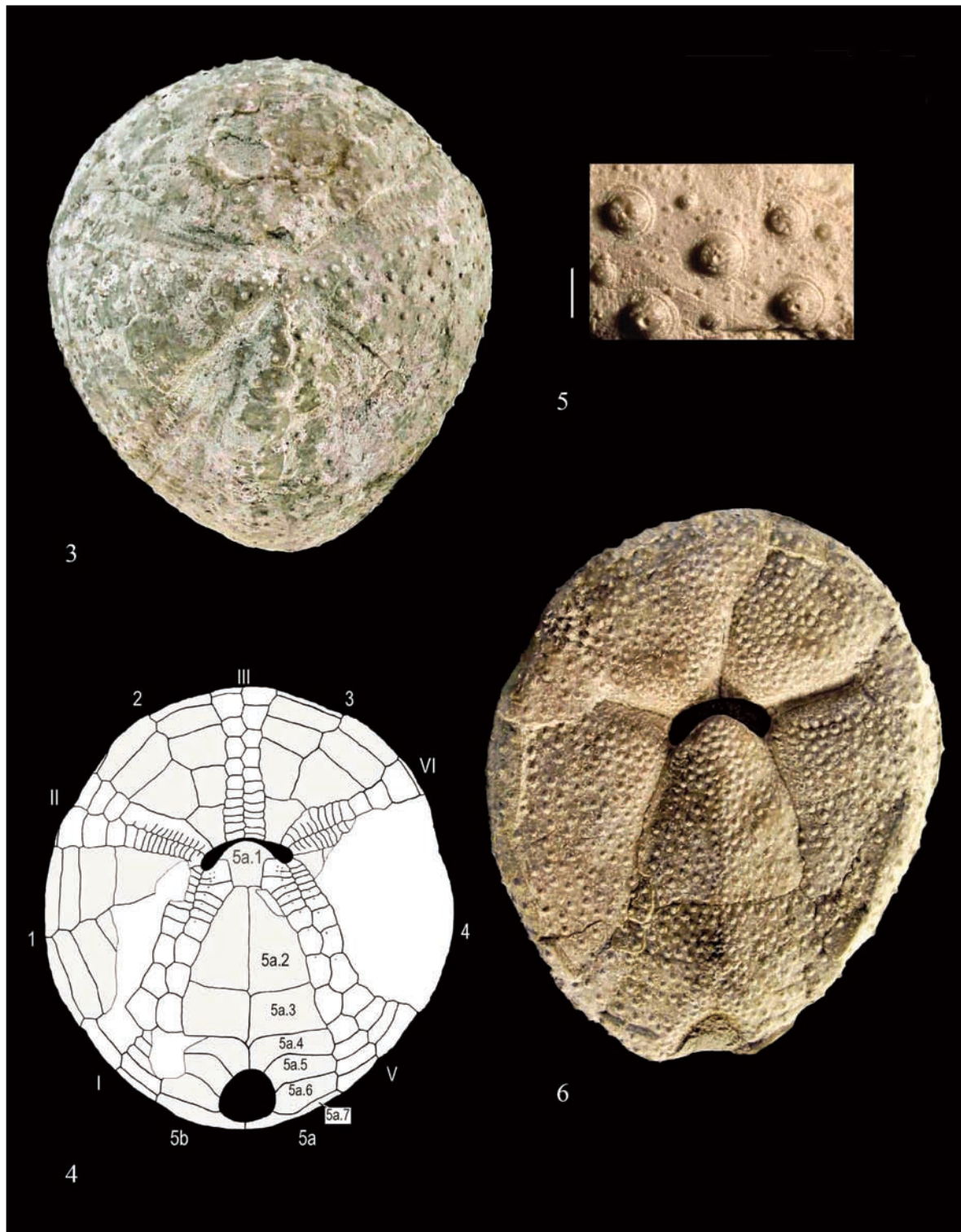
- Primary spines finely striate longitudinally, with a hollow lumen and circular section.

- Fascioles absent (at least in all the specimens with TL > 38 mm).

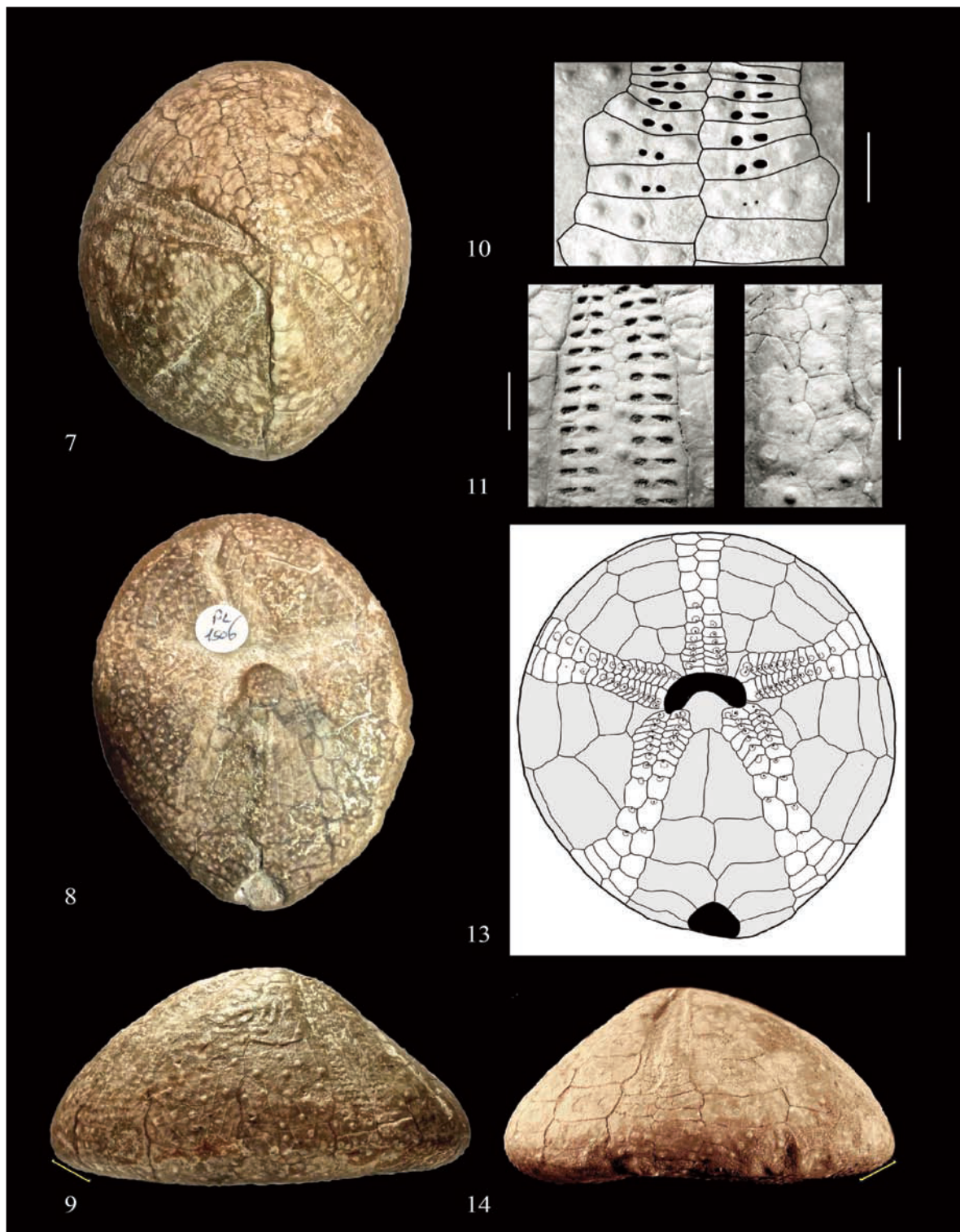
DISCUSSION

The sample from Sardinia

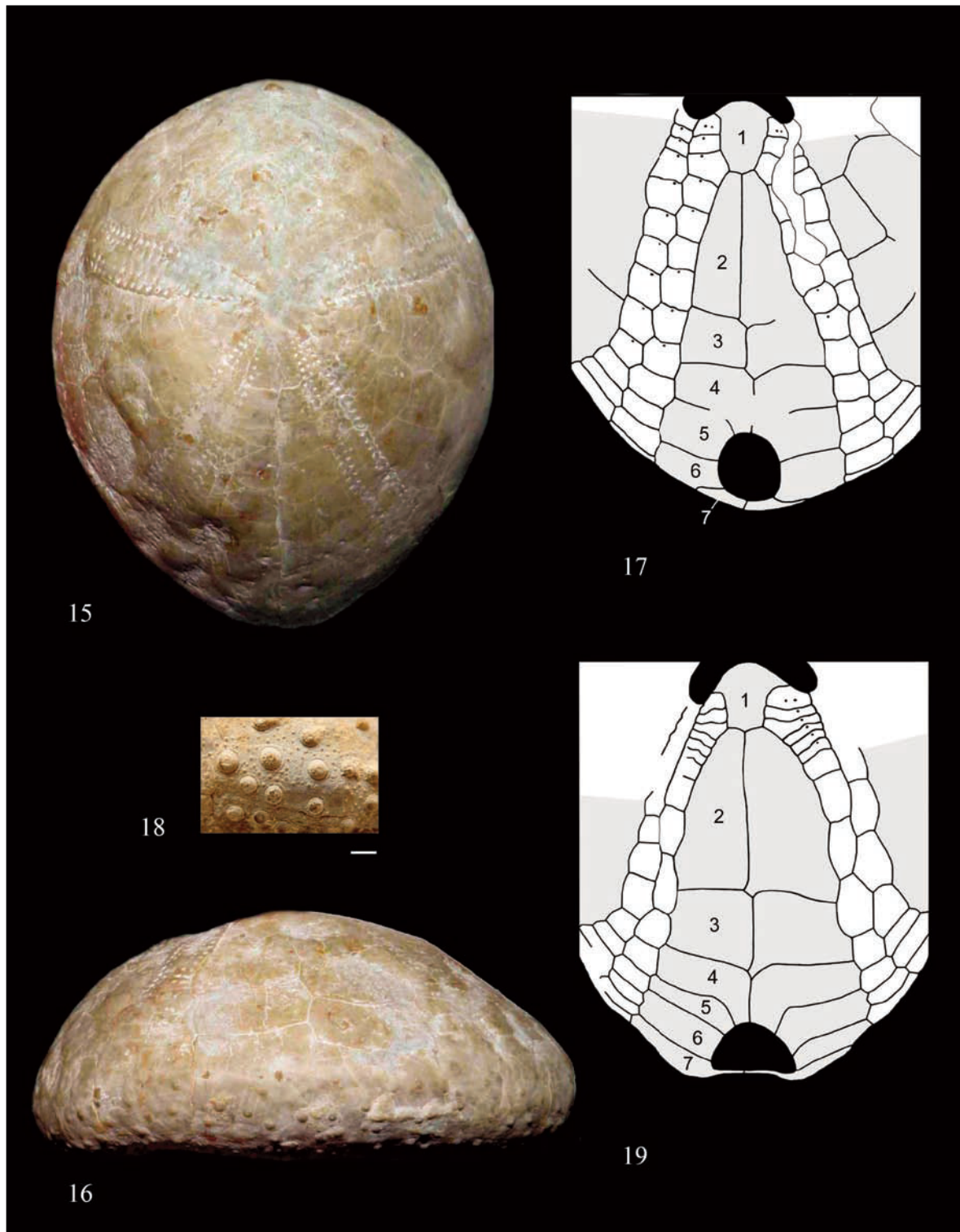
As seen above, the specimens examined from the Early Miocene of Sardinia share all the main



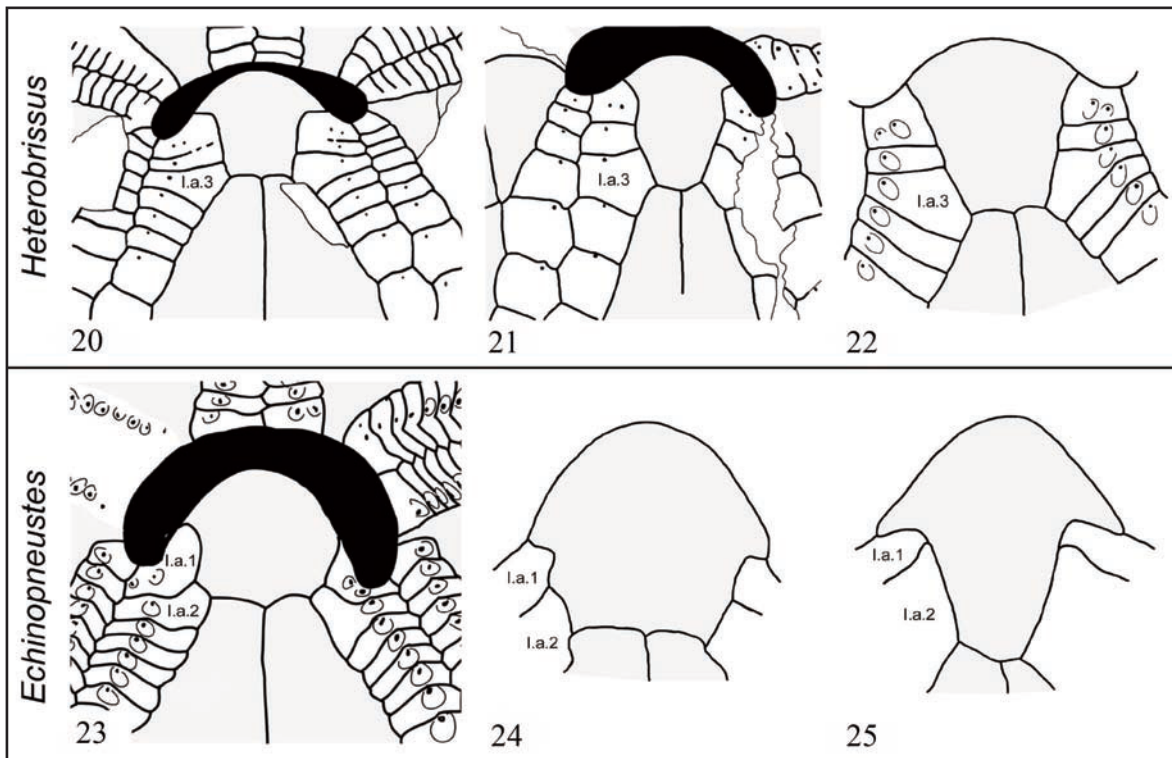
Figures 3–6. *Heterobrissus montesi* Manzoni et Mazzetti, 1878, Langhian of Emilia-Romagna. Fig. 3: aboral view of IGF.104267, a specimen figured in Stefanini (1908, pl. 14, figs. 4a,b), TL = 98 mm, Jano (Bologna). Fig. 4: oral plating diagram taken from IGF.100335, Jano. Fig. 5: close up of the primary tubercles at the ambitus in the aboral interambulacrum 4, taken from IGF.101267, Monte Valestra (Reggio Emilia). Fig. 6: oral view of IGF.101266, TL = 116 mm, Monte Valestra. The scale bar equals 1 mm.



Figures 7–14. *Heterobrissus lubellii* n. sp., Early Miocene of Sardinia. Figs. 7–9: respectively aboral, oral and lateral views of the holotype (MDLCA.23788), TL = 112 mm, Burdigalian, Isili. Figs 10–12: MAC.PL1505, Burdigalian, Isili: close up view of the tip of a petal (Fig. 10), of the mid part of the aboral ambulacrum IV (Fig. 11) and of the frontal ambulacrum III (Fig. 12); the scale bars equal 5 mm. Fig. 13: oral plating diagram of MAC.PL2097, Early Burdigalian, Baraci. Fig. 14: lateral view of MAC.PL1504, TL = 94 mm, Burdigalian of Isili; the yellow bars indicate the position of the periproct in lateral view.



Figures 15–18. *Heterobrissus salvae* (Cotteau, 1890), Late Oligocene of Monteagudo, near Novelda (Spain). Figs. 15–16: aboral and lateral views of LH.02, TL = 95 mm. Fig. 17: plastron plating in JS.01. Fig. 18: close up of primary tubercles in the aboral interambulacrum 4 at the ambitus, in CG.01. The scale bar equals 1 mm. Figure 19. *Heterobrissus montesi* Manzoni et Mazzetti, 1878: plastron plating taken from IGF.101266, TL = 116 mm, Langhian of Monte Valestra, near Reggio Emilia.



Figures 20–25. Plating schemes of the peristome area highlighting the extension of the labrum. Fig. 20: *Heterobrissus montesi* Manzoni et Mazzetti, 1878; Fig. 21: *Heterobrissus salvae* (Cotteau, 1890); Fig. 22: *Heterobrissus hystrix* (Agassiz, 1880), from Mortensen (1950); Fig. 23: *Echinopneustes niasicus* (Doderlein, 1901); Fig. 24: *Echinopneustes gigas* (Baker et Rowe, 1990); Fig. 25: *Echinopneustes erinaceus* (Baker et Rowe, 1990).

morphological features with the fossils from the Northern Apennines. Stara et al. (2012) assigned eight specimens from Baraci to *Heterobrissus montesi*. However, the availability for this study of a better preserved sample from a stratigraphically more differentiated area showed that the specimens from Sardinia differ from *H. montesi* by longer and larger petals, peristome farther from the anterior margin of the test, larger periproct and more elevate test (Table 2). Therefore, they are herein assigned to a new species, *Heterobrissus lubellii* n. sp.

Comparison with other genera

Gregory (1892) based the genus *Archaeopneustes* on the Recent species *Palaeopneustes hystrix* A. Agassiz, 1880 (Figs. 27, 31) without considering its differentiation from the pre-existing genus *Heterobrissus* Manzoni et Mazzetti, 1878.

The distinction of *Archaeopneustes* was confirmed by Mortensen (1950): “the labrum extending

to the third adjoining ambulacral plate, not to the second as in *Heterobrissus*”, and by a slightly more inframarginal periproct. But the plate structure in *H. montesi* was still unknown at that time, as well as the apical system (Stefanini, 1908). Mortensen (1950) based his concept of *Heterobrissus* on an Indo-Pacific species, *H. niasicus*, which differs from the western Atlantic *A. hystrix* in the ways described. The topo-typic material under study indicates that *H. montesi* has an inframarginal periproct and an elongate labrum that extends to the third ambulacral plate, thus sharing the main diagnostic features of *Archaeopneustes* and confirming the synonymy of the two genera, as already suggested by Smith & Gale (2009) and Kroh & Mooi (2019).

Mortensen (1950, p. 200) affirmed also that “If the character of the labrum (in *H. montesi*) should prove ultimately to agree with *Archaeopneustes hystrix*, then I do not see how it could be avoided to regard *Archaeopneustes* as a synonym of *Heterobrissus*, but it might then be desirable to create

a new genus for the species *niasicus*...". According to this sentence, *H. niasicus* (Döderlein, 1901) is here transferred into *Echinopneustes* n. gen. The main morphological characters distinguishing *Echinopneustes* from *Heterobrissus* are (Table 4): the labrum reaching only the middle plate 2 of the adjoining ambulacra (Fig. 23), not plate 3 as in *Heterobrissus* (Figs. 20, 22); the peristome farther from the anterior test margin (mean $L9 > 38\% TL$); periproct marginal (Figs. 30, 37; mean $L3 \geq 9\% TL$), commonly not visible in oral view (Figs. 28, 35) and bounded by the fifth plates in the interambulacrum 5, whereas the periproct is inframarginal to almost oral ($L3 \leq 6\% TL$) and framed adorally by the fourth plates, in *Heterobrissus*. Additionally, in *Echinopneustes* gen. nov. the test outline is commonly less constricted posteriorly (Figs. 28, 35) and the posterior face is not, or only slightly, undercut (Fig. 36). *Heterobrissus erinaceus* Baker et Rowe, 1990 and *H. gigas* Baker et Rowe, 1990 share these diagnostic characters (Figs. 24–25) with *E. niasicus*, consequently, they are transferred into the new genus. After Kohler (1914) in *H. hemingi* (Anderson, 1902) the labrum extends only "to the margin of the first adjoining ambulacral plate"; however, since Kohler did not provide a scheme and no specimens are available to study this rare species, its generic attribution is left open.

Mortensen (1950) noticed that in *E. niasicus* the primary spines are flattened and densely thorny and the ophicephalous pedicellariae are numerous, while in *H. hystrix* the primary spines are smooth and roundish and ophicephalous valves are lacking. However, spines in *Echinopneustes* are heterogeneous, since *E. erinaceus* has numerous fine and short spines and even in *E. niasicus* the spines may have sometimes a roundish section, with fine thorns. The difference regarding the ophicephalous pedicellariae is valid for the extant species belonging to these two genera (including also *E. erinaceus* and *E. gigas*, Table 4), but these minute morphological particulars are not preserved in the fossil material thus preventing comparison.

Pygospatagus Cotteau, 1890 is similar to *Heterobrissus*, but relevant characters of the oral face and the apical disc in the type species have so far remained unknown (Smith & Kroh, 2011). Newly reported material from the Oligocene of Novelda (Spain; Figs. 15–17, 18, 21, 29, 33) allows to illustrate the structure of the plastron (Fig. 17), which was not visible in the holotype (MHNM R62327), the sole specimen described by Cotteau (1890: p. 17, pl. 14, fig. 13). The test outline is ovate with convex anterior and weakly pointed posterior (Figs. 15, 29). The oral face is flat, the

Morphological characters	<i>Heterobrissus</i>				<i>Echinopneustes</i>		
	<i>montesi</i>	<i>hystrix</i>	<i>salvae</i>	<i>tubellii</i> sp. nov.	<i>niasicus</i>	<i>erinaceus</i>	<i>gigas</i>
Labral plate extending to the ambulacral plate 2					2	2	2
“ “ “ “ plate 3	3	3	3	3			
Distance of the peristome from the anterior margin:							
mean $L9 > 38\% TL$					42.5	38.7	38.3
mean $L9 < 37\% TL$	32.5	35	33	37			
Periproct marginal, mean $L3 \geq 9\% TL$					9	x	x
“ inframarginal, mean $L3 \leq 6\% TL$	0	6	2	0			
Periproct bounded adorally by plates 5.a.5 and 5.b.5					x		
“ “ “ “ 4.a.4 and 4.b.4	x	x	x	x			
Ophicephalous pedicellariae present					x	x	x
“ “ “ “ absent		x					

Table 4. Main morphological features distinguishing the genus *Heterobrissus* Manzoni et Mazzetti, 1878 from *Echinopneustes* n. gen.

apical disc is ethmolytic and corresponds to the scheme provided by Lopez & Sillero (2006; figs. 241 B–C), the labral plate always extends to the third adjacent ambulacral plate (Fig. 21), the oral interambulacra 1–4 are amphiplacous; the oral plates 5.a.4 and 5.b.4 are “L” shaped (Fig. 17). Aborally, in the lateral ambulacra the pore-pairs terminate 3–4 plates above the ambitus and no occluded plates are present distally. The pore-pairs in the ambulacrum III are small and subcircular adapically, elsewhere the pores are in form of small single oblique slits. The pores of the outer columns in the paired ambulacra are drop-shaped and larger than those of the inner columns. Fascioles are absent (Lopez & Sillero, 2006). The peristome is lunate and rather close to the anterior test margin (Fig. 29; range L9 = 31–34% TL). The periproct is rather large, occupying most of the short and undercut posterior face (Fig. 33). It is marginal, well visible in oral view (Fig. 29) and bounded by four plates on each side (5.a.4 to 5.a.7 and 5.b.4 to 5.b.7; Fig. 17). The oral ambulacra do not indent the posterior interambulacrum. The tuberculation is coarse and heterogeneous and consists of scrobiculate, perforate and crenulate primary and secondary (rare) tubercles and numerous miliars (Fig. 18). Primary spines are slender and longitudinally finely striate; they are 10–15 mm long in a specimen (CG.03) with TL = 60 mm. All these features match with those in *H. montesi*. The test in the holotype of *P. salvae* is very thick (up to 8–9 mm), as illustrated in Smith & Kroh (2011). However, in all the other specimens under study the test is relatively thin aborally and, although the thickness increases adorally particularly in the plastron and around the periproct, it is not very different from that in *Heterobrissus montesi*. *Pygospatangus salvae* differs from *H. montesi* also by the plates in the proximal part of the oral ambulacra I and V, that are longer and, as a consequence, the sternal plates extend only to the ambulacral plates 7–8, not to the plates 9–10 as in *H. montesi* (compare Figs. 17–19). The oral posterior ambulacra lack large primary tubercles from the peristome almost to the margin; however, some specimens of *H. montesi* from the type-area (e.g., IGF.100335) and from Cyprus share the same feature. These differences point to a distinction only at the specific level, consequently this species is here renamed *Heterobrissus salvae* (Cotteau, 1890), new combination.

Antillaster Lambert, 1909 is known from the Eocene to Miocene of the Caribbean and the Eocene of the Caucasian area (McNamara et al., 2002). The type-species, *A. cubensis* Cotteau, 1871, has only 3 gonopores. Kier (1984) revised this genus and separated it into two informal “groups”, “pointing to the occurrence of a number of intermediate forms. The oldest group (Eocene-Oligocene) is morphologically more similar to *Heterobrissus* and shares the presence of four gonopores and the shape of the phylloides. However, the species belonging to this group differ from *H. montesi* by a more depressed test, oral face convex, not flat, narrower petals extending farther towards the test edge and a different position of the periproct. Occluded plates are always present at the end of the paired petals in all the species of *Antillaster* in which the plate sutures are visible (Kier, 1984), whereas they are absent in *H. montesi* and in *H. salvae*.

The genus *Brissolampas* Pomel, 1883 was based on *Palaeopneustes conicus* Dames, 1877, from the Aquitanian of Veneto (Northern Italy). The main characters stated for this species match with those in *Heterobrissus* but the ambulacrum III is described as “petaloid”. Since the sole specimen so far known of this species (Dames, 1877: p. 47, pl. 8, fig. 1) has the frontal ambulacrum only partially visible, new topotypic material is needed to confirm the separation of this genus from *Heterobrissus*.

Systematic placement of *Heterobrissus* and *Echinopneustes* n. gen.

On account of the ethmolytic apical disc, the petaloid ambulacra (at least adapically) and the amphisternous plastron, *Heterobrissus* and *Echinopneustes* are members of the order Spatangoida. Earlier studies attributed *Heterobrissus* to various families. Mortensen (1950) suggested that *Heterobrissus*, *Archaeopneustes* and *Pygospatangus* should be placed under the *Palaeopneustidae*. Later on, *Heterobrissus* and *Pygospatangus* were placed into the Asterostomatina by Fischer (1966). However, the grouping together of spatangoid taxa that lack fascioles as adults into Mortensen’s *Palaeopneustidae* or Fischer’s Asterostomatina has historically been regarded as unsatisfactory (Fischer, 1966; Chesher, 1968). In particular, the attribution to the Asterostomatidae was strongly rejected by the

results of the cladistic analysis in Stockley et al. (2005, fig. 1): the polyphyletic arrangement of the fasciole-less “asterostomatids” highlighted by both molecular and morphological analyses strongly implied that there were multiple origins for these deep-sea spatangoids. Only a few genera originally attributed to the paleopneustids by Mortensen (1950) are today retained in this family (Smith & Kroh 2011). The Paleopneustidae appear to represent a small clade basal to prenasterids and schizasterids (Stockley et al., 2005; Kroh & Smith 2010); they are characterized by the lack of a frontal groove, long labral plate extending to the third or fourth ambulacral plate and marginal and/or peripetalous fascioles, at least in juveniles. After Smith & Kroh (2011) these characters fit well with *Heterobrissus* and *Pygospatangus*, which were included in the “*Paleopneustina* Incertae sedis B”. Kroh & Mooi (2019) actually confirm this location, accepting it as a “temporary name”.

One of the major problems in firmly reconstructing relationships between spatangoida lacking fascioles, just as *Heterobrissus* and *Echinopneustes*, is the common occurrence of secondary loss of fascioles in adults. Many deep-sea groups appear to have undergone secondary morphological simplification involving the loss of fascioles and/or reduction or complete loss of petals. In fact, fascioles are essential structures for an infaunal mode of life, but they serve no purpose in epibenthic species and are therefore commonly lost in deep sea forms. The absence of petals and fascioles is commonly interpreted as plesiomorphic, but when additional data are available, including the fasciole bearing in juveniles, such absence is recognized as being secondary reversals and a different topology results in cladistic analyses (Stockley et al., 2005). Recent analyses, such as Kroh & Smith (2010) and Kroh in Stara et al. (2016), based on the matrix proposed by Stockley et al. (2005, p. 21-22), under exclusion of the fasciole characters, resulted in a largely unresolved tree and failed to conclusively resolve the systematic placement of *Heterobrissus* (represented in the analysis by *H. hystrix*). To fully resolve the placement of *Heterobrissus*, *Echinopneustes* and several other atelostomates, additional data on ontogenetic development of fascioles is needed. Unfortunately, no information about the presence of fascioles in juveniles is so far available for the genera under study.

SYSTEMATIC PALEONTOLOGY

Superordo ATELOSTOMATA von Zittel, 1879

Ordo SPATANGOIDA L. Agassiz, 1840

Subordo PALEOPNEUSTINA Markov et Solovjev, 2001

Familia PALEOPNEUSTINA incertae sedis B (Smith et Kroh, 2011)

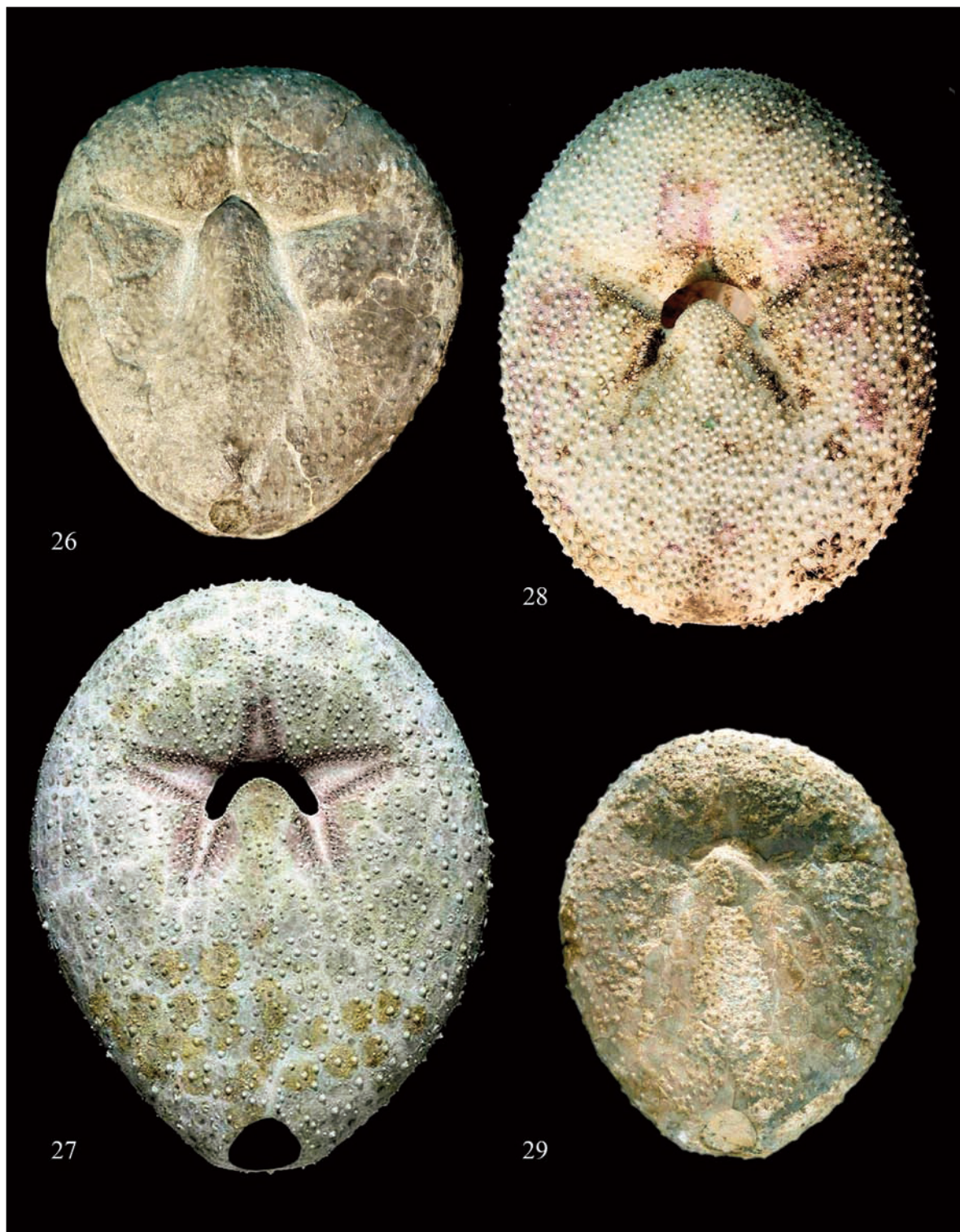
Genus *Heterobrissus* Manzoni et Mazzetti, 1878

Heterobrissus Manzoni & Mazzetti, 1878, p. 354, by original designation. [= *Pygospatangus* Cotteau, 1890, p. 17, type species *Pygospatangus salvae* Cotteau, 1890, p. 17; = *Archaeopneustes* Gregory, 1892, p. 163, type species *Paleopneustes hystrix* Agassiz, 1880].

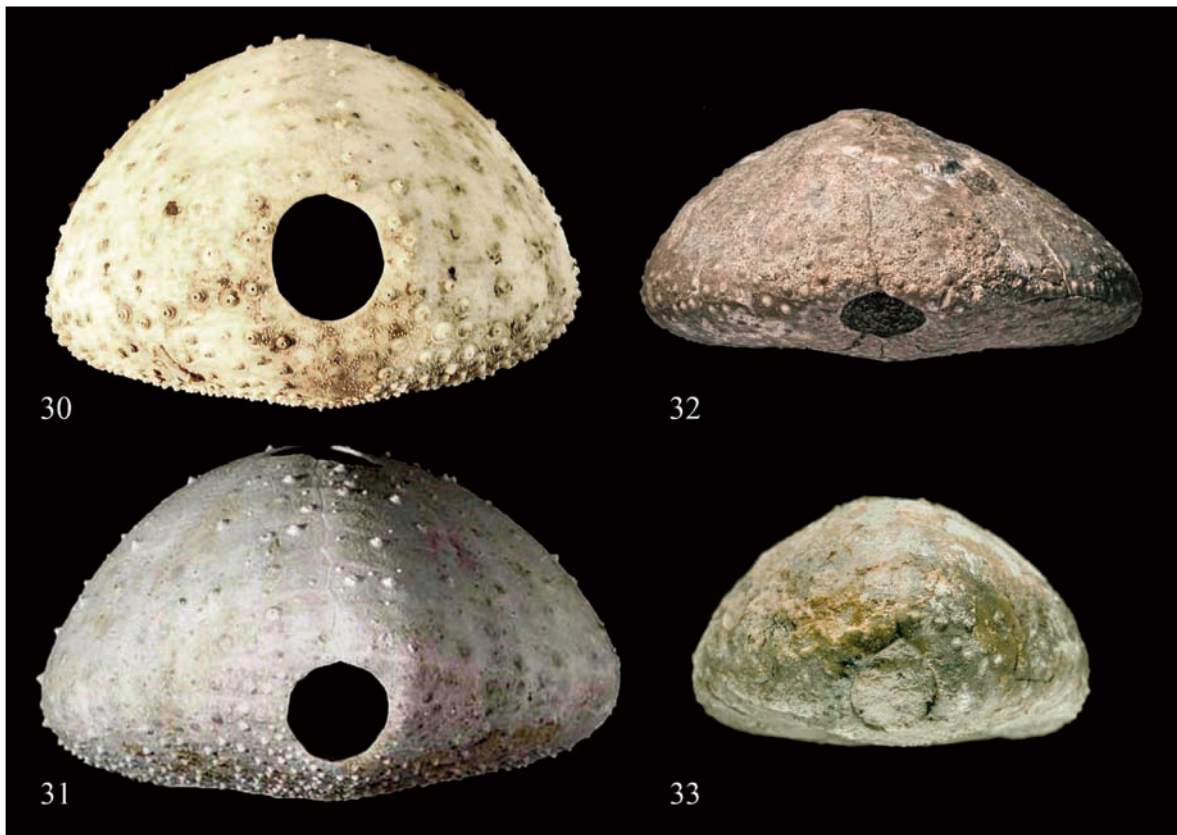
TYPE SPECIES. *Heterobrissus montesi* Manzoni & Mazzetti, 1878, p. 354.

DIAGNOSIS. Test ovate without anterior sulcus; anterior convex, posterior face short, truncate and undercut. Test domed in profile, with flat base. Apical disc ethmolytic, with four gonopores, a little anterior of centre. Anterior ambulacrum narrow, flush; pore-pairs minute adapically, elsewhere in form of small single oblique slits. Paired ambulacra flush, petaloid adapically, almost parallel-sided and largely open distally; enlarged pore-pairs extending almost to ambitus. No occluded plates at the end of the petals. Peristome lunate, facing forward into frontal groove, with rather projecting labrum. The labral plate extends to the adjacent ambulacral plates 3. Perioral area sunken. Phyllodes well developed. Sternal, episternal and post episternal plates almost symmetrical, opposite rather than alternate and not indented by the adjacent ambulacral plates. Periproct inframarginal to almost oral, well visible in oral view; adorally it is bounded by the plates 5.a.4 and 5.b.4. Fascioles absent, at least in all the examined specimens with TL > 38 mm. Aboral tuberculation coarse and heterogeneous, made of scrobiculate, perforate and crenulate primary and (rare) secondary tubercles and numerous granules. Posterior ambulacra on oral surface covered in tubercles behind phyllodes. Partially modified from Smith & Kroh (2011).

SPECIES INCLUDED. • *H. montesi* Manzoni & Mazzetti, 1878; Langhian, Italy; Serravallian, Cyprus.



Figures 26–29. Oral face views. Fig. 26: *Heterobrissus montesi* Manzoni et Mazzetti, 1878 (IGF.101267, TL = 102 mm), Langhian, Monte Valestra, near Reggio Emilia. Fig. 27: *Heterobrissus hystrix* (Agassiz, 1880), MCZ ECH-7813, TL = 127 mm, Recent, off Florida. Fig. 28: *Echinopneustes niasicus* (Doderlein, 1901), MAC.IVM210, TL = 124 mm, Recent, Southern China Sea. Fig. 29: *Heterobrissus salvae* (Cotteau, 1890), CG.01, TL = 62 mm, Late Oligocene of Monteagudo, near Novelda (Spain).



Figures 30–33. Posterior face views. Fig. 30: *Echinopneustes niasicus* (Doderlein, 1901), MAC.IVM292, TL = 124 mm, Recent, Southern China Sea. Fig. 31: *Heterobrissus hystrix* (Agassiz, 1880), MCZ ECH-7813, TL = 127 mm, Recent, Florida. Fig. 32: *Heterobrissus lubellii* n. sp. (MAC.PL1506a, TL = 113 mm), Burdigalian, Isili (Sardinia). Fig. 33: *Heterobrissus salvae* (Cotteau, 1890), CG.01, TL = 84 mm, Oligocene, Monteagudo, near Novelda (Spain).

- *H. hystrix* (Agassiz, 1880): Recent, Caribbean.
- *H. salvae* (Cotteau, 1890); ?Eocene and Late Oligocene (Chattian), Spain.
- *H. lubellii* n. sp., Late Oligocene-Early Aquitanian and Burdigalian, Sardinia (Italy).

DISTRIBUTION. ?Eocene and Late Oligocene of Spain; Late Aquitanian to Langhian of Italy; Serravallian of Cyprus. Recent, Caribbean.

Heterobrissus montesi Manzoni et Mazzetti, 1878 - Figs. 3–6, 19, 20, 26

1878 - *Heterobrissus Montesi* Manzoni & Mazzetti, 354–355, pl. 19, fig. 2.

1879 - *Heterobrissus Montesi* Manzoni & Mazzetti - Manzoni, 162.

1880 - *Heterobrissus Montesi* Manzoni & Mazzetti - Manzoni, 189, pl. 3, figs. 24–26.

1881 - *Heterobrissus Montesii* Manzoni & Mazzetti - Mazzetti, 10.

1901 - *Heterobrissus Formai* Airaghi, 210, pl. 26, fig. 6 (fide Stefanini, 1908).

1908 - *Heterobrissus Montesii* Manzoni & Mazzetti - Stefanini, 95–97, pl. 14, figs. 4–5, pl. 15, fig. 1.

1935 - *Heterobrissus cypriotes* Currie, 32, pl. 3, fig. 1.

2009 - *Heterobrissus montesi* Manzoni & Mazzetti - Smith & Gale, 123–124, figs. 6–8.

2012 - *Heterobrissus montesi* Manzoni & Mazzetti - Stara et al., 36, pl. 3, fig. 1a–c.

TYPE MATERIAL. The holotype, from Montese (Modena), is missing; it was poorly preserved and the oral face was not visible (Manzoni & Mazzetti, 1878, pl. 19, fig. 2). After Stefanini (1908), the holotype and the other specimens figured in Manzoni (1880: pl. 3, figs. 24–26) were already missing at that time.

TYPE LOCALITY. Montese (Province of Modena), Langhian, Pantano Formation.

OTHER EXAMINED MATERIAL. Twelve specimens from Jano, near Sasso Marconi (Province of Bologna) housed at the IGF, including the two figured in Stefanini (1908, pl. 14, figs. 4 and 5) and those reported in his description as “specimens II, III and IV”. Five specimens from Monte Valestra, Province of Reggio Emilia (IGF.101266-7, IGF.100345-6), and one from Pescale, Province of Modena (IGF.101268). All of them from the Langhian, Pantano Formation.

DESCRIPTION. Large sized species (TL up to 123 mm). Test longitudinally elongate (mean TW = 84% TL) and more or less constricted posteriorly, with maximum width in front of mid-length (Fig. 3). Test with low domal upper surface and flat oral face, sinking towards the peristome (Fig. 6). Posterior face short and undercut, sometimes almost facing downwards. Test height variable (mean TH = about 40.5% TL). Ambitus low with rounded margin.

Apical disc - Small, slightly anterior to centre (mean L8 = 55.5% TL), ethmolytic; it has four gonopores, the anteriors are placed closer together than the posteriors.

Ambulacra - Ambulacrum III narrow, flush over the aboral surface (Fig. 3), slightly depressed only as it approaches the peristome (Fig. 26). Adapically there are minute pore pairs; then, starting from the sixth-tenth plate, each plate bears a small slit-like unipore oriented almost vertical to the lower suture, as in *H. hystrix* (compare Mortensen, 1950, fig. 146b); these pores become lost towards the ambitus. Paired ambulacra petaloid adapically, almost flush, only slightly depressed in their upper half; they extend, slightly diverging, almost to the ambitus, remaining open distally. Pore-pairs become slightly smaller towards the end, where no occluded plates are present. In the anterior paired petals the anterior columns of pore-pairs are smaller than those in the posterior columns as they approach the apex. Pore-pairs are drop-shaped isopores, with a narrow, flush interporal zone. Anterior paired petals (mean L4 = 45% TL, L5 = 10% TL) slightly flexed to the anterior and diverging from each other at about 130°. Posterior petals longer (mean: L6 = 49.5% TL, L7 = 11.5% TL), more or less straight and diverging at about 65°. Adorally, the paired ambulacra enlarge and plating becomes crowded as they approach the

peristome. Phyllodes well developed, with 6-8 pores in a column in the posterior and the anterior ambulacra and 10-12 in the lateral ambulacra. The pores are single in the phyllodes. There are no enlarged subanal pores.

Interambulacra - Slightly inflated adapically (Fig. 3).

Plastron - Plastron not raised. The labrum strongly indents the peristome (Figs. 6, 26). Labral plate wedge-shaped, with convex surface and always extending to halfway along the third plate in the adjacent ambulacra (Fig. 20). Sternum almost as long as wide, with sternal plates symmetrical and extending to plate 9-10 in the adjacent ambulacral columns (Figs. 4, 19). Episternal plates also paired and about half as long as the sternal plates. Plates 5.a.4 and 5.b.4 weakly offset, “L” shaped and forming the oral border of the periproct. Ambulacral plates do not indent the Interambulacrum 5. All other interambulacra amphiplacous. In the interambulacra 1 and 4 the plates a.5 and b.5 or the a.6. and b.6 form the ambitus.

Peristome - Sunken, lunate, much wider than long and eccentric anteriorly (mean L9 = 32.5% TL, range 28.5–36.5% TL).

Periproct - Inframarginal to almost oral and framed by plates 5.a.4, 5.b.4 to 5.a.7, 5.b.7. (Figs. 4, 26); it is rather small and slightly longitudinally elongate (mean L1 = 10% TL, L2 = 9% TL).

Tuberculation - Primary tubercles scrobiculate, perforate and crenulate (Fig. 5), scattered over the entire aboral face; they become denser approaching the apex and along the mid-line of the posterior interambulacrum. All plates have a covering of sparse miliary granules and occasional smaller tubercles. A few small tubercles also occur within the petals and the frontal ambulacrum. The oral face is fully covered by smaller and denser primary tubercles, including the labral plate and the plastron (Fig. 6). Ambulacral zones have almost identical tuberculation to that in the interambulacral zones, with scattered primary tubercles, except in the phyllodes.

Spines - Primary spines are almost straight aborally, slightly curved in the oral side, some 20–25 mm long in adults with TL = 70–90 mm; they are longitudinally finely striate with a subcircular section and a hollow lumen.

Fascioles - Absent also in well preserved adult specimens. According to Mortensen (1950), the absence of an adproctal widening of the plates in the

ambulacra I.a and V.b adjoining the episternal plates typically confirms the absence of a subanal fasciole.

REMARKS. The morphological variability includes: test more or less posteriorly constricted and elevated, labrum more or less projecting over the peristome. In the smallest specimens under study (TL 38–50 mm) the test outline is sometimes less elongated (Fig. 4), the margin is more inflated, the tuberculation may be less dense and the labrum less projecting over the peristome (Stefanini, 1908).

Heterobrissus salvae (Cotteau, 1890) differs by the plates in the proximal part of the oral ambulacra I and V, that are longer and, as a consequence, the sternal plates extend only to the ambulacral plates 7–8, not to the plates 9–10 as in *H. montesi*. Additionally, the shell is thicker.

Archaeopneustes abruptus Gregory, 1892, from the Oceanic series of Bissex Hill (Barbados) is represented by a sole specimen of uncertain age (Gregory, 1892). Although not completely preserved, the holotype shows closer affinity to the genus *Antillaster* Lambert, 1909 based on test profile and petal shape. Indeed, it was assigned to *Antillaster* by Lambert & Thiery (1924) and Mortensen (1950). It differs from *H. montesi* also by the anterior paired petals much more diverging (at almost 180°) and extending farther towards the ambitus, by “V” shaped aboral plates and less projecting labrum.

Heterobrissus formai Airaghi, 1901, from Pino Torinese (Piedmont, Italy), was distinguished mainly by the scarcity of the primary tubercles on the aboral surface. Based on the available information (Airaghi, 1901), the holotype and only known specimen of this species was collected from the Baldissero Formation (Langhian). The holotype was lost in 1943 (personal communication, D. Ormezzano, MTPL, June 2007) and no other specimens have been subsequently recorded from that area. Stefanini (1908) had the opportunity of examining the type and affirmed that the lack of primary tubercles was due to abrasion; consequently he considered *H. formai* as a junior synonym of *H. montesi*.

Heterobrissus cypriotes Currie, 1935, from the Pakhna Formation (Serravallian) of Alessa near Limosol (Cyprus), was originally based on badly preserved material. Smith & Gale (2009), with access to better material from the same locality, found no significant differences with the type material from Italy and proposed *H. cypriotes* to be a junior synonym of *H. montesi*. In addition, the oral plating

and the structure of the apical disc in the specimens of *H. montesi* under study match with the schemes reported by Smith & Gale (2009; figs. 7a–c).

Archaeopneustes moorefieldi Hall, 1966, from the Early Pliocene Pismo Formation of California, was based on a sole specimen whose preservation prevents confirmation of the presence of the diagnostic characters of *Heterobrissus*. The outer pores of the paired petals are not conspicuously larger than the inner ones, as in *Heterobrissus* (Kier, 1984). Its generic position remains uncertain.

Heterobrissus montesi shows a close similarity with the Recent *Heterobrissus hystrix* (Agassiz, 1880) from the Caribbean. According to Smith & Stockley (2005) and Smith & Gale (2009), in *H. hystrix* the peristome is more anteriorly located and more rounded, and the labral plate projects more strongly. Although the difference in the position of the peristome is not confirmed by our dataset (Table 2), *H. montesi* differs also by its periproct, smaller and almost oral, and by much denser tuberculation aborally; additionally, the primary spines are slender and finely striated longitudinally, not stout and smooth as in *H. hystrix* (Mortensen, 1950).

DISTRIBUTION. Langhian of Emilia-Romagna and Piedmont (Northern Italy).

Heterobrissus lubellii n. sp. - Figs. 7–14, 32 - <http://zoobank.org/2830b226-6f5b-4324-9614-da27d4d93c1f>

TYPE MATERIAL. The holotype (MDLCA 23788) and seven paratypes (MDLCA 23789, 23790 and 23792; MAC PL1505, PL1506a, PL1508 and PL1861) from the Early Burdigalian of Baraci and Nuraghe Longu, near Isili (Cagliari Province). Other two paratypes (MDLCA 23791 and MAC PL2095) respectively from the Late Burdigalian of Nureci (Oristano Province) and of Genoni (Oristano Province).

TYPE LOCALITY. Baraci and Nuraghe Longu, near Isili (Cagliari Province) 39°44'45.54"N - 9°10'07.78"E.

OTHER EXAMINED MATERIAL. Twenty-five specimens from the Early Miocene of Sardinia: 18 of them from the Early Burdigalian of Isili, 3 from the Late Burdigalian of Nureci, 3 from the Late Burdigalian of Genoni, 1 from the Late Oligocene-Early

Aquitanian of Calada Bianca, near Funtanazza (Oristano Province).

DIAGNOSIS. A species of *Heterobrissus* with the paired petals longer and larger than those in the other species belonging to this genus (L4 = 52%; L5 = 13.5%; L6 = 55%; L7 = 17% TL in the holotype) and with the peristome farther from the anterior margin (L9 = 38% TL in the holotype) (Table 1); the periproct is larger (L1 = 14; L2 = 12% TL in the holotype) than that in the type-species of the genus.

DESCRIPTION. Large sized species (TL up to 127 mm in the studied sample). Test longitudinally elongate (mean TW = 84% TL) and more or less constricted posteriorly, with maximum width in front of mid-length (Fig. 7). Test with low domal upper surface (Figs. 9–14) and flat oral face, sinking towards the peristome (Fig. 8). Posterior face short, undercut and almost facing downwards (Figs. 9–14). Test height variable (mean TH = 46% TL). Ambitus low with rounded margin (Fig. 32).

Apical disc - Small, slightly anterior (mean L8 = 57% TL), ethmolytic, with four gonopores, the anterior pores are placed closer together than the posterior pair.

Ambulacra - Ambulacrum III narrow, flush over the aboral surface, slightly depressed only as it approaches the peristome. In the frontal ambulacrum the pores are double only adapically, farther down they are replaced by a narrow slit-like unipore oriented almost vertical to the lower suture (Fig. 12); these pores disappear towards the ambitus. Paired ambulacra petaloid adapically, almost flush, only slightly depressed in their upper half; they extend, slightly diverging, almost to the ambitus, remaining largely open distally (Fig. 7). Pore-pairs become slightly smaller towards the tip of the petal, where no occluded plates are present (Fig. 10). In the anterior paired petals the anterior columns of pore-pairs are smaller than those in the posterior columns as they approach the apex. Pore-pairs are drop-shaped isopores, with a narrow, flush interporal zone. Anterior paired petals long and wide (mean L4 = 49% TL, L5 = 12.5% TL), diverging from each other at about 130°. Posterior petals more or less longer and wide (mean: L6 = 57% TL, L7 = 14% TL), more or less straight and diverging at about 65°. Adorally, the paired ambulacra enlarge and the plating becomes crowded as they approach the peristome (Fig. 13). Phyllodes well developed, with 6–8 pores in a column in the ambulacra I, III,

V, and 10–12 in the lateral anterior ambulacra. The pores are single in the phyllodes.

Interambulacra - Only slightly inflated adapically.

Plastron (Fig. 13) - Plastron not raised. The labrum strongly indents the peristome (Fig. 8). Labral plate wedge-shaped, with convex surface and extending to halfway along the third plate in the adjacent ambulacra. Sternum almost as long as wide with sternal plates symmetrical and extending to plates 9–10 in the adjacent ambulacral columns. Episternal plates also paired and about half as long as the sternal plates. Plates 5.a.4 and 5.b.4 weakly offset, “L” shaped and forming the oral border of the periproct. The ambulacral plates do not indent the Interambulacrum 5. All the other interambulacra are amphiplacous. In interambulacra 1 and 4 the plates a.5 and b.5 or the a.6. and b.6 form the ambitus.

Peristome - Sunken, lunate, much wider than long and with a strongly projecting labrum. It is eccentric anteriorly but rather far from the test edge (mean L9 = 37% TL, range 34–38.5% TL).

Periproct - Inframarginal to almost oral (Fig. 32) and framed by plates 5.a.4, 5.b.4 to 5.a.7, 5.b.7. (Fig. 13); it is subcircular to slightly longitudinally elongate (mean L1 = 13.5% TL, L2 = 11% TL).

Tuberculation - Primary tubercles scrobiculate, perforate and crenulate, scattered over the entire aboral surface. All plates have a covering of sparse miliary granules and occasional smaller tubercles. A few small tubercles also occur within the petals and the frontal ambulacrum. The oral face is fully covered by smaller and denser primary tubercles, including the labral plate and the plastron (Fig. 8). Ambulacral zones have identical tuberculation to that in the interambulacral zones, with scattered primary tubercles, except in the phyllodes.

Fascioles - Absent in well preserved adult specimens. According to Mortensen (1950) the absence of an adproctal widening of the plates in the ambulacra I.a and V.b adjoining the episternal plates, typically confirms the absence of a subanal fasciole.

ETYMOLOGY. Dedicated to Giuseppe Lubelli (1938–2013), a collector from Cagliari who provided the authors with the first specimen of *Heterobrissus* found at Isili (Sardinia).

REMARKS. *Heterobrissus salvae* (Cotteau, 1890) differs by thicker shell and by the plates in the proximal part of the oral ambulacra I and V, which are longer and, as a consequence, the sternal plates extend only to the ambulacral plates 7–8, not to the plates 9–10 as in *H. lubellii*.

Heterobrissus lubellii n. sp. mainly differs from the Recent *H. hystrix* from the Caribbean area by lower test, periproct more inframarginal (Fig. 32), larger paired petals and much denser aboral tuberculation.

DISTRIBUTION. Late Oligocene-Early Aquitanian and Burdigalian of Sardinia.

Genus *Echinopneustes* n. gen. - Figs. 23–25, 28, 30, 34–38 - <http://zoobank.org/ee07de29-90d8-4eed-8719-bdbc0653f7b5>

TYPE SPECIES. *Palaeopneustes niasica* Döderlein, 1901 (p. 22).

TYPE MATERIAL. Döderlein (1901) did not designate a type. A syntype (MCZ.2817), dredged from Nias (Indonesia) during the Valdivia expedition, is housed at the Museum of Comparative Zoology, Harvard University (Downey, 1968).

DIAGNOSIS. Test ovate without anterior sulcus (Fig. 34); anterior convex, posterior face truncate. Test domed in profile, with flat base (Fig. 36). Apical disc ethmolytic, with four gonopores, anterior of centre. Anterior ambulacrum narrow, flush; pore-pairs minute adapically. Paired ambulacra petaloid adapically, most parallel-sided and largely open distally; enlarged pore-pairs extending almost to ambitus. No occluded plates at the end of petals. Peristome lunate with projecting labrum (Figs. 28, 35). Labral plate extending to the adjacent ambulacral plate 2 (Figs. 23–25). Perioral area sunken. Phyllodes well developed (Fig. 35, 38). Sternal, episternal and post episternal plates almost symmetrical, opposite rather than alternate; ambulacral plates not indenting the oral interambulacrum 5. Periproct large and flush, marginal to supramarginal, located rather high on the posterior test face (Figs. 30, 37), and bounded by the plates 5.a.5 and 5.b.5 in the oral posterior interambulacrum. Fascioles absent, at least in adult specimens. Aboral surface covered in coarse and heterogeneous tuberculation, made of scrobiculate, perforate and crenulate primary tubercles and numerous granules. Oral posterior ambulacra covered in tubercles behind phyllodes. Primary spines sharply pointed; in the type-species they are flattened and densely thorny, and only close to the base they may be round in section.

SPECIES INCLUDED. • *E. niasicus* (Döderlein, 1901): Recent, Indo-Pacific.

• *E. erinaceus* (Baker et Rowe, 1990); Recent, Australia.

• *E. gigas* (Baker et Rowe, 1990); Recent, Australia.

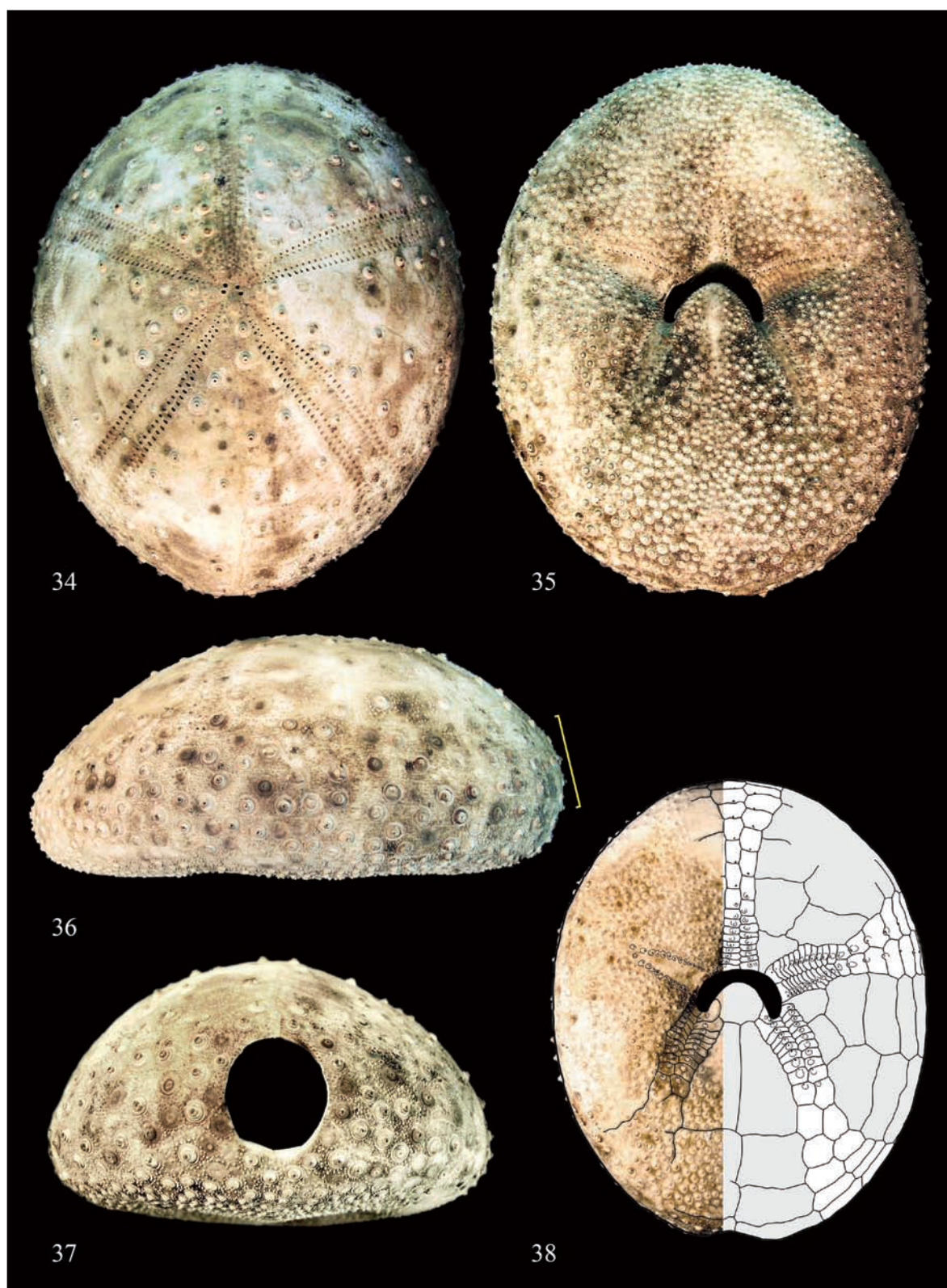
DISTRIBUTION. Recent, Indo-Pacific.

DIFFERENTIAL DIAGNOSIS. *Echinopneustes* n. gen. differs from *Heterobrissus* mainly in the labral plate being shorter and reaching only plate 2 of the adjoining ambulacra, instead of plate 3 as in *Heterobrissus*. Additionally, the test outline is not restricted posteriorly (Figs. 28, 35) and the posterior face is larger and steeper (Figs. 30, 36, 37), sometimes almost vertical, so that the periproct cannot be seen in oral view (Figs. 28, 35). The peristome is farther from the anterior margin of the test (Tables 2–3, Figs. 28, 35, 38). The periproct in the type-species is bounded by the interambulacral plates 5.a.5 and 5.b.5, not the 5.a.4 and 5.b.4 as in *Heterobrissus* (Fig. 38). In *Echinopneustes niasicus* the primary spines are thorny and flattened distally, whereas they are smooth and round in *H. hystrix* and round and finely striated in *H. montesi*. Ophi-cephalous pedicellariae are present, whereas they are absent in *H. hystrix*.

ETYMOLOGY. It derives from the Greek words echinos (sea urchin) and pneuma (breath), referring to the inflated shape of the test.

REMARKS. *Echinopneustes* n. gen. has no near relation with *Palaeopneustes*, in which the type species was originally placed by Döderlein (1901). In particular, the oral posterior ambulacra are highly characteristic in being wholly covered with large and small tubercles, not at all naked as it is otherwise usual in *Palaeopneustes* (Mortensen, 1950).

Echinopneustes erinaceus differs from *E. niasicus* by the presence of many short spines and the labrum longer than wide. *Echinopneustes gigas* differs from the other species attributed to *Echinopneustes* by its larger maximum size (TL up to 165 mm), coarser tuberculation, narrower phyllodes area and the presence of large short-bladed globiferous and rostrate pedicellariae (Baker & Rowe, 1990). A detailed key to distinguish among the Recent species attributed to this genus has been provided by Baker & Rowe (1990, p. 310).



Figures 34–38. *Echinopneustes niasicus* (Doderlein, 1901), MAC.IVM291, TL = 121 mm, Recent, Southern China Sea: respectively aboral, oral, lateral and posterior views, and oral plating scheme.

PALAEOECOLOGY

The presence of an outer shelf setting was prospected in the Pantano Fm at Jano, near Sasso Marconi (Panini et al., 2005), as well as in the Pakhna Fm of Cyprus (Smith & Gale, 2009). In both the examined areas, a low diversity fauna has been recorded. In particular, in the Serravallian of southern Cyprus the echinoid assemblage is dominated by just two genera of spatangoids, *Palaeobrissus* A. Agassiz, 1883 and *Heterobrissus*, both of them today confined to bathyal muddy settings (Smith & Gale, 2009). In the Langhian of Emilia-Romagna, *Heterobrissus* is commonly associated with *Mazettia paretii* (Manzoni, 1879) and *Faorina maullui* Stara et Borghi, 2012. According to Smith & Gale (2009), *Mazettia* is a probable sister taxon to *Linopneustes* A. Agassiz, 1881, which today lives in 55–710 m water depth, with maximum frequency between 200–500 m (Mortensen, 1950). *Faorina* Gray, 1851 today inhabits the Indo-Pacific at depths of 41–220 m, associated with *Echinopneustes niasicus* and *Linopneustes* spp. (Lane et al., 2000).

Heterobrissus montesi is closely related to *H. hystrix*, today living on muddy bottoms in the Caribbean, at 220–1610 m depth, (Mortensen, 1950; Serafy, 1979). Young et al. (1998) studied the distribution of *H. hystrix* and the thermal tolerances of its embryos and echinopluteus larvae. They found that embryos could tolerate temperatures as high as 25 °C, but larvae died at temperatures above 20 °C. The population of *H. hystrix* inhabiting the slopes of the Bahamian Islands had adult distributions centred at a depth of 550 m, with the upper limit corresponding closely to the thermal tolerances of larvae. At 200 m, in the Caribbean, the water temperature ranges from 15–16° along the northern Colombian coast to a maximum of 20–21° in the Cuba-Florida area. (Fuglister, 1954). At 1600 m, the maximum reported bathymetry for this species, the temperature is about 5 °C (NOAA data, 2009).

Heterobrissus is a large and flat-based echinoid with a heterogeneous aboral spine canopy and without fascioles. The lack of fascioles points to echinoids living epibenthic or inhabiting coarse permeable sediments (Smith & Stockley, 2005); the first hypothesis is more likely also for the fossil *Heterobrissus*, since groups of *H. hystrix* have been observed “patrolling” the bottom surface at

the Bahamas Islands (NOAA Photo Library, 2009).

Based on the available evidence and on comparison with living sister taxa and their bathymetric ranges, *H. montesi* was an epibenthic echinoid, inhabiting muddy bathyal settings and harvesting organic detritus from the sediment-water interface.

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