

Analysis of some astriclypeids (Echinoidea Clypeasteroidea)

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ABSTRACT

The systematic position of some astriclypeid species assigned through times to the genera *Amphiope* L. Agassiz, 1840 and *Echinodiscus* Leske, 1778 is reviewed based on the plating pattern characteristics of these two genera universally accepted, and on the results of new studies. A partial re-arrangement of the family Astriclypeidae Stefanini, 1912 is herein proposed, with the institution of *Sculpsitechinus* n. g. and *Paraamphiope* n. g., both of them characterized by a peculiar plating-structure of the interambulacrum 5 and of the ambulacra I and V. Some species previously attributed to *Amphiope* and *Echinodiscus* are transferred into these two new genera. Two new species of Astriclypeidae are established: *Echinodiscus andamanensis* n. sp. and *Paraamphiope raimondii* n. sp. Neotypes are proposed for *Echinodiscus tenuissimus* L. Agassiz, 1840 and *E. auritus* Leske, 1778, since these species were still poorly defined, due to the loss of the holotypes and, for *E. auritus*, also to the unclear geographical/stratigraphical information about the type-locality. A number of additional nominal fossil and extant species of "*Echinodiscus*" needs revision based on the same method.

KEY WORDS

Astriclypeidae; *Amphiope*; *Paraamphiope*; *Echinodiscus*; *Sculpsitechinus*; Oligo-Miocene.

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INTRODUCTION

The classification of the astriclypeid echinoids *Amphiope* L. Agassiz, 1840 and *Echinodiscus* Leske, 1778 have been traditionally based on the external morphological features, mainly test outline, size and shape of lunules and petals (see Durham, 1955). Structural characters, largely used in the taxonomy of other clypeasteroids, were practically ignored in earlier studies dealing with these genera, and although several species have been described in the literature, important features for species-level taxonomy, such as oral plating, were poorly illustrated or omitted completely.

MATERIAL AND METHODS

The studied specimens are housed in the following public institutions: MAC (Museo di Storia Naturale Aquilegia) and UNICA (Department of Animal Biology and Ecology, University of Cagliari) Cagliari, Italy; MSNDG (Museo di Storia Naturale Doria, Genoa) and UNIGE.SM (Dip. Te. Ris, University of Genoa), Genoa, Italy; NHMUK (National History Museum of United Kingdom) London, England; ZM (Zoological Museum of Denmark, University of Copenhagen) Copenhagen, Denmark; PMBC (Phuket Marine Biological Centre), Phuket District, Thailand.

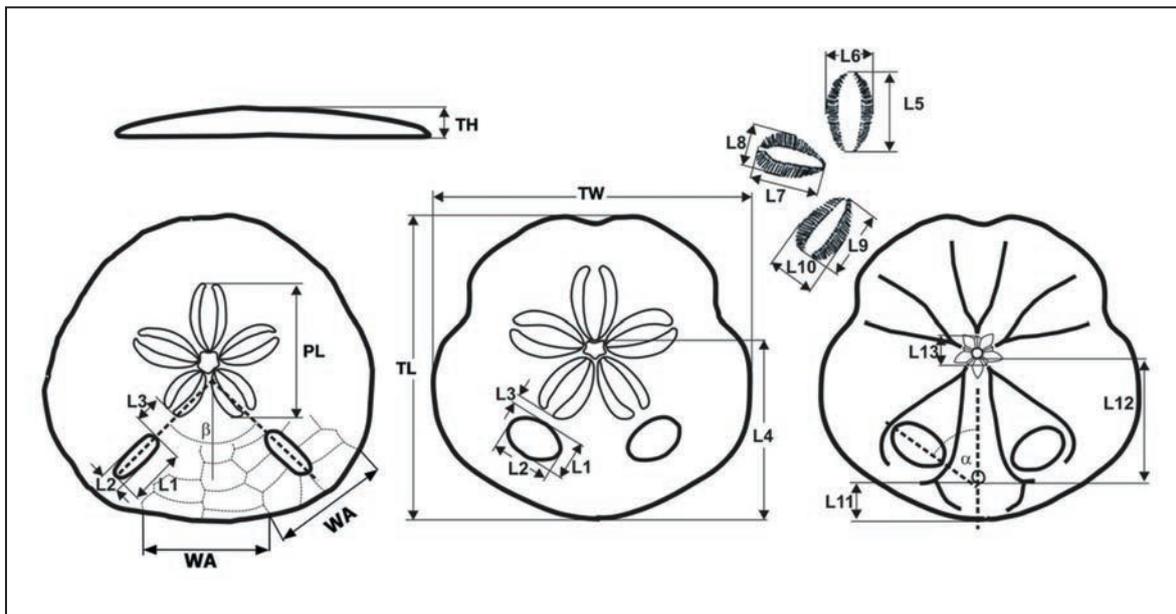


Figure 1. Biometric parameters measured in the studied samples.

Some other specimens, used for comparison, are kept in private collections, as cited.

43 specimens attributed to *Echinodiscus* and 29 to *Amphiope* were examined. 8 *Amphiope* fossils from Touraine, France; 1 *Echinodiscus* fossil from Hurgada, Egypt; 1 “*Amphiope*” fossil from Liguria, Italy and, 1 “*Echinodiscus*” Recent from Lembeh, North Sulawesi, Indonesia; 2 *Echinodiscus* Recent from Nosy Be, Madagascar; 33 “*Echinodiscus auritus*” Recent from Mangili, Madagascar; 10 “*Echinodiscus*” Recent from Philippines; 1 “*Echinodiscus*” Recent from Indonesia (Borneo) are housed in MAC; after study, some specimens will be deposited at the UNICA; 3 “*Amphiope*” fossils from Liguria, housed to the MSNDG and 2 fossil specimens of “*Amphiope*” at the UNIGE.SM (Dip. Te. Ris); 21 *Echinodiscus* and 10 “*Amphiope*” at the NHMUK; 1 “*Echinodiscus*” at the ZM; 6 *Echinodiscus* at the PMBC.

Three specimens of “*Echinodiscus*” used for comparison belong to private collections; some plating patterns were taken from illustrations reported in the literature.

Measures taken as in figure 1. The plating pattern follows Durham (1955) and, when possible, includes both sides of the specimen. To highlight the sutures, humidification by denatured ethyl alco-

hol has been used for extant species, a mixture of water and hydrochloric acid (ca. 2%) for some fossil specimens. The internal structure was studied by sectioning the test, and in some cases by X-ray. Morphological abbreviations as in figure 2: β = angle between major axis of the two lunules; TL = test length; TW = test width; TH = test height; L1-L2 = lunule length and width, respectively; L3 = distance between posterior petal-tip and lunule, L4 = distance between apical system-posterior margin, L5-L6 = length and width of the frontal petal, respectively; L7-L8 = length and width of the anterior paired petal, respectively; L9-L10 = length and width of the posterior petal, respectively; L11 = distance between periproct-posterior margin test; L12 = distance between the posterior border of the peristome and of the periproct, L13 = front-rear diameter of the ambulacral basicoronal circlet. PL = petalodium length; WA = ambulacral and interambulacral width at ambitus; \varnothing pc = periproct diameter; \varnothing ps = peristome diameter; Σ = summation. To describe the lunules shape and dimension into a numeric value, we introduced a Shape Index (SI) corresponding to the ratio $L2/L1$ and a Width Index (WI) = $(L1 + L2) / 2$.

Species with doubtful taxonomic attribution are marked by quotation marks.

I. DESCRIPTION OF THE SAMPLES EXAMINED

“*Amphiope*” sp.
Plates 1, 2; Tables 1, 2

EXAMINED MATERIAL. Eight specimens from Channay-sur-Lathan, Touraine, France, Late Serravallian-Early Tortonian, TL 47 - 73 mm.

DESCRIPTION. Small to medium sized echinoid with low test and small rounded lunules. The lunules show a low variability range: SI ranges from 1 to 1.6 (lunules roundish to slightly transversely elongated), WI ranges from 9 to 10.5 (small lunules). In this sample, the lunules variability equals on the average 34% L1 and 27% L2.

In the oral interambulacrum 5 there are only the post-basical plates 2a, 3a and 2b, 3b and, in some cases, a small portion of 4b. The plate 2a is long and staggered with respect to 2b; the periproct opens between 2a/3b. Aborally, the tips of the posterior petals are separated from the lunules by 1 or 2 couples of plate.

“*Amphiope*” *pedemontana* Airaghi, 1901

EXAMINED MATERIAL. Rupelian, Piedmont and Liguria, Italy. The holotype was housed in the Civic Museum of Natural History of Milan; it was lost during the Second World War. The specimens in the

Genoa museum indicate the occurrence of two different morphotypes under this name: one of them corresponds to the description of “*Amphiope*” *pedemontana* Airaghi, 1901, the other seems different.

First morphotype
Figures 2a, b; Table 3

EXAMINED MATERIAL. Three specimens: MSNDG. N25 from Pareto, MSNDG. N1214 from Cairo Montenotte and MSNDG.N1218 from unknown locality, TL 53 ÷ 61 mm; two illustrations given by Airaghi (1899 and 1901) of a specimen from Deago and another one from Santa Giustina; one specimen from Merana: MAC.PL2014, TL, 71 mm, TH 7 mm.

DESCRIPTION. Small to medium sized form, with small axial lunules, small and open petals, very depressed test and drop-shaped periproct. In the oral interambulacrum 5 there are only the post-basical plates 2a, 3a and 2b, 3b, all of them large and paired; the periproct opens between plates 2a/3b (Figs. 2a, b).

Second morphotype
Fig. 2c; Table 3

EXAMINED MATERIAL. Two whole specimens (UNIGE.SM-VI-P-(5)-DN and UNIGE.SM-VI-DR) and 2 test fragments, from Pareto.

Specimen	TL	TW	TH	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13	oPc	oSto
PL1668	68	101	12	8.5	9	9	58	25	13	24	15	23	15	5.5	43	13	2	3
PL1669	70	101	12	7.5	12	7.5	56	26	15	25	15	24	14	5.5	43	14	2	4
PL1921	47	104	15	8.5	10	9.5	55	25	13	24	13	22	13	3.5	46	14	1	5
PL1822	50	100	15	10.5	10	7.5	56	26	14	23	14	24	14	5	43	12	1.5	5
PL1823	49	106	14	9	10	9.5	56	24	14	23	14	22	14	4.5	44	12	1.8	4.5
PL1824	55	102	16	9	12	7	57	26	15	23	15	22	15	3.5	46	13	1.8	4.5
PL1825	61	101	16	8	10	8.5	56	26	14	24	15	23	15	5	44	12	1.8	5
PL1826	73	101	16	9	12	6.5	57	26	15	25	15	24	15	7	43	13	1.5	2.5
mean		102	14	8.7	11	8.1	56	25	14	24	14	23	14	4.9	44	13	1.6	4.2

Table 1. Morphometric data of *Amphiope* sp. 3. TL in mm, other measures in % TL.

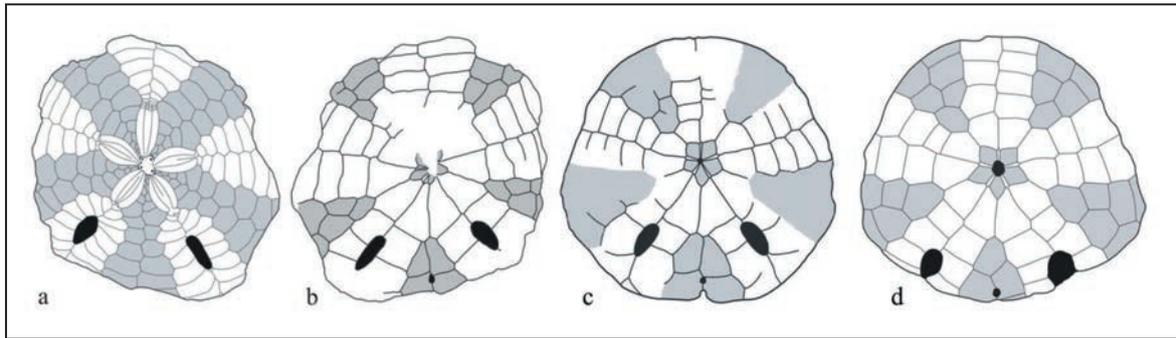


Figure 2. “*Amphiope*” *pedemontana* (Oligocene, Liguria and Piedmont, Italy): a, b: respectively, aboral and oral plate structure of MSNDG.1218; c: “*Amphiope*” sp. 1 (Oligocene, Liguria and Piedmont, Italy), oral plate structure of UNIGE.SM-VI-P5-DN; d: “*Amphiope*” *arcuata* (Miocene, Libya), oral plate structure.

<i>Amphiope</i> sp. 3	TL	Apx	PL	WA	α
PL1668	68	8	51	36	52°
PL1669	70	8	53	33	64°
PL1821	47	8	52	29	54°
PL1822	50	8	52	32	71°
PL1823	49	8	50	32	-
PL1824	55	8	53	-	67°
PL1825	61	8	53	-	64°
PL1826	73	8	53	30	53°
mean		8	52	32	60.7°
range			50-53	29-36	52-71

Table 2. Apx, PL, WA and α data of *Amphiope* sp. 3. TL in mm, α in degree, other measures in % TL.

DESCRIPTION. Small sized form with closed petals and a notch along the posterior margin, close to the periproct. The periproct is rounded and opens between plates 2a/3b. In the interambulacrum 5 there are only the post-basicoronal plates 2a, 3a and 2b, 3b, that are large and paired.

“*Amphiope*” *arcuata* Fuchs, 1882

Fig. 2d; Table 4

EXAMINED MATERIAL. Five specimens from the “Miocene” of the Libyan desert (locality not specified), housed in the NHMUK (code E1671-2, E1674-6), TL 35-79 mm.

DESCRIPTION. Small to medium sized echinoid, with very low test and thin ambitus; test outline rounded or sub-trapezoidal. In the interambulacrum 5 there are two plates per column: 2a, 3a and 2b 3b; the plates 2a/2b are staggered. These specimens are characterized by small ovoid axial lunules, distant from the corresponding petal tips. Lunules show a low variability since SI ranges from 0.45 to 0.76 (axially elongated lunules) and WI ranges from 8 to 10.5 (small lunules). On average the lunules variability equals 34% of L1 and 27% of L2. PL ranges from 42 to 46% TL.

“*Amphiope*” *duffi* Gregory, 1911

Plate 3 Figs. 1–6

EXAMINED MATERIAL. Rupelian, Libya. Two syntypes housed in the NHMUK: CY66/E11350, from Sidi Rof Diasiasia, Cyrenaica, TL = 37 mm and Cy264/E11349, from Ain Sciahat, Cyrenaica, TL = 39 mm.

DESCRIPTION. Small and low test with thin ambitus; test outline sub-rounded. Adoral face unknown. Width of the interambulacrum 5 at the ambitus about 23% TL. In Cy66 the petals are distally open. Petals are sub-equally sized; PL = 47%

TL. Lunules are apparently open (notches?), but it is not clear whether this is due to damage; in C66 they are very small and ellipsoidal. β measures 65° . On the aboral side each lunule is separated from the petal tip by 3-4 couples of plates and is surrounded by 3 - 4 couples of plates. The apical disc is small ($\approx 8\%$ of TL) and star-shaped. The internal structure is unknown. Number of plates per column only partially visible (see Table 7).

“*Echinodiscus tenuissimus*” L. Agassiz, 1847

EXAMINED MATERIAL. Recent, Indian Ocean, In-

donesian Archipelago, Oceania and China Sea.

REMARKS. The holotype was established by L. Agassiz (1847) in Agassiz & Desor (1847) on the basis of a specimen with small axial lunules, from Waigiu (New Britannia, Western Papua, Indonesia) and housed at the Museum of Natural History, Paris. Actually the holotype is wanting (personal communication by Sylvain Charbonnier, June.03.2014). The group of Recent specimens under study indicate the occurrence of three different morphotypes: one of them shows some characteristics of the genus type *E. bisperforatus* Leske, 1778, the others seem different.

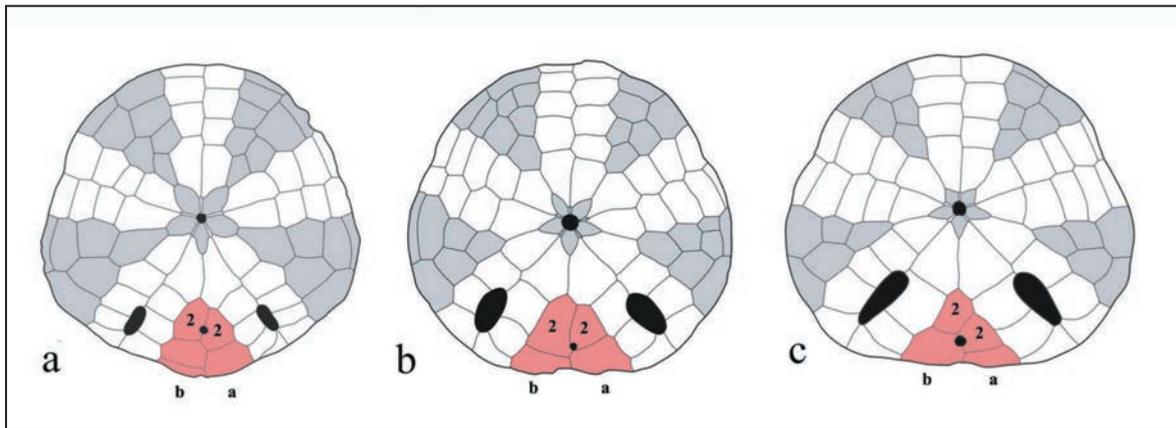


Figure 3. Plate structures of adoral side of the “*Echinodiscus tenuissimus*” morphotypes; postbasiconoral plates of interambulacrum 5 colored - a, first morphotype; b, second morphotype; c. third morphotype.

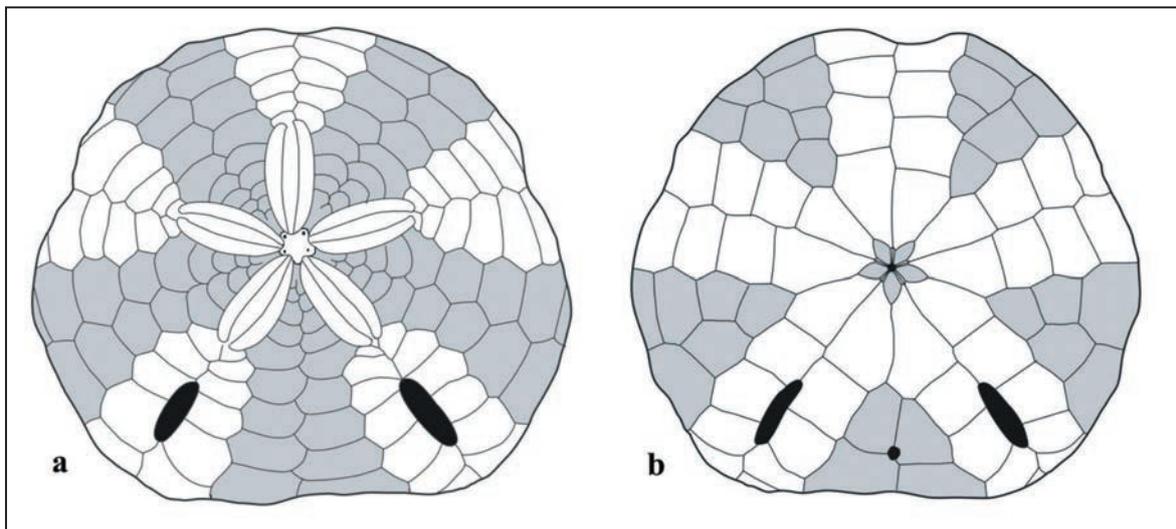


Figure 4. “*Echinodiscus bisperforatus truncatus*“, plate pattern of oral (a) and aboral sides (b).

Specimen	TL	TW	TH	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13	øPc
MSNDG.25	61	103	13	18	7.5	7	52	21	8.5	18	8	17	8.5	7	38	-	3.5
MSNDG.1214	55	118	14	15	7.5	8	55	-	11	20	11	20	11	7	-	-	-
MSNDG.1218	53	95	14	13	7	8	54	20	9	18	9.5	16	9.5	7	38	-	3.5
MAC.PL2014	71	112	10	10	5	8	56	21	8.5	20	9	20	8	7	43	-	2.5
Mi-Ai-1901	53	90	15	15	6	9	52	23	10	18	8.5	18	10	6	-	-	-
Mi-Ai-1899	-	85	-	18	5	6	50	22	10	17	8	20	9.5	>5	46	-	-
UNIGE.SM-IV-DN	76	104	10	15	7	8	54	23	9	20	9.5	18	8	7	43		-
UNIGE.SM-VI-DR	75	197	11	15	7	-	54	24	12	22	12	-	-	-	-	-	-
Mean		101	10	15	7	8	52	22	9.7	19	9.5	18	9.2	6.7	42		

Table 3. M morphometric data of *Echinodiscus pedemontanus* (former *Amphiope pedemontana*) and *Echinodiscus* sp. 1. TL in mm, other measures in % TL.

I	TL	TW	TH	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13	øPc	øSt _o
NHMUK.E76161	79	102	6	9.5	6.5	15	55	22	11	20	11	21	12	12	39	13	1.8	3.5
NHMUK.E76162	66	103	6	12	7	15	55	20	10	19	10	20	10	13	-	-	2	-
NHMUK.E76166	49	100	12	11	5	14	55	22	10	18	11	18	10	13	33	13	1.8	4
NHMUK.E76165	40	100	11	12	9.5	15	54	22	11	18	19	18	10	5	45	15	2	4
NHMUK.E76164	35	106	11	12	8.5	15	54	22	11			21	11	4				
Mean		102	9	11	7.3	15	55	22	11	19	12	20	11	9.7	39	14	1.9	3.8

Table 4. Morphometric data of *Paraamphiope arcuata* (former *Amphiope arcuata*). TL in mm, other measures in % TL.

First morphotype

Fig. 3a

EXAMINED MATERIAL. One specimen from Lembeh Channel, North Sulawesi (Indonesia), MAC.IVM 207, TL = 50 mm; one specimen from New Caledonia, NHMUK.1981.11.2.25, TL = 112 mm; one specimen from Palau, Micronesia, NHMUK.59.7.1.14, TL = 120 mm; two specimens from Lembeh Channel, North Sulawesi (Indonesia) TL 50-65 mm from the M. Fantin collection and one from Noumea, Baie des Citrons, New Caledonia, TL 68 mm, from the F. Hattemberger collection.

DESCRIPTION. Middle size test echinoids with small slit like axial lunules and small petals. Very flat test and thin ambitus, with an elongated and more rounded anteriorly outline. In the oral interambulacrum 5 there are two-three plates in column a (2a, 3a, 4a) and three in column b (2b, 3b, 4b); in which the plates 2a and 2b are more or less staggered and the periproct opens between plates 2a/2b. The β angle is low (65-70°, mean 67°) and WA at interambulacrum 5 is small (mean 32% TL).

Second morphotype

Fig. 3b

EXAMINED MATERIAL. Two specimens from Pak Meng Beach, Trang Province, Thailand; PMBC.26346, 2842, TL = 81 and 66 mm; two specimens from Noparat Tara Beach, Krabi Province, PMBC.2843, 2830, TL = 66,2 and 54,6 mm; one specimen from PMBC Jetty South, Phuket, PMBC2844, TL = 66,2 mm; one specimen from West side of Ko Yao Yai, Phuket, housed in the NHMD.Z n° ZMUC-ECH-1001, TL 37 mm (see also Warèn & Crossland, 1991: figs. 10a, c); one specimen from "Thailand", Recent (based on a illustration in "www.Echinoids NL" by Bas van der Steld, Netherlands).

DESCRIPTION. Small size tests echinoids, with ovoidal axial lunules, very flat test and thin ambitus, sub-rounded in shape. In the oral interambulacrum 5 there are two postbasiconal plates per column (2a, 3a and 2b, 3b), paired and wide. The β angle is small (75,5°). The WA at interambulacrum 5 is about 38% TL. Since only a small sample is available to study, it is not possible to verify the variability of the lunules.

Third morphotype

Fig. 3c

EXAMINED MATERIAL. One specimen from Indonesia (Borneo), Recent, MAC.IVM206, TL = 53 mm.

DESCRIPTION. Small sized echinoid, with a flat test and slit-like axially elongated lunules. Petals small, closed distally. In the oral interambulacrum 5 there are 2 postbasiconal plates per column (2a, 3a - 2b, 3b), with the first two staggered. The 2b is in amphiplacous contact with the first postbasiconal plates of ambulacra I and V. Between the petal tips and the notches there are 3 couples of plates, and the periproct opens between plates 2a/3b. The WA at the interambulacrum 5 is 38% TL; the β angle is 80°.

Echinodiscus bisperforatus truncatus

(L. Agassiz, 1841)

EXAMINED MATERIAL. Some Recent specimens examined in the Fantin collection (Venice, Italy), labeled *E. truncatus* (Fig. 4a, b), recently dredged near Singapore, allowed to observe the plate structure and other characteristics. It differs from the previous "second morphotype" by some noticeable features. The echinoids collected in Singapore have the plate pattern that match with those of the second morphotype, but have the peristome smaller, more branched food grooves, the apex much further forward, lunules longer and slit-like and the ambital outline with the posterior margin truncated. To compare other characters we took some pictures of *E. truncatus* in situ, from www.wildsingapore.com (Mega Marine Survey of Singapore) and we have established new differences, as we will see in the discussion ad in the systematics chapters.

***Echinodiscus bisperforatus* Leske, 1778**

Plates 4, 5; Table 5

EXAMINED MATERIAL. Recent, Red Sea and Indian Ocean. Seven specimens from South Africa (locality not specified) NHMUK: NHMUK 2013.7-13, TL = 26 - 62 mm, eleven specimens from Wakiro, Massawa, Eritrea, Red Sea, NHMUK.1965.1.11-20, TL = 46 ÷ 69 mm, one specimen from Pangani, Tanga, Tanzania, NHMUK.1957.5.21.3. TL = 84 mm; two specimens from Nosy Be Island, Northern Madagascar, TL = 25 and 45 mm, the smaller one housed at the (MAC.IVM208), and the large one from a private collection.

Specimen	TL	TH	TW	L1	L2	L11	WA	PL	β
NHMK. 1965-6-1-11	69	9.8	115	28		12.5	54	45	101
NHMK. 1965-6-1-12	67.5	9	120	28	2.5-5	8.5	48	47	109
NHMK. 1965-6-1-13	67	11	119	31.5	2.5-5	9	51	42	103
NHMK. 1965-6-1-14	65	8.5	122	34	2.5-5	9	46	41	102
NHMK. 1965-6-1-15	65	9	113	32	-	12	-	-	-
NHMK. 1965-6-1-16	64	10	115	31	-	8	-	40	-
NHMK. 1965-6-1-17	63	9	119	28	-	9.5	52	39	110
NHMK. 1965-6-1-18	60	7.5	112	30	-	8.5	51	41	107
NHMK. 1965-6-1-19	59	8	113	31	-	7	49	38	107
NHMK. 1965-6-1-20	51	6.5	113	29	-	8	-	-	104
NHMK. 1965-6-1-21	46	6.5	109	-	-	-	47	38	-
mean		8.6	115.4	30.2	-	9.2	48	41.2	105
range		6.5-11	109-120	28-34	2.5-5	7-12.5	46-54	38-47	101-109
Specimen	TL	TH	TW	L1	L2	L11	WA	PL	β
MAC.IVM 208	30	7	113	31	6	3.5	44	38	86
Specimens	Dap	H	Dt	L1	L2	L11	WA	P	β
NHMK.3013.7	62	9.5	115	34	3-3-4	5.5	50	43	103
NHMK.3013.8	56	9	115	33.5	3-4-4.5	5.5	47	50	105
NHMK.3013.9	54	7	116	36	3-3-3.5	5	45	45	106
NHMK.3013.10	53.5	8	114	33.5	3-4-5	4	-	43	106
NHMK.3013.11	47	7	115	33	3-4-5	5	47	46	108
NHMK.3013.12	39	8	122	38	4-4-4	4	53	-	117
NHMK.3013.13	26	7	113	31	6-6-6	3	53	-	102
mean		7.9	115.7	34	--	4.5	49	45	107
range		7-9.5	113-122	31-38	--	3-5.5	45-53		102-117
Specimen	TL	TH	TW	L1	L2	L11	R	PL	β
NHMK.1957.5.21-3	84	11	111	24	3.5-3.5-3	10	49	43	111

Table 5. Simplified morphometric data of *Echinodiscus bisperforatus* from different localities; TL in mm, β in degree, other measures in % TL.

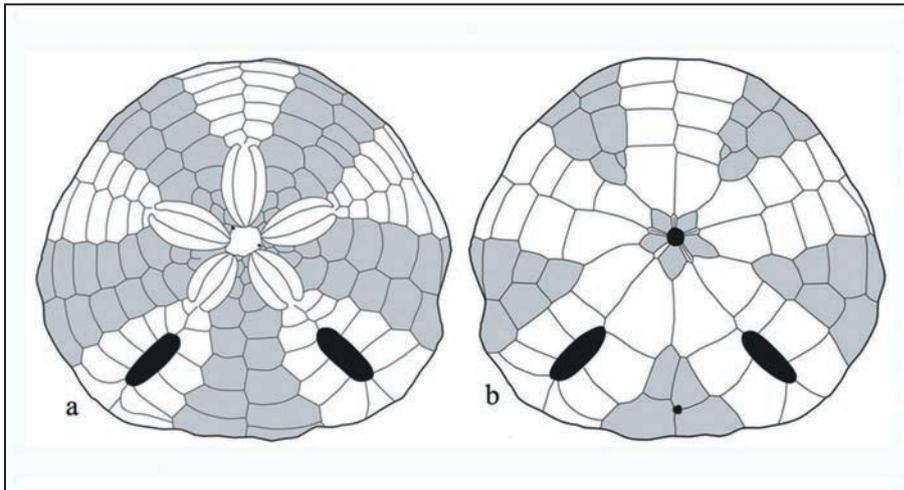


Figure 5. “*Echinodiscus* sp. 2” (Pleistocene-Holocene, Hurgada, Red Sea, Egypt), plate pattern of oral (a) and aboral sides (b).

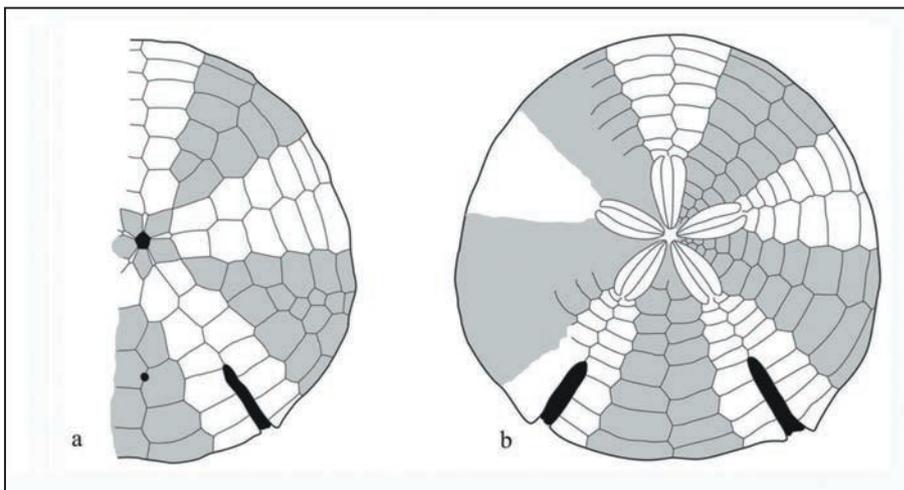


Figure 6. “*Lobophora aurita*”, plate pattern, taken from the illustration by L. Agassiz (1838–41: table 14, figs. 1, 2): adoral (a) and aboral view (b).

DESCRIPTION. Middle size tests echinoids, with flat test with rounded to sub-trapezoidal outline. In the interambulacrum 5 there are two plates per column, 2a, 3a and 2b, 3b, paired and wide (see Plate 5 Fig. 2). The β angle is about 110° ; the lunules are very long and show a low variability. The WA is high (47–50% TL).

***Echinodiscus* sp.**
Fig. 5a, b

EXAMINED MATERIAL. One specimen from the Pleistocene of Hurgada, Red Sea, Egypt, MAC.PL 1850, TL = 21 mm.

DESCRIPTION. Small sized echinoid, with flat test, thin ambitus and test outline rounded. In the oral in-

terambulacrum 5 there are two plates per column (2a, 3a, 2b, 3b), paired and wide. and the periproct opens between plates 2a/3b. The β angle is 80° .

Echinodiscus desori Duncan et Sladen, 1883
Plate 6 Figs. 1–6

EXAMINED MATERIAL. Four specimens from the Miocene of the Gujarat State, northern India: NHMUK.E78129, TL 49 mm; NHMUK.E724b, TL 39 mm; NHMUK.E78128a (TL 47 mm) and b (TL 47.5 mm).

DESCRIPTION. Small size and very depressed test (TH = $7 \div 11\%$ TL). The ambitus is thin and with sub-rounded outline. The oral surface is exposed only in specimen NHMUK.E78128a, with the plat-

ing pattern only partially visible. The WA at the interambulacrum 5 is about $30 \div 35\%$ TL in NHMUK.E724b. The petals are sub-equal in size, they are distally open or tend to opening (e.g. in NHMUK.E724b). The axial lunules are medium sized, ellipsoidal shaped. In NHMUK.E78129 they are both incomplete. The β angle is low (68° to 74°).

“Amphiope bioculata” des Moulins, 1835

Plate 7 Figs. 1–11

EXAMINED MATERIAL. Based on eleven specimens illustrated by Cottreau (1914), from the Helvetian (Burdigalian in Philippe, 1998) of Saint-Cristol, Nissan, Herault; pl. VI, figs. 1–11, TL $43 \div 67$ mm.

DESCRIPTION. Small sized echinoids, slightly wider than long ($TW = 103 \div 110$, the mean measure is 106% TL). Test depressed, however the measure of the height is unknown. The ambitus outline is sub-rounded. Inflections occur in the ambitus in correspondence with the ambulacra II, III and IV. The adoral surface is flat or slightly concave; plating not detectable. The petals are closed and sub-equal; PL ranges between 42 to 55% TL (mean 49.5% TL). The lunules are very distorted, relatively small and rounded and close to the tips of the corresponding petal. It is clear that the size variability of the lunules is high (Table 6; Figs. 11, 12), with a variation range of L1 which exceeding 50% on the average value and that of L2 which exceeds 45% on the average value. However, the SI varies from 0.95 to 1:47

Specimens	L1	L2	SI	WI
Fig. 1	10	9.5	0.95	9.75
Fig. 2	8	10	1.25	9
Fig. 3	12	13	1.08	12.5
Fig. 4	12	13	1.08	12.5
Fig. 5	8.5	10.5	1.23	9.5
Fig. 6	7.5	10	1.33	8.75
Fig. 7	7.5	10	1.33	8.75
Fig. 8	8	9	1.12	8.5
Fig. 9	10	14	1.47	12
Fig. 10	9	12	1.33	10.5
Fig. 11	8	11	1.37	9.5
mean	9.13	11	1.22	10.20
range	7.5-12	9-14	0.95-1.47	9-12.5
variance	49.2	45.4		

Table 6. Variability data of the lunules in *Amphiope bioculata* in Cottreau's sample.

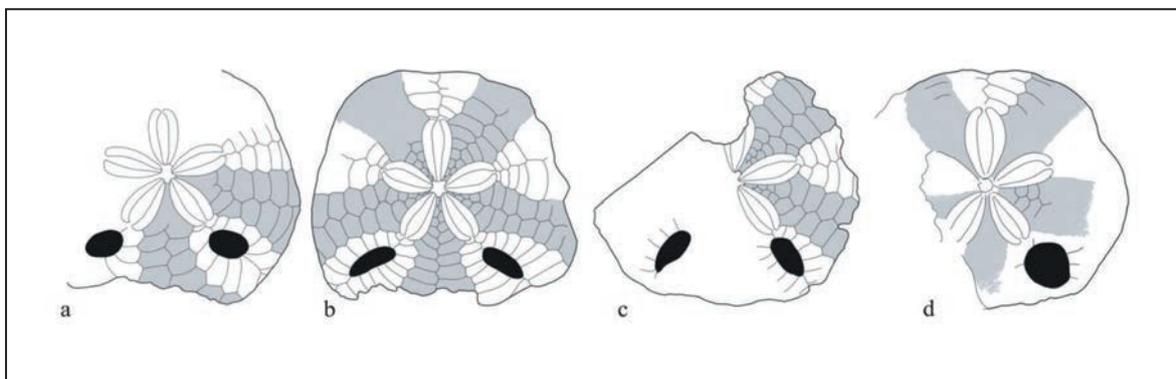


Figure 7. Aboral plate structures of “*Echinodiscus*” from Taiwan and Japan; a: *E. formosus*, ?Eocene-Miocene, Taiwan (from an illustration in Tokunaga, 1901, pl.1, figs. 1, 2); b: *E. yeliuensis*, Miocene, Taiwan (from Wang, 1984, pl. 1, fig. 2a, b); c: *E. cikuzenensis*, Oligo-Miocene, Japan (from Takano et al., 2007, pl. 1, fig. 12); d: “*E.*” *transiens*, Miocene, Japan (from Nisiyama, 1966, pl. 17, fig. 1).

while the WI ranges from 9 to 12.5, indicating that the lunules are always rounded, while varying especially in amplitude.

“*Echinodiscus auritus*” Leske, 1778

Fig. 6a, b

EXAMINED MATERIAL. Based on the illustration of *Lobophora aurita* by L. Agassiz (1841), as *L. aurita*, pl. 14, fig. 1, 2; TL 110 mm, TH 11% of TL; Recent, Red Sea, Egypt.

DESCRIPTION. Medium to large-sized echinoid with polygonal ambitus outline and two long posterior notches. The adoral surface is flat or slightly plano-concave. In the oral interambulacrum 5 there are four postbasiconal plates per column (2a, 3a, 4a, 5a and 2b, 3b, 4b, 5b); the periproct opens far from the posterior margin (L11 = 19% TL) between plates 3b/3a. Aborally, there are 5-6 couples of plates between the notches and the posterior petal tips.

REMARKS. The illustration given by L. Agassiz (1841) was the first to highlight the plate structure of this echinoid. These data are not even reported in the recent works, for which we detect the complete plating, which is very different from those of Mangili and from the Philippines, examined by Stara & Fois M. (2014).

Echinodiscus formosus Yoshiwara, 1901

Fig. 7a

EXAMINED MATERIAL. Based on the illustration by Tokunaga (1901–3: pls. 14 and I, fig. 2); TL 100 mm. 1 specimen from Middle Eocene? to Miocene, Hatto, Kelung, Taiwan. Plating of the aboral side taken from fig. 2, pl. I; inclination of the lunules as in pl. II fig. 2.

DESCRIPTION. Medium to large sized echinoid (max TL = 140 mm), with depressed test and with sub-ellipsoidal ambitus outline. The estimated WA of the interambulacrum 5 obtained by measuring the half visible, seems to be the 50% TL. The petals are closed, sub-equal in size; Tokunaga affirms that the anterior odd petal is 25% and the other are 22.5% TL, but the illustration indicates that they all measure the 20% TL. The lunules are large and ellipsoidally shaped. The β angle is large (111°). The lunules are surrounded by 5 pair of plates on the aboral face. The partial number of plates per column is shown in Table 7.

Echinodiscus yeliuensis Wang, 1982

Fig. 7b

Based on illustration in Wang (1984), from the Taliao Formation (Aquitanian), of Yeliu, Taiwan, pl. I, fig. 2a, b; topotype n° NTUG - [E] - 81.42; TL = 112 mm; TW = 131 mm.

DESCRIPTION. Medium to large sized echinoid with depressed test (TH = 10% TL). The ambitus outline is sub-trapezoidal, wider near the rear. Only a part of the plating of the apical surface is detectable. The estimated measure of WA at the interambulacrum 5 is 34% TL. The petals are sub-equal in size; the petalodium is wide (PL = 52% of TL). The lunules are long and narrow, broader anteriorly, lanceolate shaped and their axis deviates substantially from the corresponding petals (β angle about 114°). There are 2 couples of plates between the petals tips and the corresponding lunules.

Echinodiscus cikuzenensis Nagao, 1928

Fig. 7c

EXAMINED MATERIAL. Based on illustration in Takano et al. (2007) pl. 1, fig. 11; 1 specimen of Education Kawai, Oligocene-Miocene in age, from Chugoku and Kyushu Province, Japan. TL unknown.

DESCRIPTION. The test outline in sub-rounded. The aboral face is incomplete. The petals are sub-equal in size; the PL is small (44% TL). The lunules are large, sub-ellipsoidal shaped and deformed and very close to the corresponding petal tip. The right lunule is surrounded by 6 couples of plates on the aboral side. The β angle is 73°.

Echinodiscus transiens Nisiyama, 1968

Fig. 7d

EXAMINED MATERIAL. Based on the specimen illustrated in Nisiyama (1966), pl. 17, fig. 1; IGPS collection, No. 37773, from the Yamaga Formation, Miocene, Yamaguchi Prefecture, Japan. TL 102 mm.

DESCRIPTION. Medium sized, with a depressed test; TH unknown. Test outline sub-rounded. The aboral face is incomplete. The petals are sub-equal and the petalodium is wide (52% TL). The unique visible lunule is large and sub-rounded shaped.

Specimens		Ia5	Σ	amb I	Σ	amb V	Σ	Ia1	Σ	Ia4	Σ	amb II	Amb IV	Ia2	Ia3	amb III	Σ
<i>Echinodiscus formosus</i> Middle Eocene	a b	- x+6		x+6 x+6				x+6 x+6				x+5 x+5		-		-	
<i>Echinodiscus pedemontanus</i> Rupelian	a b	x+9 x+8		x+8 x+8		- X+7	↓	- -				- -		-		-	
<i>Echinodiscus cikuzenensis</i> Oligo – Miocene	a b	- -		x+6 x+6				x+10 x+9				x+4 x+5		x+8 x+8		X+5 -	
<i>Echinodiscus yeliuensis</i> Early Miocene	a b	x+10 x+10		x+7 x+8		X+8 X+8+		x+11 x+11		X+10 X+10		- -		-		-	
<i>Amphiope nuragica</i> MAC.PL1684, Oligo-Miocene	a b	4+9 5+10	13 15	7+9 8+10	16 18	8+9+ 7+9	17 16	4+11 3+10	14 13	4+10 x+11	14	5+4 5+4	5+4 4+4	4+6+ 5+6+	4+8 4+7	5+5 6+5	10 11
<i>Amphiope nuragica</i> MAC.PL1680, Oligo-Miocene	a b	4+15 5+14	19 19	7+10 7+11	17 18	8+11 7+10	19 17	4+12 x+12	16	x+13 4+13	17	- 5+5	x+5 x+6	4+10 4+11	4+10 X+10	5+6 6+5	11 11
<i>Amphiope</i> sp. 2 MAC.PL549, Late Burdigalian	a b	3+11 4+11	14 15	7+8 7+7	15 14	7+7 6+7	14 13	4+7 x+8+	11	x+8 4+7	11	6+5+ 6+5+	x+4 x+5	5+10 4+11	4+11 5+10	5+5 5+6	10 11
<i>Amphiope</i> sp. 2 MAC.PL552, Late Burdigalian	a b	3+11 5+10	14 15	8+8+ 8+9	16 17	8+7 8+8	15 16	4+10 3+10	14 13	3+ 4+		6+4 6+5	6+4+ 6+6+	4+9 4+9	5+9 4+9	6+5 6+4	11 10
<i>Amph</i> sp. 3 MAC.PL1669 Serravallian - Tortonian	a b	3+10 4+11	13 15	6+7 7+7	13 14	7+7 6+7	14 13	4+11 3+11	15 14	3+10 4+9	13 13	5+4+ 5+4	5+5 6+4	4+9 4+10	4+10 3+9	6+4 5+4	10 9
<i>Sculpsitechinus tenuissimus</i> Recent	a b	3+6 4+6		7+8 7+7	15 14	7+6 7+6	13 13	5+8 4+6	13+ 10+	4+9 5+10	13 15	5+6 6+(-)	6+(-) 6+(-)	4+(-) 5+(-)	5+(-) 4+(-)	6+ 6+	
<i>Sculpsitechinus auritus</i> MAC.IVM87, Recent	a b	4+10 5+10	14 15	7+7 7+8	14 15	7+7 6+7	14 13	5+11 4+11	15 14	4+10 5+10	14 15	6+6 7+5+	6+6+ 6+6	5+9 5+9	5+10 4+10	6+6 5+7	12 12
<i>Sculpsitechinus</i> sp. 1 MAC.IVM210, Recent	a b	4+11 4+11	15 15	7+7 8+7	14 15	7+8 7+6	15 13	5+11 4+11	16 15	4+10 5+11	14 16	6+6 6+7	6+7 6+6	4+10 5+10	5+11 5+11	6+6 7+6	12 13
<i>Echinodiscus andamanensis</i> Thailandia, Recent	a b	3+9 3+9	12 12	5+6 5+5	11 10	5+5 5+5	10 10	4+8 5+8	12 13	4+8 4+8	12 12	5+5 6+4	5+5 6+4	5+9 4+9	4+6 4+5	6+5 6+6	11 12
<i>Echinodiscus truncatus</i> Singapore, Recent	a b	3+10 3+9	13 12	6+6 6+5	12 11	6+4 5+6	10 11	4+10 4+9	14 13	3+9 4+9	12 13	5+6 5+5	5+5 5+5	4+8 4+8	4+8 4+8	5+5 5+5	10 10
<i>Echinodiscus bisperforatus</i>	a b	3+9 4+9	12 13	7+6 8+5	13 13	8+6 7+6	14 13	5+11 4+10	16 14	4+9 4+10	13 14	6+5 6+5	6+4 6+4	4+10 4+10	5+10 5+10	7+4 7+4	11 11

Table 7. Number of plates in some Astrictlypeids species. Ia = interambulacrum; Amb = ambulacrum; Σ = summation of oral and aboral plates per column.

II. MAIN CHARACTERISTICS DISTINGUISHING AMPHIOPE FROM ECHINODISCUS

Durham (1955: 154, fig. a, b) and Smith & Kroh (2011) indicated some characteristics of the oral plating which distinguish *Amphiope* from *Echinodiscus*. In species belonging to *Amphiope* in the oral interambulacrum 5 there are two postbasalcoronal plates in column a (2a, 3a) and three in column b (2b, 3b, 4b), with the plate 2b more elongated and staggered than the 2a and in amphiplacous contact with the first two adjacent postbasalcoronals ambulacral plates (Fig. 8a). In species belonging to *Echinodiscus*, in the oral interambulacrum 5 there are two postbasalcoronal

plates per column in which the first two plates 2b/2a are similar-sized and paired (Fig. 8b).

From Kroh (2005), Pereira (2010) and Stara & Borghi (2014), we have taken other characteristics that distinguish *Amphiope* from others genus. Since the shape of the lunules in *E. bisperforatus* is hardly distinctive, we found the other characters of this genus by a number of samples stored in a museum, how above documented.

In the aboral face of *Amphiope*, there are always one-two pairs of plates between the petal tips and the corresponding lunules and the plates surrounding the lunules are arranged in a radial manner (Plate 8 Figs. 1, 2; Plate 9 Figs. 1, 2; Plate 10 Figs. 1, 2). In the aboral face of *E. bisperforatus*, there

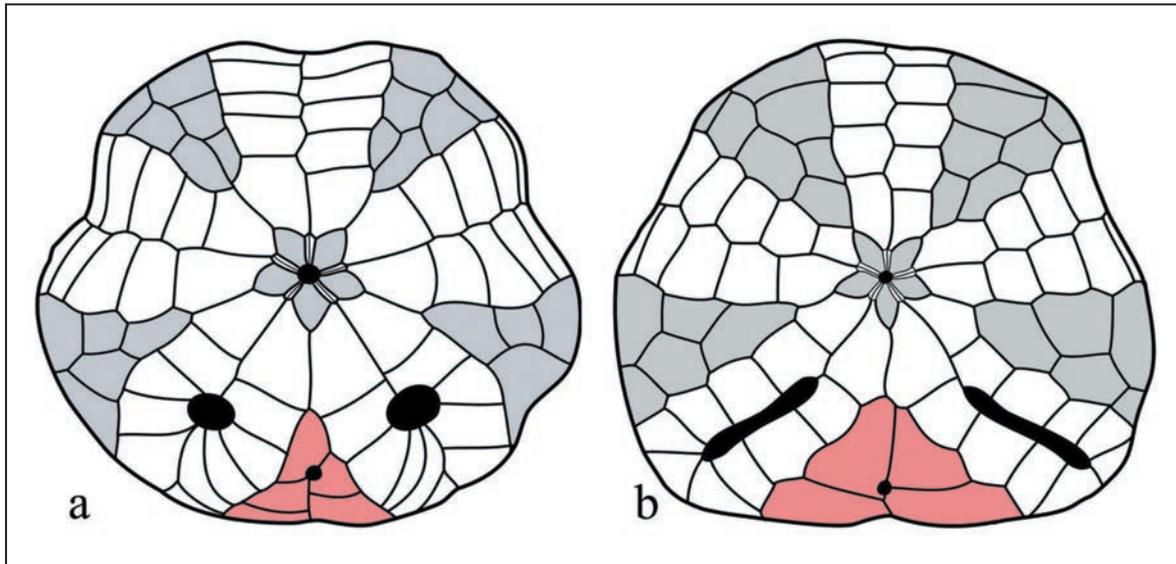


Figure 8. Plate patterns of adoral sides of *Amphiope* “*bioculata*” and *Echinodiscus bisperforatus* from Durham (1955: p. 154, figs. a, b) and Smith & Kroh (2011); in red the oral postbasalcoronal interambulacral structures.

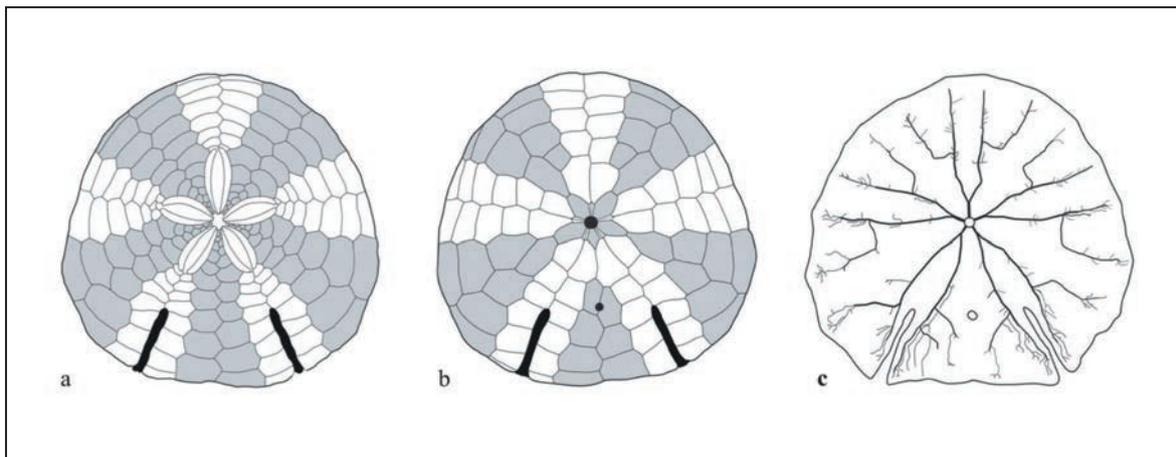


Figure 9. *Sculpitechinus auritus* from Mangili (Recent, Tulear, Madagascar); a, b: respectively, aboral and oral plate structure of MAC.IVM 87; c: food grooves scheme.

are similarly one-two pairs of plates between the petal tip and the corresponding lunules, but the plates surrounding the lunules are arranged in a linear manner (Plate 9 Fig. 5). Finally, Smith & Kroh (2011), state that *Amphiope* have roundish-ovoid transverse lunules, while *Echinodiscus* have ovoidal axial lunules or notches.

Based on these characters, and others that have already been published in the pages of *Amphiope* and *Echinodiscus* genus in Smith & Kroh (2011), we have included in these genera the morphotypes

whose the plate patterns of interambulacrum 5, coincided with those described by Durham (1955) and Smith & Kroh (2011).

According to logic, the forms that do not match with any of the two types have been treated by us and characterized as belonging to several new genera. Then, in the following we will use the terms *Amphiope* and *Echinodiscus* to indicate any form of astriclypeids corresponding to the description summarized above.

DISCUSSION ON SYSTEMATICS ASPECT

The specimens of "*Echinodiscus auritus*" described by Stara & Fois (2014) do not match with the above reported concepts of *Echinodiscus* and *Amphiope*. The first two postbasalcoronal plates 2b and 2a in the oral interambulacrum 5 are partially staggered and the total number of plates per column is higher (4 in column b and 3–4 in column a) than those of *Echinodiscus* and *Amphiope* (see Plate 10 by comparison). Also the couples of plates present between the tip of each petal and the corresponding notch is higher than those of *Echinodiscus* and *Amphiope* (see Plate 9).

Furthermore, the size of the petalodium (PL) is significantly lower than that of *Amphiope*, where as WA is lower than that of both genera. Even the complicate and dense food grooves branching is peculiar. Based on these characters this form is attributed to a new genus, *Sculpsitechinus* genus novum. The definition of the corresponding type species is reported in the following systematics chapter (see Figs. 9a–c).

The oral structure of the sample of "*Amphiope*" sp. from Channay-sur-Lathan (Plate 2 Fig. 6) matches the schemes published by Durham (1955), Pereira (2010), Smith & Kroh (2011) and Stara & Borghi (2014). The plate 2b of the interambulacrum 5 is longer and staggered with respect to the 2a; the lunules are more or less roundish and surrounded by plates arranged in a radial manner. The size of the lunules do not correspond to the samples from Sardinia (Stara & Borghi, 2014). It is clear that this form belongs to the genus *Amphiope*. However it is left in open nomenclature, *Amphiope* sp. 3, since the type species of *A. bioculata* Des Moulins, 1837 still needs definition.

Both the morphotypes recognised within the sample of "*Amphiope*" *pedemontana* Airaghi, 1901 have an oral plate structure corresponding to the plating pattern of *Echinodiscus* given by Durham (1955) and Smith & Kroh (2011). Also the axially elongate lunules and the plate arrangement around them indicate that they belong to the genus *Echinodiscus* (Figs. 2a–c).

The first morphotype corresponds to the original description and is herein assigned to *E. pedemontanus* (Airaghi, 1901). The other form is left in open nomenclature, *Echinodiscus* sp. 1, since only two are available to study and they are poorly preserved.

The specimens of "*Amphiope duffy*" Gregory, 1911, from Cyrenaica (Libya) (Plate 3 Figs. 1–6), show a plate structure in the aboral side which is quite different from the plate patterns of *Amphiope* and *Echinodiscus*. The arrangement of the plates surrounding the lunules is linear as in *Echinodiscus* but there are 3–4 couples of plates between the lunules and the corresponding petal tips. It is noticeable that one of the petals is open distally, as in *E. pedemontanus*. Since the oral plating of these echinoids is not visible, better preserved material is needed to clear the systematic position of this form.

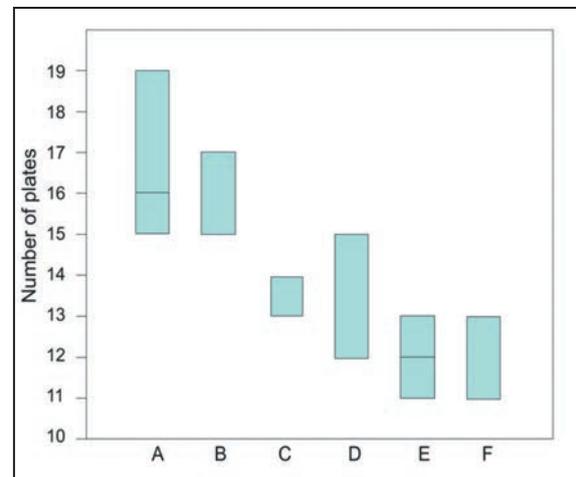


Figure 10. Numbers of post-basical plates comparison in *Amphiope* from different geological age. A, B: *A. nuragica*, Oligo-Miocene, respectively inter. 5 and ambulacrum III. C, D: *Amphiope* sp. 2, Late Burdigalian, respectively inter. 5 and amb. III. E, F: *Amphiope* sp. 3, Late Serravallian, Tortonian, respectively, inter. 5 and amb. III.

The oral and aboral structures of the large sample of *E. bisperforatus* from various localities of the Indian Oceans and the Red Sea match with the plating schemes given by Durham (1955), Jansen & Mooi (2011), Smith & Kroh (2011). It seems likely that different species may be present within the studied sample (Plate 4 Figs. 1–8; Plate 5 Figs. 1–3), however further studies are needed to clear the question.

Samples attributed to "*E. tenuissimus*" L. Agassiz, 1847. The first morphotype (Fig. 3a) has both the oral and aboral plate structure that does not match those of *E. bisperforatus* Leske, 1778, and is closer to "*E. auritus*" studied by Stara & M. Fois

(2014). The plates arrangement of the oral interambulacrum 5 and the number of couples of plates between the petal tips and the corresponding lunules is high and matches those of “*E. auritus*” (Fig. 9a, b). Also the particular branching of the food grooves matches with that of “*E. auritus*”. Based on these observations this morphotype is placed into *Sculpsitechinus* n. gen.

Since the holotype of *E. tenuissimus*, from Wai-giou, eastern Indonesia is wanting, a specimen from Lembeh, North Sulawesi (eastern Indonesia) is proposed as neotype of *Sculpsitechinus tenuissimus* (L. Agassiz, 1847) (Plate 11 Figs. 5, 6).

The second morphotype from Andaman Sea of Thailand, has the plating structures of oral and aboral faces that match with *Echinodiscus*, since in the oral interambulacrum 5 the postbasicoronal plates 2b and 2a are paired as well as 3b and 3a (Fig. 3b). Also the axial lunules and the structure of the plates surrounding them matches with those of *E. bisperforatus*.

This morphotype which is a true *Echinodiscus* and, given the differences between it and the other species of this genus, as we shall see in the chapter of the systematic, is here named *E. andamanensis* n. sp.

The third morphotype from Indonesia (Borneo), has the plating structure of the oral interambulacrum 5 with the two first postbasicoronal plates staggered as in *Amphiope* (Fig. 3 c), but it has the plate arrangement that encircling the lunules as in *Echinodiscus*.

It is evident, now, that this form belongs to a new genus. Therefore, we introduce *Paraamphiope* n. g., as it has some similarities with *Amphiope*. This morphotype is named *Paraamphiope raimondii* n. sp., after the collector who donated the specimen to our museum.

The specimens labeled *Echinodiscus truncatus* from Singapore, has a plate structure of the oral interambulacrum 5 that matches with that of *Echinodiscus* (see Fig. 4), but they differ from other species of *Echinodiscus* in many features, that make us consider this a true *E. truncatus* (L. Agassiz. 1841).

Also the specimen collected from Hurgada, Red Sea, shows the plate structure of the oral interambulacrum 5 corresponding with that of *Echinodiscus* (Figs. 5a, b). They differs from *E. andamanensis* n. sp. and *E. truncatus* by the position of the periproct, that opens more rearmost, between the plates 2a/3b/3a. This is likely a different

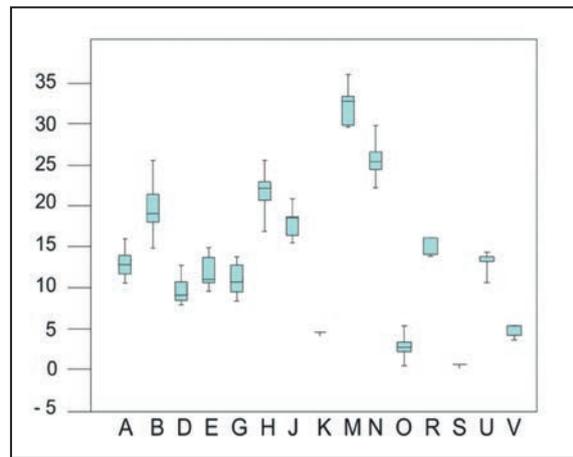


Figure 11. Comparison of lunules size variability in *Amphiope*, *Echinodiscus* and *Sculpsitechinus* species. A-B: respectively, L1 and L2 variability in *A. lovisatoi*. D, E: respectively, L1 and L2 variability in “*A. bioculata*” in Cottreau (1914). G, H: respectively, L1 and L2 variability in *A. nuragica*. J, K: respectively, L1 and L2 variability in *E. truncatus*. M, L1 variability in *E. bisperforatus*. N, O: respectively, L1 and L2 variability in *S. auritus*. R, S: respectively, L1 and L2 variability in *E. andamanensis* n. sp. U, V: respectively, L1 and L2 variability in *S. tenuissimus*.

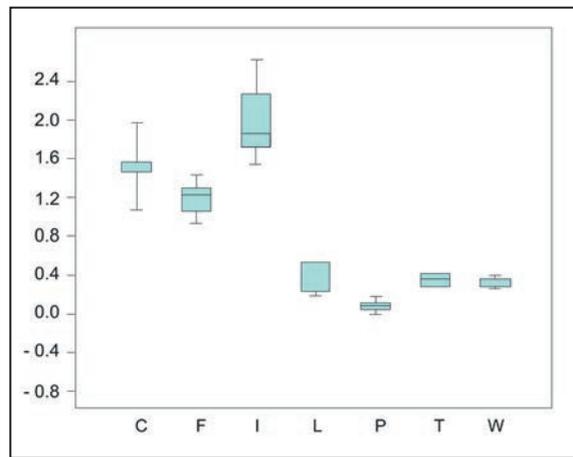


Figure 12. Comparison of differences and variability in lunules shape utilizing SI. C: *Amphiope lovisatoi*. F: “*A. bioculata*” in Cottreau (1914). I: *A. nuragica*. L: *Echinodiscus truncatus*. P: *Sculpsitechinus auritus*. T: *E. andamanensis* n. sp. W: *S. tenuissimus*.

species but, since the sole specimen available to study is poorly preserved, it is left in open nomenclature: *Echinodiscus* sp. 2.

The examined specimens of “*Amphiope*” *arcuata* Fuchs, 1882, from the “Miocene” of

Libya, has the oral plate structure on interambulacrum 5 (Fig. 2d) that matches with *Paraamphiope raimondii* n. sp. It differs by *P. raimondii* by greater distance between petal tips and lunules and by longer lunules. Based on these characters this form is attributed to *Paraamphiope* genus novum and assigned to *Paraamphiope arcuata* (Fuchs, 1882).

The specimens labeled as *Echinodiscus desori* Duncan et Sladen, 1883 are incomplete and the sole oral face visible is only partially legible. Using the available data, these echinoids probably belong to *Echinodiscus*, by the shape of the lunules and by the arrangement of the plates surrounding them (Plate 6 Figs. 1–6). Also the petals, clearly open distally, connect them to *E. pedemontanus*.

The sample of “*Amphiope bioculata*” des Moulins described by Cottreau (1914) (Plate 7 Figs. 1–11) likely belongs to the genus *Amphiope* L. Agassiz, 1840, by the large petalodium, that in some specimens gets up to 60% TL, the roundish lunules with a SI value of about 1.5, and the distance of the lunules from the tips of the petals which is very short. However, it is not possible to attribute these specimens to *A. bioculata*, since their plate structure was not reported by Cottreau (1914) and, on the other hand, the type species of *Amphiope* still needs defining.

The “*Lobophora aurita*” illustrated by L. Agassiz 1840 (Fig. 6), clearly belongs to the *Sculpsitechinus* n. gen., by the plate structures, close to that of *S. auritus* (Leske, 1778) and *S. tenuissimus* (L. Agassiz, 1847) (see Plate 11 by comparison). The oral interambulacrum 5 has 4 couples of postbasical plates, with 2b and 2a partially staggered and low WA value. There are six couples of plates between the petal tips and the corresponding notches and the PL is very small. It differs from the above mentioned species by the periproct that opens between plates 3a and 3b.

Since the original specimen is wanting, this species is left in open nomenclature: *Sculpsitechinus* sp. The species *E. formosus*, *E. yeliuensis*, *E. cikezenensis* and *E. transiens* were based on specimens with the oral face covered by sediments. Lacking the important characters of the oral face, such as the interambulacral plating, a comparison with the type species *E. bisperforatus* is unreliable.

For any other consideration see the conclusions chapter.

DISCUSSION ON MORPHOMETRIC AND MORPHOLOGICAL ASPECTS

In the following some relevant characters and morphometric values highlighted by the studies of Stara & Fois (2014) and Stara & Borghi (2014) are compared with the results of this study. This can be useful for further studies to improve the knowledge of this interesting family of echinoids.

The sample of *Amphiope* examined by Stara & Borghi (2014) and in this work, represents a time span that ranges from the Chattian-Aquitania to the Serravallian-Tortonian (about 13–14 Ma). Furthermore, this sample confirms what has been observed by Stara & Borghi (2014): in the echinoids belonging to this family, during the geologic time, there was a downward trend with a decreasing total number of plates. The sample examined in this study also includes other genera of astriclypeids like *Echinodiscus*, which are present from Rupelian to Recent, *Paraamphiope*, which runs from the middle Miocene to the present and *Sculpsitechinus* that may have been present in the Miocene and is very wide spread in the Recent.

Durham (1955) noted that the number of plates on the oral face is fixed at the end of metamorphosis, whereas some new plates are formed in the aboral face during the early stages of growth (e.g. from 2–3 mm to 10–15 mm TL). No significant variation in the total number of plates per column was observed by Durham on both oral and aboral faces of the examined adult individuals (TL = 50 to 62 mm).

The same result emerges also from the available sample of *Sculpsitechinus auritus* (former *E. auritus*) from Mangili, consisting of about thirty specimens with TL ranging from about 70 mm to 150 mm (see Stara & Fois M., 2014). Smith (2005) confirmed that the number of plates in adult clypeasteroids remains almost unchanged during the stages of growth in this group of echinoids (see Fig. 10).

In samples of *Amphiope*, on the other hand, we can see one particularity: there is a decrease in the overall plate number as a consequence of the “geological age”. Kier (1982) noted that there was a trend within cassiduloids for a decrease in the number of plates through time, and this may reflect a general trend towards fewer and earlier formed plates (from Smith, 2005).

We can deduce that the *Amphiope* with greater number of plates is more archaic than that with

lower number of plates. It would be logical that this should also be observed in "*Echinodiscus*", but it is not obvious, in part due to the heterogeneity of the treated samples, which look more like a paraphyletic group than a monophyletic one, and in part due to the presence of too many gaps in the fossil records.

On the variability in size and shape of the lunule/notches

From the comparison between the samples examined, we observed that lunules are variable in shape and in dimension, and that the greater variability seems to affect only some species and some populations.

The sample utilized by Cottreau (1914) seems to show the largest variability range of the lunules (variance), which is respectively 49% on L1 average and the 45% on L2 average; the other samples decidedly show a lower variability, which ranges between 22% in *E. bisperforatus* and 41% in *Paraamphiope arcuata*.

Moreover, the finding of distorted lunules has been the normality, as noted by Stara & Borghi (2014) on over 100 complete specimens of *Amphiope* from Sardinia and many fragments with lunules belonging to different species and localities, and this can often make worthless the measures.

Comparing in a graph the size of L1 and L2, detected in a larger sample [40 specimens of *A. lovisatoi* (data from Stara & Borghi, 2014); 11 "*A. bioculata*" in Cottreau; 25 *A. nuragica*] however, we see that the sample of Cottreau's "*Amphiope*" is not the more variable, but that the more variable is *A. lovisatoi* from Sardinia. The graph (Fig. 11) shows that, despite the significant variability in the size of lunules, remain clear the specific differences (see in particular the difference between "*A. bioculata*" in Cottreau and *A. nuragica*).

Using the SI and WI data, in "*A. bioculata*" in Cottreau, SI range from 0.95 to 1.47 (mean 1.22) (Table 6); in *A. nuragica* the SI range from 2 to 3 (mean 2.4). As demonstrated (see Table 8), this system highlights the real differences very well.

Now, if we compare the SI of the various samples utilized in the first graph (Fig. 11), the specific differences between *A. lovisatoi*, "*A. bioculata*" and *A. nuragica* become very evident, (Fig. 12 C, F and I). About the samples of the other genera (*Echinodiscus* and *Sculpsitechinus*), instead, it is seen that the vari-

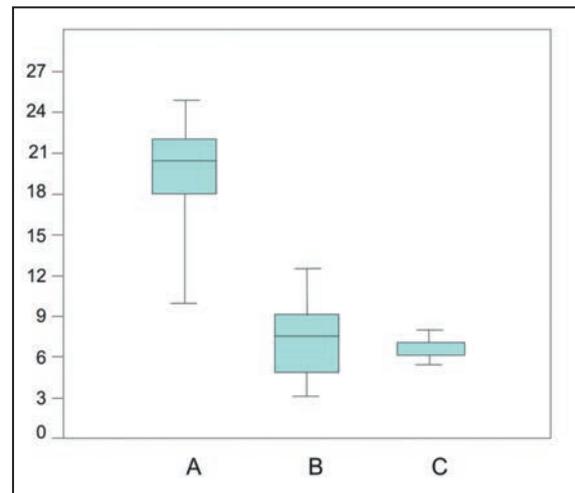


Figure 13. L1 comparison, respectively with *Sculpsitechinus* species (A), *Echinodiscus bisperforatus* group (B) and others *Echinodiscus* (C).

ability of lunules is much lower and the specific difference is highlighted much more through the measurement of L1 and L2 (see Fig. 11, samples J–V).

Finally, the lunules variability exists, but this does not make difficult to specific distinction. Indeed, it is demonstrated that the shape of the lunules (measured with the SI) becomes really distinctive between species.

On the plates arrangement encircling lunules/notches

The position of the lunules along the ambulacrum has visibly changed during time, but we can evaluate this change in the oldest species only partially, given that in most of the literature only the aboral face is shown and is sometimes incomplete.

Now, there are at least two possibilities: different starting point or finishing point of the lunules, and different number of couples of plates surrounding the lunula in the oral and aboral side.

As noted by Stara & Borghi (2014) the number of couples of plates that surround the lunules can vary greatly from species to species, and in particular look different between geologically younger species from geologically older ones.

In *Amphiope* from Chattian-Early Aquitanian from Cuccuru Tuvullao, the couples of plates that encircle aborally the lunules are 8–9, while in the oral face are 4–4 (about half); in the specimens

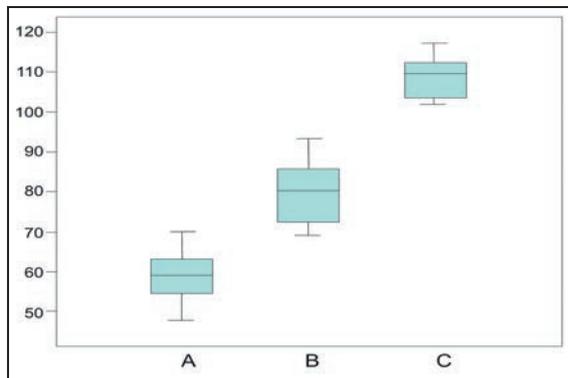


Figure 14. β angle comparison, respectively with: *Sculpsitechinus* species (A), *Echinodiscus andamanensis* n. sp., *E. truncatus*, *Echinodiscus* sp. 1, *Echinodiscus* sp. 2 (B), and *E. bisperforatus* group (C).

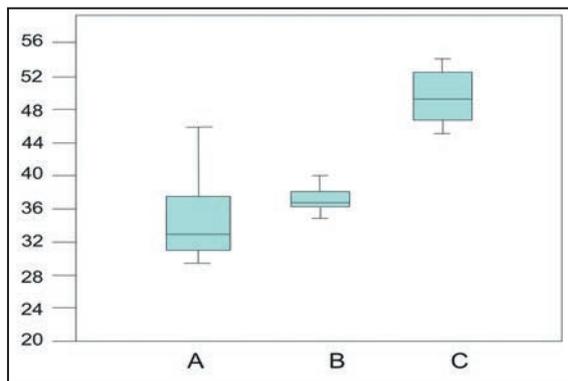


Figure 15. W_a comparison, respectively, with: *Sculpsitechinus* species (A), *Echinodiscus* and *Paraamphiope* species (B), and *Echinodiscus bisperforatus* group (C).

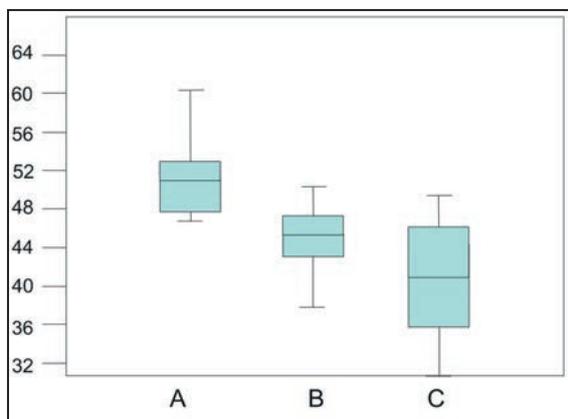


Figure 16. PL comparison, respectively, with: *Amphiope* species (A), *Echinodiscus* and *Paraamphiope* species (B), and *Sculpsitechinus* species (C).

from Channay-sur-Lathan the situation is 6–6 against 3–4, with an aboral/adoral ratio sharply decreasing.

In *E. pedemontanus* the couples of plates on aboral side ranges among 4–5 and 5–6; in the adoral side, however, they range from 2–2 to 3–3. It seems clear that the more archaic characteristics (greater number of plates) are located in *A. nuragica* (Comaschi-Caria, 1955), so this last one can not descend from *E. pedemontanus*, but could derive from a more archaic ancestor.

In other *Echinodiscus* fossils, we can observe the following: in *E. cikuzenensis*, on aboral side, the couples of plates are 6–6, the highest number between the fossils of their genus, but we do not know the number of the corresponding adoral ones (assuming that they are 8, the highest number known, the total number will be 14 plates per column, very far from the 16–20 of *A. nuragica*).

On the other hand, *E. bisperforatus* shows more plates than *E. andamanensis* n. sp., which has the lowest number of plates of all (see Table 6).

In all samples of *Amphiope*, between the lunules and the corresponding petal tips there are one or two pairs of plates (not occluded); while on the oral side the lunules begin constantly from the second pair of the post-basicoronal plates. (see Plate 9 Figs. 1, 2; Plate 10 Figs. 1, 2)

In *E. pedemontanus* there are 3–4 couples of plates between lunules and the corresponding petals tip, as in *Paraamphiope arcuata*.

Summarizing, in other forms of *Echinodiscus*, excluding *E. bisperforatus*, between the petal tip and the corresponding lunula/notch there are two-three pairs of plates (Plate 9 Fig. 4), and these are arranged in a linear manner, as in *E. bisperforatus*. Therefore these characteristics seem constant and diagnostic and in the future it will be necessary to take them into account. For more information see the respective plates and the plate patterns reported in plates 9, 10.

Migration of the periproct

The migration of the periproct is one of the main evolutionary processes of irregular echinoids (Durham, 1955; Kier, 1982); from the apical disc the periproct migrates towards the peristoma, viz, from the aboral surface shifts to the oral one. Echinoids of this family always have the periproct in the oral

face, between the peristome and the ambitus and it is clear that the periproct does not change its position with respect to individual plates after those plates have started to form, at the end of the metamorphosis, except for occasional cases (Durham, 1955).

But with the passing of geological time, its position is not fixed and immutable, nor is the plating that surrounds it. Thus, the "migration" of the periproct occurs simultaneously with changes in the plating and width of the plates, and in the internal structure, too. We noticed plate pattern modifications, that we believe to be diagnostic, as well as an increase or decrease in number, or breadth and shape changes, of the post-basicoronal interambulacral plates on inter. 5 and on the ambulacra I and V.

Considering the *A. nuragica*, *Amphiope* sp. 2 (in Stara & Borghi, 2014) and *Amphiope* sp. 3 series, which covers a Chattian-Aquitanian to Serravallian-Tortonian time-span, the position of the periproct to the relative plates seems to be indicative to the effect of time and evolution; indeed, the distance from the posterior margin has even decreased (L11 varies from a minimum of 10% of TL in *A. nuragica* to 4% TL in *Amphiope* sp. 3) simultaneously to the decreasing in size of the last echinoids.

In *A. nuragica* sample the periproct position relative to the plates is very variable; and this last one may open both between the plates closest to the rear edge (3a/4b), both between the most anterior ones (2a/3b), never between 2b/2a. We also noted that in this archaic form, the periproct position with respect to the related plates and their number, appear very inconstant, unlike the most recent forms.

In the sample of *Amphiope* sp. 2 the position-plates ratio is more steady, so the periproct always opens between plates 2a/3b, as in *Amphiope* sp. 3. However, in Cuccuru Tuvullao outcrop one can also find the morphotype with predominantly transverse lunules, *Amphiope* sp. 1 (see Stara & Borghi, 2014), with the periproct opened along the suture between the first two plates 2b/2a. This could indicate a convergent evolution of two close species, evolved at different speeds and in different environments, and probably found themselves in the same locality only by accident (in a slightly different times).

This last situation may depend on the well differentiated Oligo-Miocene faunas, and on the incomplete scene of the previous evolutionary steps, due to the fossil record gaps. Perhaps it will be

Sample	range SI	mean SI	range WI	mean WI	Variance L1	Variance L2
<i>Amphiope bioculata</i> , in Cottreau, 1914	0.95 ÷ 1.47	1.22	9 ÷ 12.5	10.20	49.2	45.4
<i>Amphiope nuragica</i>	2 ÷ 3	2.4	11.5 ÷ 15	13.5	36	22
<i>Amphiope</i> sp. 2	1.2 ÷ 1.5	1.3	11 ÷ 16	13	36	27
<i>Amphiope</i> sp. 3	1 ÷ 1.6	1.26	9 ÷ 10.5	9.8	34	27
<i>Echinodiscus pedemontanus</i>	0.26 ÷ 0.54	0.37	9.2 ÷ 11.2	10.4	--	--
<i>Paraamphiope arcuata</i>	0.45 ÷ 0.76	0.63	8 ÷ 10.5	9.3	36	41
<i>Sculpsitechinus</i> sp. 1	--		--		34	--
<i>Sculpsitechinus auritus</i>	--		--		29	--
<i>Echinodiscus bisperforatus</i>	--		--		20	--

Table 8. Comparison of index and data variation, between *Amphiope* samples and other astriclypeids genera.

possible to answer to this question by furthering studies on the structure of the samples from Provence and the Bay of Biscay ones.

In samples of *Sculpsitechinus* from Mangili and from Philippines the periproct always opens along the suture between the post-basical plates 2b/2a, while in the specimen from the Red Sea, illustrated by L. Agassiz (1840: pl. 14 fig. 2) and reproduced here in figure 6, it opens in the rearmost position, between the plates 3b/3a.

In the group of living *Echinodiscus andamanensis* n. sp., *E. truncatus* and *E. bisperforatus*, the periproct opens along the suture between the plates 2a/2b or at the junction 2a/2b/3b. In any case, these forms differ from the *Sculpsitechinus* "group" in which the periproct-posterior margin distance and the plates number on the inter. 5 is higher. In fact, within this group of living echinoids, the periproct distance (L11) varies from 11 to 25% TL, within a plating with more plates per column in interambulacrum 5 (2–3 in column "a" and 4–4 in column "b").

Plates number and shape on the interambulacrum 5 and periproct position

In plate 10 are summarized the results of our observations about these characteristics. Highlighting the diversity in the genera there are three platings. The distance between the periproct from the rear edge, its position along the perradial suture in the inter. 5, the shape and the relationship established between the various plates that form in particular the inter. 5 and the ambulacra I and V, seem highly diagnostic at the level of genus and species.

The distance of the periproct from the posterior margin is a characteristic which is considered to be very important by ancient authors. As we have already seen, its position is partially related to the arrangement, shape and size of the plates of the inter. 5. However, for the same plating, the distance may be diagnostic for the species, if it is confirmed by statistically significant numbers. Here we simply report what, in general, has been detected in the small samples which we examined (Fig. 13).

Angle β and WA

Given that rounded lunules can not show angles with respect to the corresponding petal, the

problem could be solved only studying the morphotypes with elongated lunules and in particular those elongated axially. In particular, the β angle seem very significant; important data are drawn by the quantification of this peculiar situation in tables 9. These data highlight different groups, corresponding to different species and / or genera, and in particular highlight *Sculpsitechinus* ($\beta = 55^\circ$ to 67°), *Echinodiscus* and *Paraamphiope* ($\beta = 70^\circ$ to 85°) and *E. bisperforatus* ($\beta = 105^\circ$ to 111°).

A characteristic which, up until now has been underestimated, is the size at the ambitus of the various ambulacral and interambulacral sectors. In particular, the WA at interambulacrum 5 appears to be very important, seeing it differentiates two of the genus studied by us: *Echinodiscus* and *Sculpsitechinus*. Furthermore, the *E. bisperforatus* group differentiates itself from the other.

Petalodium

One of the important aspects in these echinoids is the petalodium length (PL), which can be very different from group to group. In this comparison we considered a total of 54 specimens of *Amphiope*, according to the table 10. On the specimens from 11 different Sardinian localities (see also Stara & Borghi, 2014), the PL size ranges from 47 to 57% TL (mean 52 N42). In the totality of the specimens from Italy, Spain, France and Iran, the dimensions range from 45 to 60% TL (see Plate 8 Fig. 1), with the majority between 48 and 53%. In the sample of *Sculpsitechinus auritus* from Mangili in Stara & Fois (2014) PL is 34–45% TL, as in the sample of *S. tenuissimus* (29–45% TL) (see Plate 9 Fig. 8).

In *E. bisperforatus* PL is very variable, reaching from 40 to 52% TL. In this species, the front odd petal is always longer than the rear ones, which are always decidedly shorter. The size of the remaining "*Echinodiscus*" is very diversified and difficult to interpret, given the scarcity of the material available.

Another interesting feature is the presence of open petals in different species. In particular in *E. pedemontanus* the petals are all open. Some open petals are visible, however, also in *E. desori*, "*Amphiope*" *duffi* and, occasionally, even in *E. bisperforatus* (Fig. 16).

Sample	PL	WA	WA - range	β	β - range
<i>Amphiope nuragica</i>	49 - 53	42	38 - 46	--	--
<i>A. sp. 2</i>	50 - 54	38	37 - 40	--	--
<i>A. sp. 3</i>	50 - 53	32	29 - 36	--	--
<i>A. bioculata</i> in Cottreau, 1914	48 - 54	--	--	--	--
<i>Sculpsitechinus sp. 1</i>	41 - 48	33	30 - 38	57°	54 - 59°
<i>Sculpsitechinus tulearensis</i>	36 - 47	32	29 - 37	55°	48 - 62°
<i>Scupsitechinus auritus</i>	35	31	28 - 34	55	51 - 59°
<i>Sculpsitechinus tenuissimus</i>	30 - 45	32	31 - 35	67°	65 - 70°
<i>Paraamphiope arcuata</i>	42 - 46	31	33 - 35	85°	75 - 100°
<i>Paraamphiope raimondii</i>	47	38		80°	
<i>Echinodiscus desori</i> (India)	46 - 48	33	30 - 35	71°	68 - 74°
" <i>Amphiope</i> " <i>Duffi</i>	47	23		65°	
<i>Echinodiscus pedemontanus</i>	40 - 44	36	35 - 37	85°	73 - 93°
<i>Echinodiscus sp. 1</i>	44 - 46	37		69°	70 - 87°
<i>Echinodiscus sp. 2</i>	44	—		80°	
<i>E. andamanensis</i>	45.5 - 53	38	37 - 38	75.5°	68 - 85°
<i>E. cikuzenensis</i>	44	--		73°	
<i>E. bisperforatus</i> (Red Sea)	38 - 47	48	46 - 54	105°	102 - 110°
<i>E. bisperforatus</i> (S.Africa)	43 - 50	49	45 - 53	107°	102 - 117°
<i>E. bisperforatus</i> (Tanzania)	43	49		111°	
<i>E. formosus</i>		50		111°	
<i>E. Jeliuensis</i>	52?	34		114°	
<i>E. transiens</i>	52	--		--	

Table 9. Comparison of PL, WA and β range data in a large sample of astriclypeids. β in degree, other measures in % TL.

<i>Amphiope</i> (Sardinia, Italy)	47-57	52 N42
<i>Amphiope</i> (Alicante, Spagna)	48-51	49 N2
<i>Amphiope</i> (Channay-sur-Lathan, France)	51-53	53 N10
<i>Amphiope bioculata</i> in Cottreau, 1914	48-55	50 N11
<i>Amphiope serasini</i> (France)		50
<i>Amphiope deyderi</i> (France)		48
<i>Amphiope baquiei</i> (France)		48
<i>Amphiope elliptica</i> (France)		52
<i>Amphiope hollandei</i> (Corsica)		52
<i>Amphiope</i> cf. <i>bioculata</i> (Iran)		60

Table 10. Comparison of PL data in a large sample of *Amphiope*. Data in % TL.

Variability of the disjunction/contact between basicoronal and post-basicoronal plates

Random disjunctions between the basicoronal interambulacral plates and the related post basicoronal ones can be observed in many samples. For example, *Sculpsitechinus tenuissimus* from New Caledonia, *S. auritus* from the Red Sea and from Tulear, Madagascar, *E. bisperforatus* from Eastern Africa (see Jansen & Mooi, 2011) have high variability. The problem has already been studied by Durham (1955), who pointed out that more archaic scutellids show the basicoronal plates in contact with the following postbasicoronals, and that the separation is observable only in the most recent genera. He also noted that in *Dendraster excentricus* (Eschscholtz, 1831) from the Pacific coast of United States, juvenile individuals shown the basicoronal plates in full contact with the following ones. Furthermore, during growth, the second plate of each ambulacra grew faster than the others until its

separation from the second interambulacral ones, as indeed is observed in most representatives of the Astriclypeidae family.

Of all the species studied by Durham where this variation occurred, *Echinarachnius* showed the largest variability. Lohavanjiaya & Swan (1965) also studied this problem in more detail on some populations of *Echinarachnius parma* (Lamarck, 1816) from the coasts of New Hampshire (USA). These authors noted that there was a wide variability in the loss of contact between the basicoronal interambulacral plates and the corresponding post-basicoronal ones for each column, but it also varied the amphiplacous or meridoplacous conditions of the contact, when it was present. It demonstrated that the variation in the number of plates involved in the phenomenon followed individuals growth (size increase), and conceived that the phenomenon was caused by a selective response to genetically-induced modifications, at least partially, by different environmental factors for the different places where the tested samples lived. As for Durham's observations, we believe as normal (not diagnostic) the presence of basicoronal interambulacral plates in contact with the following post-basicoronal ones.

From the results obtained in particular from Stara & Fois M. (2014) on the sample of *Sculpsitechinus auritus* (Former *Echinodiscus* cf. *auritus*) from Mangili it is clear that the disjunction between the basicoronal and post-basicoronal plates in Inter. 5 is constant, but also that there is no constancy in disjunctions between the corresponding plates in other interambulacra (see Plate 5 Figs. 3–5). Moreover, from what emerges from the analysis of our sample, but especially from the sample (about 100 specimens) observed by Stara & Borghi (2014) were not basicoronal interambulacral plates in contact joint in *Amphiope*.

Differences in internal structure

As we have seen in the tested sample, while the morphology of these two groups of astriclypeids may be similar, the difference in the internal structures can be substantial. All groups have a single central visceral hollow with peripheral walls and pillars, but the floor reinforcement systems of the central cavity are profoundly different.

In *Sculpsitechinus* the floor is supported by a dense network of thin trabeculae or ribs (see Stara

& Fois M., 2014: pl. 2 fig. 7; pl. 4 figs. 6, 7), whereas in *Amphiope* the floor is supported by a system of thick masses, with appearance of callosity, modeled in different shapes depending on the species (see Plate 2 Figs. 2–4). Also the floor of the central cavity of *Parascutella* (personal observation) (but also of *Astriclypeus*) seems to have the same floor support structure that characterize *Amphiope* species.

Instead, the ballast system of all the astriclypeids is crossed by a different number of cavities more or less large, and by several micro-channels, which are distributed differently. A characteristic that does not appear to have been recognized enough so far is the size of Aristotle's lantern.

In percentage, the Aristotle's lantern is much larger in *Sculpsitechinus* sample from the Philippines than in the sample from Mangili, Madagascar (see pl. 6 in Stara & Fois, 2014).

However, some results obtained so far are very interesting. For example, the size of the Aristotle's lantern in *Paraamphiope raimondii* n. sp. is very large [27% of TL in a central hollow that measure 46% TL (Plate 19 Fig. 6) if compared to the 15–18% TL that characterize the Aristotle's lantern of *S. auritus* from Mangili (see Plate 23 Fig. 4) or the 15% TL of the Aristotle's lantern of *Sculpsitechinus tenuissimus* from Lembeh.

Other peculiarities

In *Amphiope*, the food grooves are always simple (Plate 1 Fig. 7), while they are always more or less branched in *Echinodiscus* and largely branched in *Sculpsitechinus* (Plate 22 Fig. 4).

INFLUENCE OF PALEOGEOGRAPHY DURING EOCENE-MIOCENE

Stara & Rizzo (2014), hypothesized that the Oligocene closure of the pre-Pyrenean corridor caused a separation (or the exchanges decreasing) between the North-Western Atlantic faunas and the Mediterranean ones. To understand the consequences of this, we need to study the evolutionary course of these faunas, in particular on the basis of the structural aspects.

From initial observations it appears that already in the late Rupelian-Early Chattian the scutellids

faunas of the Bay of Biscay were well differentiated. Even the "*Amphiope*" bearing axial lunules from Rupelian of Val Bormida had at least two morphotypes (Stara & Rizzo, 2013; 2014). In Early Miocene, the Rhône Basin was inhabited by "*Amphiope*" *boulei* Cottreau, 1914, a particular morphotype with small ellipsoidal axial lunules positioned far from their petals (Plate 14 Fig. 1); also during the middle Miocene, in Libya a similar morphotype appeared characterized by smaller and rounded lunules positioned far from the petals tip (Plate 14 Fig. 2). At the same time in India, *Echinodiscus desori* lived together *E. placenta* Duncan et Sladen, 1883, a form characterized by ellipsoidal axial lunules far away from the corresponding petals tip (Plate 14 Fig. 3). During Middle Miocene in Papua New Guinea lived another similar form, with long and narrow lunules (comparable with those of *Sculpsitechinus tenuissimus* (Plate 14 Fig. 4). Other morphotypes not appear so clear, as the "*Echinodiscus*" sp. from Miocene of Libya (Plate 14 Fig. 6), which has lunules open posteriorly, resembling the Recent *Sculpsitechinus auritus*.

Even *Amphiope* with rounded or transverse lunules was already well-differentiated, and widespread: this morphotype is found in the Bay of Biscay, in the Rhône basin, in central Sardinia and in the Kabylies.

Stara & Borghi (2014) found two different species of *Amphiope* with transverse lunules, both originating from Cuccuru Tuvullao, Sardinia, Chattian-Aquitania in age: *Amphiope nuragica*, and *Amphiope* sp. 1. Not far from this locality (both from the spatial and temporal point of view), in the localities of Duidduru, Bruncu Montravigu Nuraghe Caiu and Tanca Sierra, also a form characterized by rounded lunules (Stara et al., 2012) was present.

To complete our knowledge of the differentiations occurred between the Biscay faunas and those of the Proto-Western Mediterranean, it will be necessary to know the structure of "*Amphiope*" *agassizi* from Middle Oligocene, and *A. ovaliflora* from the Aquitania of the Atlantic coast, and furthermore "*A.*" *boulei* from the Rhône basin. Given the wide temporal and the spatial distribution of *Amphiope*, as previously described, it is probable that numerous speciation events occurred even in different French regions, as occurred in Sardinia.

EVOLUTIONARY TRENDS

Now, as proposed by Cottreau (1914), *Amphiope* would be descended from some Atlantic-European "*Echinodiscus*", deriving also from *E. formosus*, because this last might be geologically the oldest. But the situation seems more complex and the current phylogenetic tree needs to be reviewed. Obviously, this requires a careful study of cladistics, and so for now we will only formulate hypotheses based on observations arising from this work.

Echinodiscus formosus from ?Middle Eocene and *E. yeliuensis* from Early Miocene of Taiwan, already had some features comparable to those of the living *E. bisperforatus* (e.g. a similar β angle). This character and the lack of similar forms in the Oligo-Miocene peri-Mediterranean basins, suggest that this morphotype is derived from ancient faunas of the China Sea. But that does not seem true for other forms of *Echinodiscus*.

On the other hand, other common features such as the lunules shape and their distance from the corresponding petals, seem to connect "*Amphiope boulei*", "*Echinodiscus placenta*", ecc. (see Plate 14) to the group of *Sculpsitechinus*.

To clarify the relationship between the four groups which have emerged from this study (*Amphiope*, *Echinodiscus*, *Paraamphiope* and *Sculpsitechinus*), it is necessary to study more the internal structure of the various fossil forms of the far east and those that linked the north American faunas to the European ones.

It seems clear, however, that this trend has led to the current situation, in which we can see that, while *S. auritus* is spread throughout the Indian Ocean to the islands of the Western Pacific, the form *S. tenuissimus* seems confined to the Western Pacific (see Fig. 17). In these two forms, however, may also be included various species which only by new studies, based on more consistent sampling and analysis of pedicellaria and / or DNA, can be distinguished.

Among others, the most widespread form of *Echinodiscus* remains *E. bisperforatus*, while other forms seem very localized in restricted areas (see *E. andamanensis* n. sp. in the Andaman Sea and *E. truncatus* in the Singapore coasts). Even in this case, new studies, in part based on the analysis of the structure but also (for the living species) on other analysis, may better clarify their distribution areas.

For now, in figure 17 you can see the distribution areas of living forms so far recognized in this work.

OLD AND NEW PHYLOGENETIC HYPOTHESES

From the phylogenetic point of view, although several aspects still remain unclear, today we can say with reasonable certainty that in the dispute between Stefanini (1912) and Cottreau (1914) both had a share of reason. In fact, the thesis supported by Stefanini (1912) (he thought astriclypeids bearing axial lunules were real *Echinodiscus* and not *Amphiope*) is here confirmed for *E. pedemontanus* (former *A. pedemontana*).

However, as argued by Cottreau, the ancestor of "*A. boulei*" could also be the "*Amphiope*" with small axial lunules positioned far from their petals tips [such as "*Amphiope*" sp., from the Libyan desert (Plate 14 Fig. 2) and such *E. placenta* from India (Plate 14 Fig. 3)]. We partially agree with him when he states that the living *Sculpsitechinus auritus* (former *Echinodiscus* cf. *auritus*) that colonized the entire Indo-Pacific area, could be derived from these echinoids. In fact, if we compare morphology and distance lunules-petals in these echinoids, with the one detectable in "*E. bisperforatus*" from Papua New Guinea (Lindley, 2001) (Plate 14 Fig. 4) and *S. tenuissimus* from Lembah North Sulawesi and other East Pacific locality, (Plates 21, 22), we will see that they are relatively overlapping. We do not agree with Cottreau, however, when we examine the oldest *E. formosus* and *E. yeliuensis* from Taiwan. In fact, β angle and distance between lunules and respective petals tips, seem to suggest them as being the ancestors of the living *E. bisperforatus*.

The fact that some features (shape of the plates in inter. 5 and the periproct position, etc...) accost them very closely to the *E. pedemontanus*, let us assume at least two possibilities. First presumes that already during the Middle Eocene these astriclypeids were very diversified and spread along the shores from the Atlantic to the China Sea; second, however, one presumes that from a single common ancestor who lived in the northern basins of the Atlantic Ocean during the Eocene, two forms detached. These last ones migrated then in opposite directions: one towards the inland basins of the

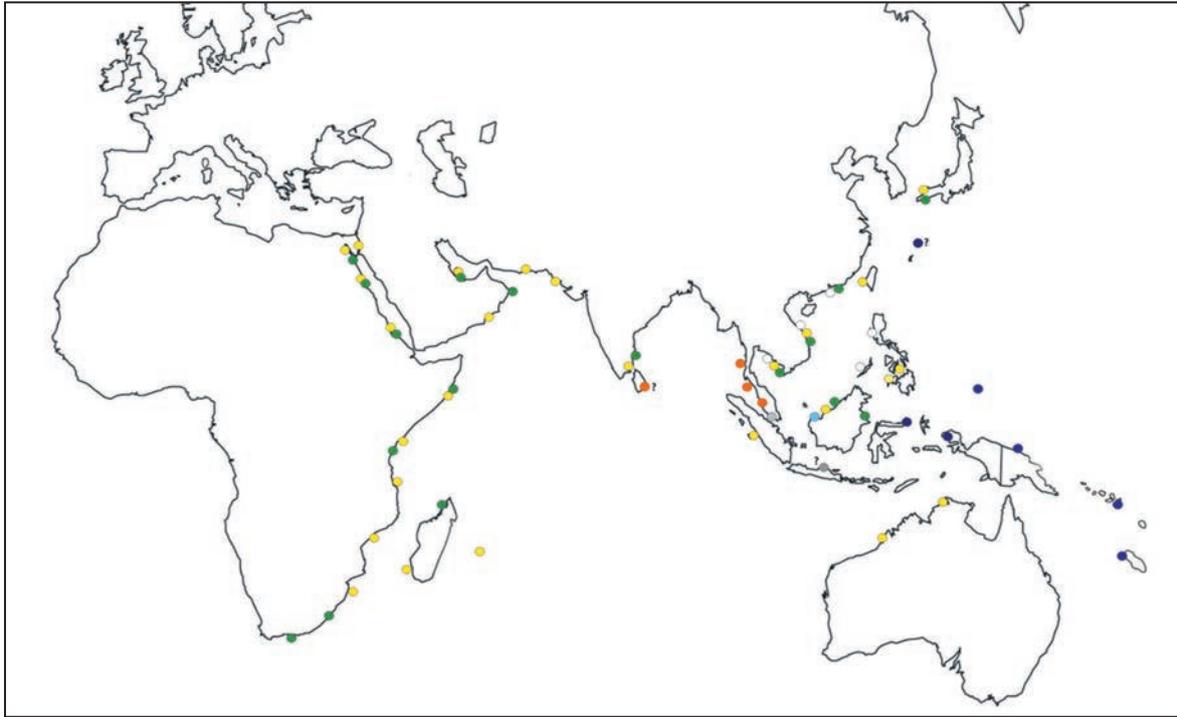


Figure 17. Distribution of extant main “*Echinodiscus*” morphotype, *Sculpsitechinus* and *Paraamphiope* species. From Mooi (2014) the GBIF portal; Ashley (personal communication, Dec. 2013); Hattenberger (personal communication, Dec. 2013), Mooi (1989). Other data by cited authors. Yellow dots: *Sculpsitechinus auritus* group. Blue dots: *S. tenuissimus*. Orange dots: *Echinodiscus andamanensis* n. sp. Grey dots: *E. truncatus*. White dots: “*Echinodiscus*” cf. *tenuissimus*. Green dots: *E. bisperforatus* group. Light blue dots: *Paraamphiope raimondii* n. sp.

Proto-Mediterranean sea and then to the Middle East; the other one towards the Western Pacific basins to the north of the Eurasian continent.

Figure 18 shows the phylogenetic hypothesis emerged from this research.

TAXONOMIC CONCLUSIONS

In the samples we analyzed there are clear internal structural differences between *Echinodiscus* and *Amphiope*. Important differences can also be observed at the specific level, especially in the morphology of the central hollow floor.

To understand some of undetermined features in the fossil individuals, the use of living species specimens for the comparison allowed us to solve several problems that were unsolved for a long time.

Despite the great variability in shape and lunules/notches size shown by some groups of astriclypeids, the shape of the lunule remains an important data for the specific distinction. We have seen that

other characters are also useful to specific and generic distinction; particularly, we should consider the platings of the two test faces, and the differences in the internal structure, where possible. The comparison of pedicellaria and spines, not always considered in this work, need further studies, particularly in the living populations and can help us in the determination of the variety and/or species, also by molecular examen.

The detection of the test plating allowed comparisons based on reliable data; the use of appropriate indicators in the statistical comparison, as operated by Stara & Borghi (2014) can provide, moreover, a further diagnostic tool.

Among the astriclypeids examined in this work, the specimens of the Chattian-Aquitainian from Cuccuru Tuvullao have the highest number of plates in the inter. 5, the backward position of the periproct (with respect to the post-basical plates on inter. 5) and also the highest number of couples of plates surrounded the lunules. These characters and the massive and strong structure make them apparently the most archaic of all the taxa included in this com-

parison group. It follows that this *Amphiope* does not descend from *E. formosus*, but from an older common ancestor. This is also true for *E. pedemontanus*, "*Amphiope*" *duffi* and *E. desori*, which can not be the ancestor of the said *Amphiope*.

Also the comparison of the internal structures between *Amphiope* and *Sculpsitechinus* makes it clear that these two groups are not as similar as they seem, but their common origin moves further back in time.

As a result of these observations, it is clear that all forms of *Amphiope* bearing round or transverse lunules, today grouped under the specific name of *A. bioculata*, as proposed by Philippe (1998) need to be revised, since their distinctive characters have not yet been published up to now or have been underestimated. It is obvious, moreover, that among the species of *Amphiope* of Sardinia and those of the group of "*Echinodiscus*" there is no direct connection.

In this group of comparison, the knowledge of the arrangement, number and size of the post-basical plates that characterizes the oral face of the inter. 5 and the aboral one, shows a different subdivision of the genera and a species distinction previously unrecognized. Referring to the data obtained with our present work, we can say that the petalodium size has a diagnostic importance at generic level: it is small in echinoids of the new group *Sculpsitechinus* (30–47%) and wider in *Amphiope* (45–60%). In any case, this characteristic must be always used together with others, since in some groups, such as the *E. bisperforatus*, it is very variable.

Given the different morphologies and morphometric diversity observed between the samples of "*E. bisperforatus*" group here examined (Plate 4 Figs. 1–8), we believe that there is also the basis for looking for the presence of different species, but this will be the subject of future research. Jansen & Mooi (2011) propose the examen of the pedicellaria of living echinoids to differentiate species. In paleontology, unfortunately, this possibility is almost always precluded, since the soft parts or the minute parts hardly preserve in the sediment. However, careful observation of the skeletal parts, such as test, internal structures, Aristotle's lantern, can partially allow the distinction between genera and also between species, acting as a support of the soft parts study.

Despite the lack of available data, we can already say that the genus of French "*Amphiope*" bearing axial lunules, such as *A. agassizi* and *A. boulei*, and of the East regions, such as *E. placenta*, from Miocene

of India, are not real *Amphiope* or *Echinodiscus*; these species should be re-studied and assigned to different genera. However, the morphological and morphometric comparison of Miocene astriclypeids as "*Amphiope boulei*", "*Amphiope*" sp. from Libya, "*E. bisperforatus*" from Papua New Guinea, with those that characterize the new genus *Sculpsitechinus*, allow us to assume that the first ones may be the ancestors of the latter one and all are detached from *Amphiope* and *Echinodiscus*.

Even the series from ?Eocene to Miocene, *Echinodiscus formosus*-*E. yeliuensis* and living *E. bisperforatus* could be consistent. In fact, all these echinoids share some distinctive characters such as the angle β and the distance between lunules and petals tips, which places themselves in a close phylogenetic relationship, and detaches them from both *Amphiope*, *Sculpsitechinus* and *Paraamphiope*. Strictly speaking, even the *Echinodiscus formosus*, *E. jeliuensis* and *E. bisperforatus* series should be moved in a separate genus, but also in this case it is needed to restudy the specimens of Taiwan and deeply study also the different forms of living "*E. bisperforatus*".

It is also evident the diversity of *E. transiens* from all other supposed congeners, in particular by the dimension of the sole visible lunule, and by the petalodium size, that would fit it between the real *Amphiope*. Even in these cases, however, nothing certain can be defined, until we know the oral face plating of the specimens in object.

With regards to the astriclypeids present in the Middle East Miocene, despite the different works published (among others, see Kier, 1972), the illustrations and platings published are insufficient to determine with any certainty the belonging to a genus rather than another. From bibliographical data we believe it could be *Echinodiscus* or *Paraamphiope*, but only a new study will clarify the real systematic position of these echinoids. We add only that, according to a specimen present in NHMUK London, *Amphiope* was also present in the Miocene of Mosul (Iraq) and in the Gulf of Aqaba (Arabian peninsula).

Finally, although we have observed that the condition of open petals is quite common in the astriclypeids and perhaps also in other scutellids of neighboring families, this important character, mentioned by Airaghi (1899;1901), joins *Echinodiscus pedemontanus* to "*Amphiope*" *duffi* and *E. desori*, and allows us to reconfirm the existing link between their regions.

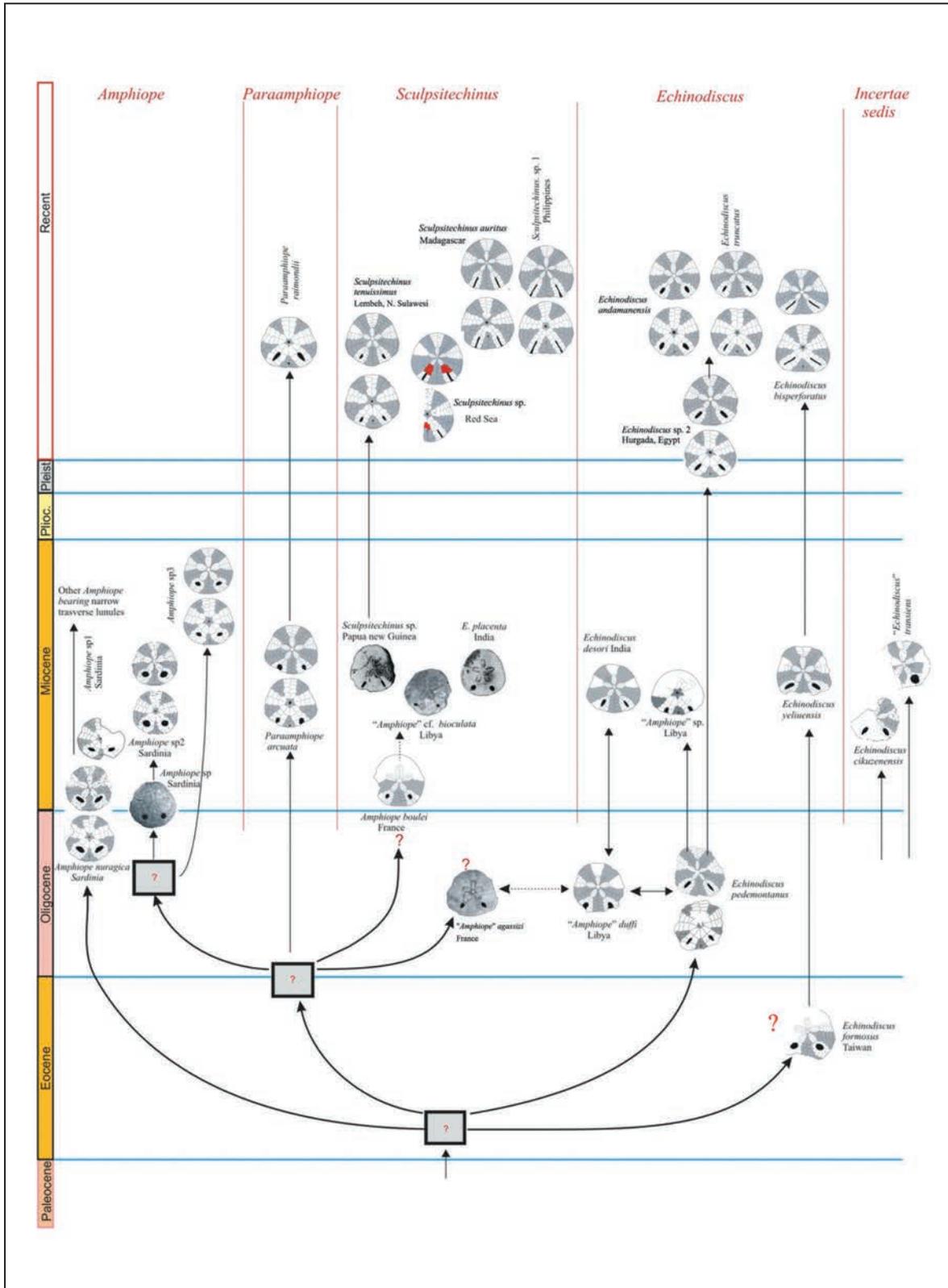


Figure 18. Hypothesis of phylogenetic relationships between *Amphiope*, *Echinodiscus*, *Paraamphiope* and *Sculpstiechinus* genera.

All three of these echinoids have some petals which are open or partially open, an uncommon (or ignored) character in echinoids of this family. Indeed, we observed in *E. bisperforatus* that even one or more petals are open or tend to be open. Based on these conclusions, in figure 18 is proposed a new phylogenetic hypothesis, waiting appropriate cladistic new studies on the genera and species of this family.

In conclusion, according to the results highlighted, four clusters emerge at the generic level of species hitherto treated and a new distribution of living species studied as in figure 17.

1. *Amphiope*, including: *A. nuragica*; *Amphiope* sp. 1; *Amphiope* sp. 2 from Bancali; *Amphiope* sp. 3 from Channay-sur-Lathan and all other species from Sardinia treated by Stara & Borghi (2014)

2. *Paraamphiope*, including “*Amphiope*” *arcuata* from Libya and “*Echinodiscus tenuissimus*” from Indonesia, here renamed *Paraamphiope arcuata* and *P. raimondii* n. sp.

3. *Echinodiscus*, including: *E. bisperforatus*; *E. andamanensis* n. sp. and *E. truncatus*; *E. formosus*, *E. cikuzenensis*, *E. jeliuensis*, *E. desori*; finally, *E. pedemontanus* and *Echinodiscus* sp. 1 from Italy and *Echinodiscus* sp.2 from Red Sea.

4. *Sculpsitechinus*, including all the “*Echinodiscus* cf. *auritus*”; “*Echinodiscus tenuissimus*” of New Caledonia, Micronesia and some “*E. tenuissimus*” from Indonesia; “*Echinodiscus bisperforatus*” of Papua New Guinea, which would be a new species. All renamed here as follows: *Sculpsitechinus auritus* from Mangili; *S. tenuissimus*, *Sculpsitechinus* sp. 1 and *Sculpsitechinus* sp. 2.

All other nominal species of “*Amphiope*” and “*Echinodiscus*” discussed herein and not included in these four groups will have to be reviewed, given the few characteristics known at the present.

Finally, a clear zonation of living *Sculpsitechinus* and *Echinodiscus* in the Indo-Pacific Seas is highlighted, as a prelude to further investigations about the old bibliographic citations on the presence of “*Echinodiscus* cf. *tenuissimus*” in the Oceania and in the Andaman Sea (see Fig. 17).

In order to facilitate the understanding of the main characteristics that differentiate the species and genera treated here, we have summarized the main differences in Tables 13 and 14.

Specimens	Apx	PL	WA	β
IVM82	4.5	39	34	55
IVM83	5	38	31	53
IVM84	4.5	38	32	57
IVM85	4.5	40	29	49
IVM86	4.5	40	33	58
IVM87	4.5	38	30	56
IVM88	4.5	36	32	56
IVM89	4.5	39	32	50
IVM90	4.5	38	32	54
IVM91	6	40	34	59
IVM92	5.5	41	32	54
IVM93	5.5	41	32	56
IVM94	5.5	38	31	57
IVM95	5	39	33	62
IVM96	5	39	33	54
IVM97	5.5	43	33	57
IVM98	5.5	41	32	53
IVM99	5.5	38	29	58
IVM100	4	39	35	56
IVM101	5	41	31	53
IVM102	5.5	41	32	53
IVM103	5	43	31	56
IVM104	5	41	33	55
IVM105	6	42	33	57
IVM106	5.5	38	31	59
IVM107	5	37	31	48
IVM108	4.5	40	37	
IVM109	5	40	31	54
IVM110	4.5	43	32	53
IVM111	4.5	38	34	65
IVM112	6	47	37	55
mean	5.6	39.8	32.3	55.4
Range	4 - 6	36-47	29-37	48 - 62

Table 11. Apx, PL, WA and β data in the sample of *Sculpsitechinus auritus*. β in degree, other data in % TL.

Table 12 (right). Simplified morphometric data of *Echinodiscus*, *Paraamphiope* and *Sculpsitechinus* samples from different localities; TL in mm, β in degree, other measures in % TL.

Specimen	TL	TH	L1	L2	S1	L4	L11	WA	PL	β
<i>Echinodiscus andamanensis</i> PMBC 26346	81	9,1	11.3	5.6	0,49	55	5.1	-	49	85
<i>Echinodiscus andamanensis</i> PMBC 2642	66	9,5	17.6	6.8	0,38	53	4.2	-	51	83
<i>Echinodiscus andamanensis</i> PMBC 2643	66	10,1	12.1	5.2	0,43	52	7.6	-	51	68
<i>Echinodiscus andamanensis</i> PMBC 2644	66	10,1	15.5	4.9	0,31	52	9.6	-	53	73
<i>Echinodiscus andamanensis</i> PMBC 2830	54,6	9,1	14.9	5.2	0,35	53	4.1	-	46	75
<i>Echinodiscus andamanensis</i> PMBC 2643.1	50	.	13	5.1	0,39	51	7.2	-	52	71
<i>E. andamanensis</i> ZMUC-ECH-1001	37	-	15	6.7	0,44	53	6.5	38	45.5	71
<i>E. andamanensis</i> NL	-	-	13.3	4.1	0,30	50	6.8	36	47	78
Mean <i>E. andamanensis</i>		9,58	14.3	5.4	0,44	52	6.6	37	49	75.5
MAC.PL 1850	31	11	18	6	0,33	56	5.5	37	44	81
MAC.IVM 206.	59	13,5	20	6,6	0,33	51	7	36	42	80
<i>E. truncatus</i> , Singapore S137a	60	-	14.6	4.2	0,28	57	9.5	37	49	68
<i>E. truncatus</i> , Singapore S137	51		15.3	3.9	0,25	57	10	37	51.5	65
<i>E. truncatus</i> , Singapore S1			19.6	4.2	0,21	57	10.8	37		71
<i>E. truncatus</i> , Singapore S2			17.6	4.2	0,21		10.3			64
<i>E. truncatus</i> , Singapore S3			17.6	3.4	0,19	57	11.5		50	67
Mean <i>E. truncatus</i>			16.9	3.98	0,22	57	10.4	37	50	67
<i>Sculpsitechinus tenuissimus</i>	TL	TH	L1	L2	S1	L4	L11	WA	PL	β
N. Cal. in Dollfus & Roman	121	-	12.5	4	0,32	54	11	31	30	65
NHMUK.59.7.1.14	112	9	10	4	0,4	54	13	31	38	70
NHMUK.1981.11.2.25	120	9	12.5	3.5	0,28	55	10	31	45	67
ANU 60549	70	—	14	4	0,28	—	..	32	46	61
MAC.IVM 207	50	10	13	4	0,30	56	11	34	35	66
Lembeh 1	62	8	13	5	0,38	—	14	33	34	74
Lembeh 2	60	-	13	5	0,30	56	16.5	35	35	68
N. Cal. 1 (Hattenb. coll)		-	16	4,5	0,28	56	17	33	37	61
Mean <i>Sculpsitechinus tenuissimus</i>		9	11,7	4,2	0,28	55	13,2	32,5	37,5	66,5

Table 13 (down). Comparison between different old and new astriclypeid genera: contact between interambulacral plate 2b and the adjacent ambulacral plates. A= amphiplacous; M=meridoplacous. β in degree, other data in % TL.

Genus	PL	Main characters of inter. 5				L11	other
		WA	A	M	β		
<i>Astriclypeus</i>	47	39		x	75	19	5 ambulacral lunules; floor of the central hollow reinforced by massive thickening; highly branched food grooves
<i>Amphiope</i>	45-61	29-46	x		----	4-13	Transverse or rounded posterior lunules; floor of the central hollow reinforced by massive thickening; simply food grooves
<i>Paraamphiope</i>	42-46	31-38	x		75-2100	3.5-12	Axial posterior lunules; floor of the central hollow reinforced by ribs; highly branched posteriorly food grooves
<i>Echinodiscus</i> "tenuissimus group"	40-50	35-38		x	70-81	5.5-8	Axial posterior lunules; floor of the central hollow reinforced by ribs; simply food grooves; sometime branched posteriorly food grooves
<i>Echinodiscus</i> "bisporatus group"	38-50	45-54		x	100-117	3.5-12	Axial posterior lunules; floor of the central hollow reinforced by ribs; sometime branched posteriorly food grooves
<i>Sculpsitechinus</i>	30-47	30-33		x	48-70	11-24	Axial posterior lunules; floor of the central hollow reinforced by network of ribs or trabeculae; highly branched food grooves

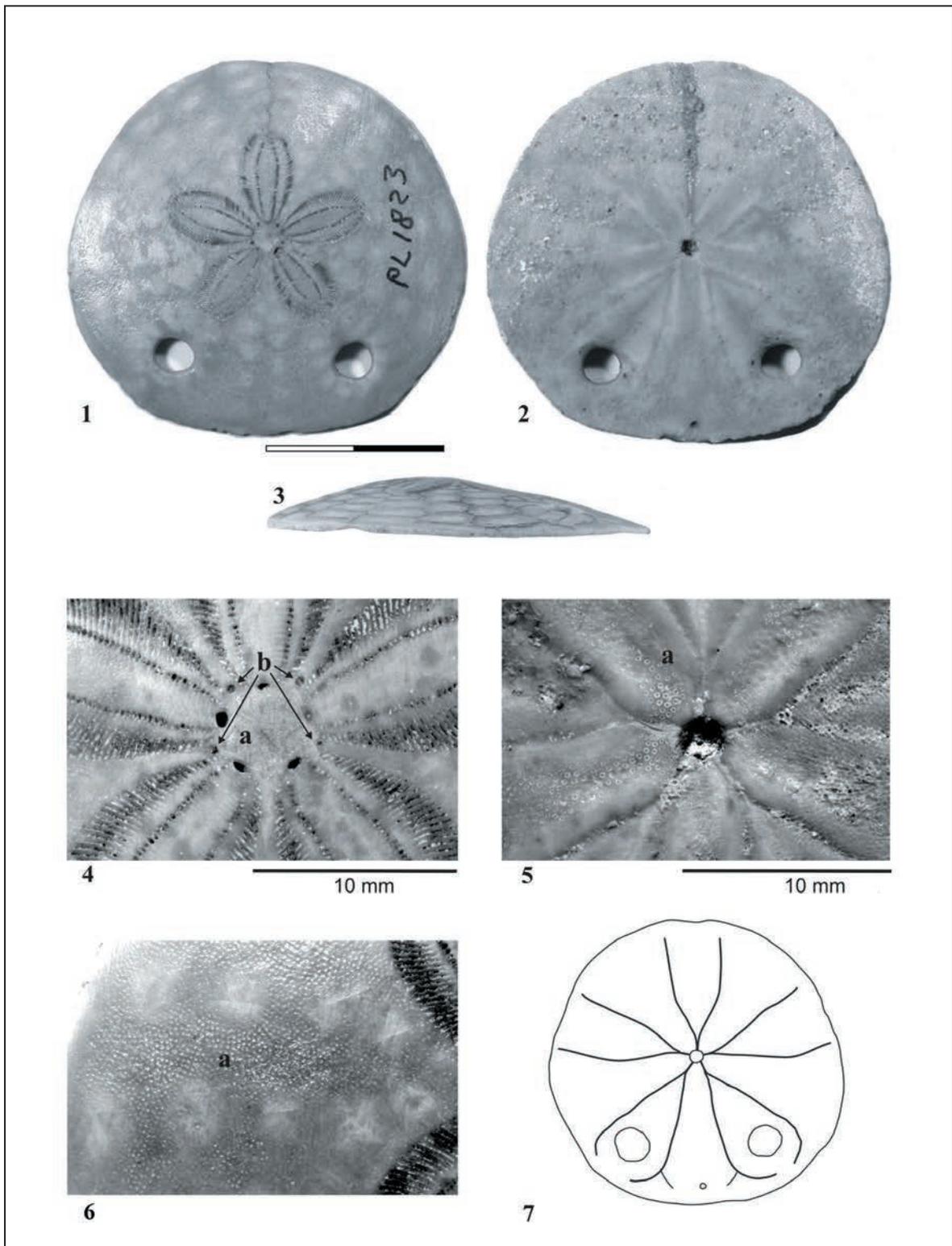


Plate 1. *Amphiope* sp. 3 from Channay-sur-Lathan, France (late Serravallian-early Tortonian): external features. Figs. 1–3. Aboral, adoral and antero (to the left)-posterior (to the right) lateral view of MAC.PL1823; Fig. 4. Apical disk with (a) madreporite (b) genital pores; the other pores at the tips of the petals are ocular pores; Fig. 5. Stoma, basicoronals circling with tuberculation and food grooves; Fig. 6. Aboral view with (a) undifferentiated tuberculation; Fig. 7. Pattern of very simple food grooves.

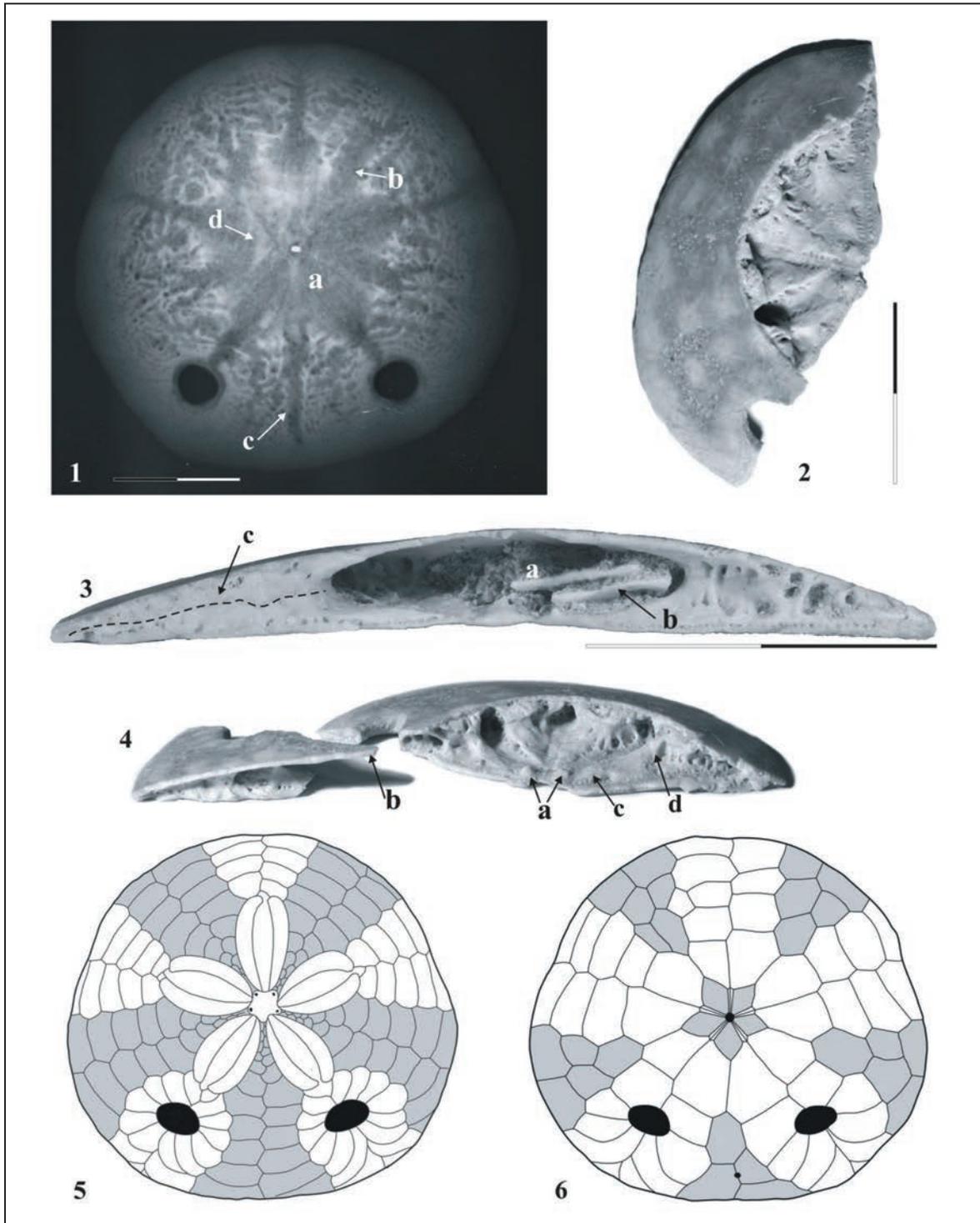


Plate 2. *Amphiope* sp. 3 from Channay-sur-Lathan, France (late Serravallian-early Tortonian): internal features and plating. Fig. 1. radiography of MAC.PL1668; a: central hollow; b: caecum cavity; c: terminal intestine cavity; d: small disarticulated Aristotle's lantern. Fig. 2. Test fragment showing the internal structures of the central hollow. Fig. 3. Cross antero (to the right)-posterior (to the left) section of the test; a: central hollow; b: wings of the Aristotle's lantern c: middle conjunction plan of the reinforcement structures. Fig. 4. Antero-posterior cross-section of the echinid; a: lantern supports; b: section of ceiling; c: massive floor reinforcement; d: pillars and buttresses of the peripheral reinforcement system. Fig. 5. Plating of aboral face of MAC.PL1668. Fig. 6. Plating of adoral face of MAC.PL1668.

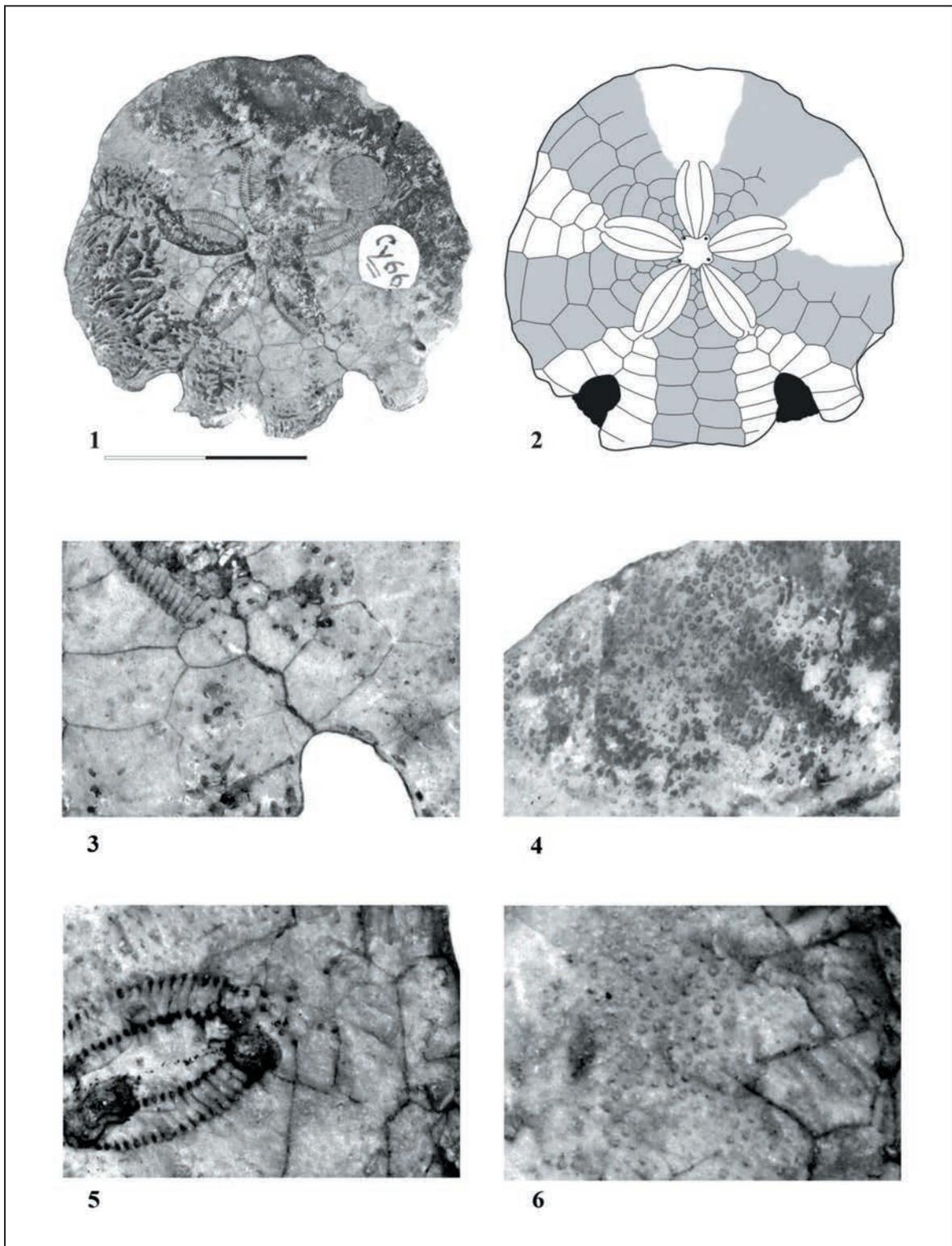


Plate 3. "*Amphiope*" *duffi* from Sidi Rof Diasiasia, Cyrenaica, Libya (early Oligocene). Figs. 1, 2. Aboral view of NHMUK: CY66/E11350 and corresponding aboral plating. Figs. 3, 4. Open posterior right petal and aboral tuberculation of NHMUK.CY66. Figs. 5, 6. Ambulacrum II with open tip and aboral tuberculation on NHMUK.CY264. In particular, from Figures 3 and 5 it is noted that in the tip of the petals no plate is occluded.

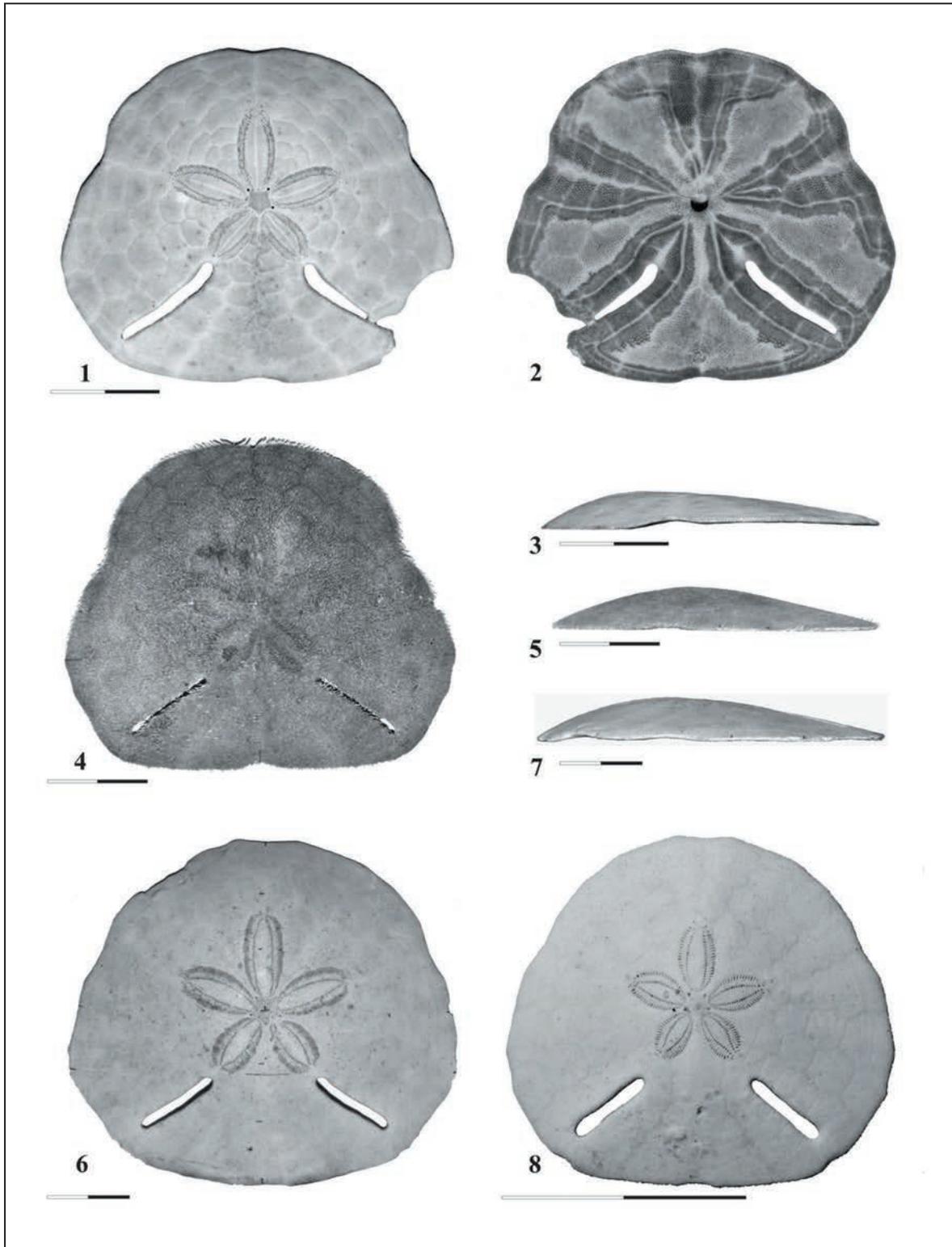


Plate 4. *Echinodiscus bisperforatus* from different localities (Recent). Figs. 1–3. Aboral, adoral and antero (to the left)-posterior (to the right) lateral view of NHMUK.2013.7 from South Africa. Figs. 4, 5. Aboral and antero (to the left)-posterior (to the right) lateral view of NHMUK.2013.3, from Eritrea. Figs. 6, 7. Aboral and antero (to the left)-posterior (to the right) lateral view of NHMUK.1957.5.21.3, from Tanzania. Fig. 8. Aboral face of juvenile IVM.206 from north Madagascar.

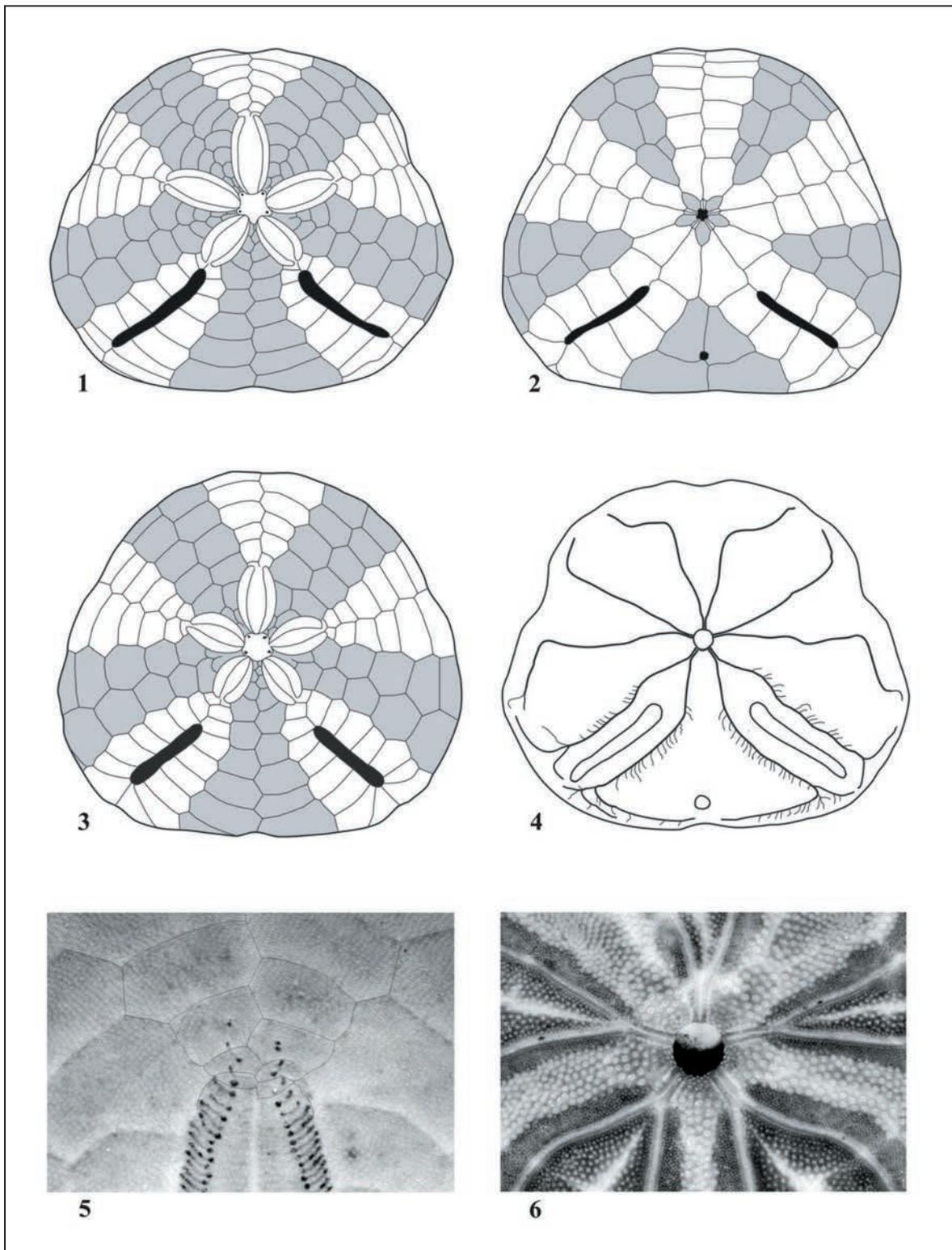


Plate 5. *Echinodiscus bisperforatus*, platings and peculiarities in specimens from different localities (Recent). Figs. 1, 2. Plating of aboral and adoral face in two specimen from South Africa. Fig. 3. Plating of aboral face in MAC.IVM.206, juvenile from Madagascar. Fig. 4. Scheme of food grooves in a specimen from South Africa. Fig. 5. Open anterior odd petal in NHMUK.2013.7 from South Africa. Fig. 6. Peri-oral tuberculation in specimen NHMUK.2013.7 from South Africa.

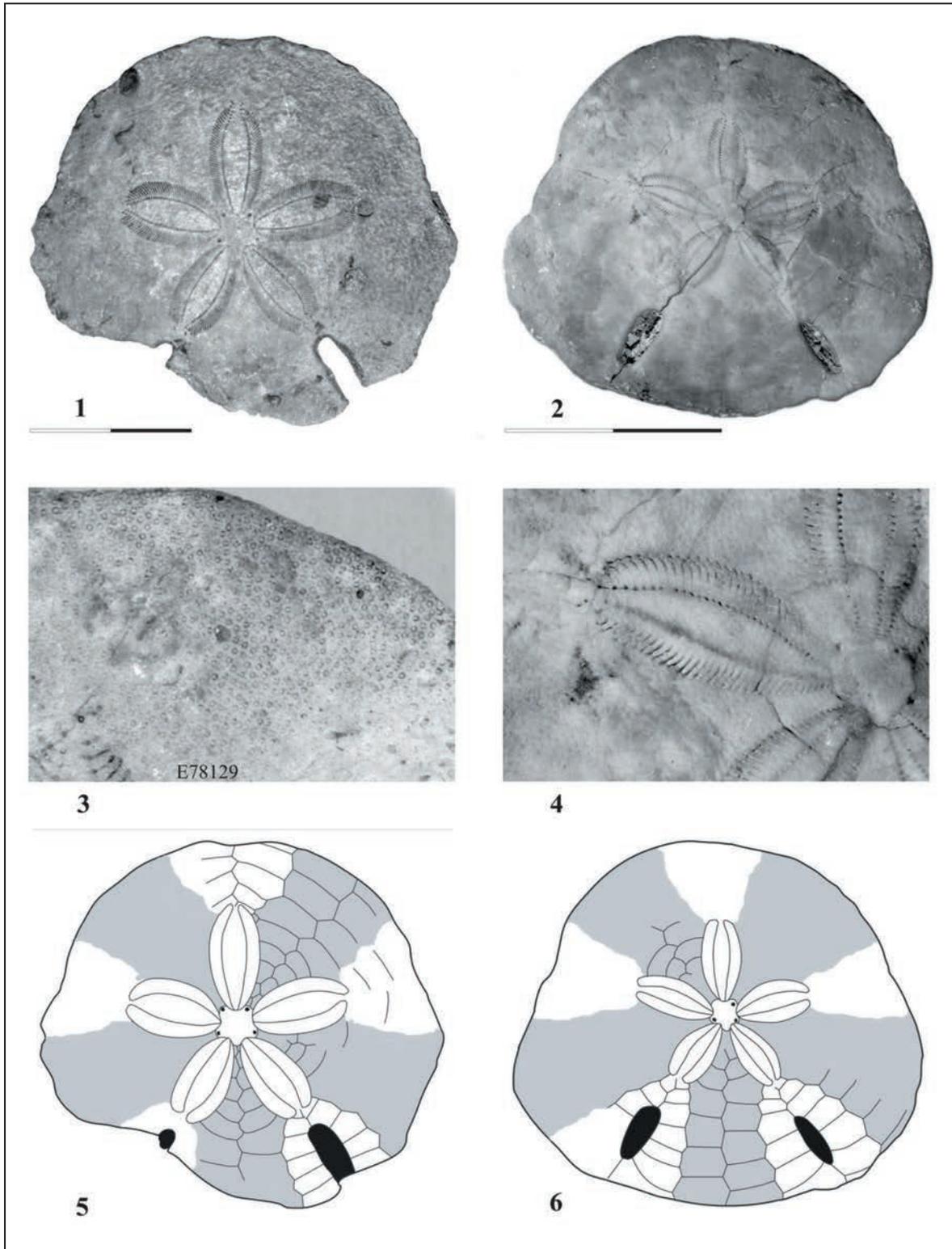


Plate 6. *Echinodiscus desori* from India (Miocene). Fig. 1. Aboral face of NHMUK.E78128a. Fig. 2. Aboral face of NHMUK.E78129. Fig. 3. Aboral tuberculation, NHMUK.E78129. Fig. 4. Ambulacrum IV with open tip, NHMUK.E78129. Fig. 5. Plating of aboral face of NHMUK.E78128a. Fig. 6. Plating of aboral face of NHMUK.E78129. Is noticeable that these samples have in common with those of Cyrenaica some petals open.

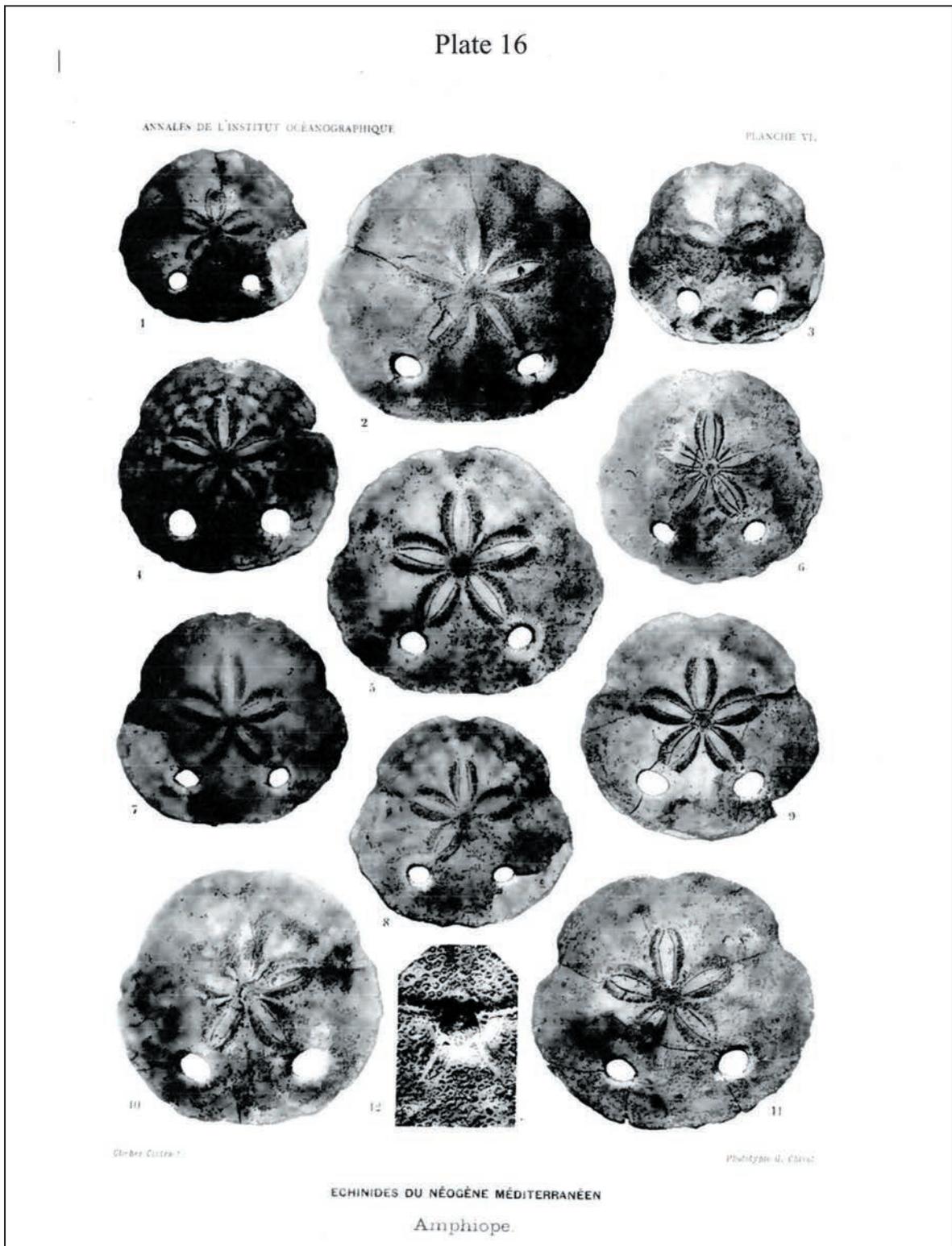


Plate 7. In this fine example of morphological variability of a small portion of *Amphiope* population, Cottreau (1914) shows visually what the morphometric data has confirmed. But inadvertently he also highlights that none of these forms can match with those of other species, such as, for example, *A. nuragica*. However, looking closely at the lunules, one can also see the normal deformations and growth differences between the two lunules of the same specimen.

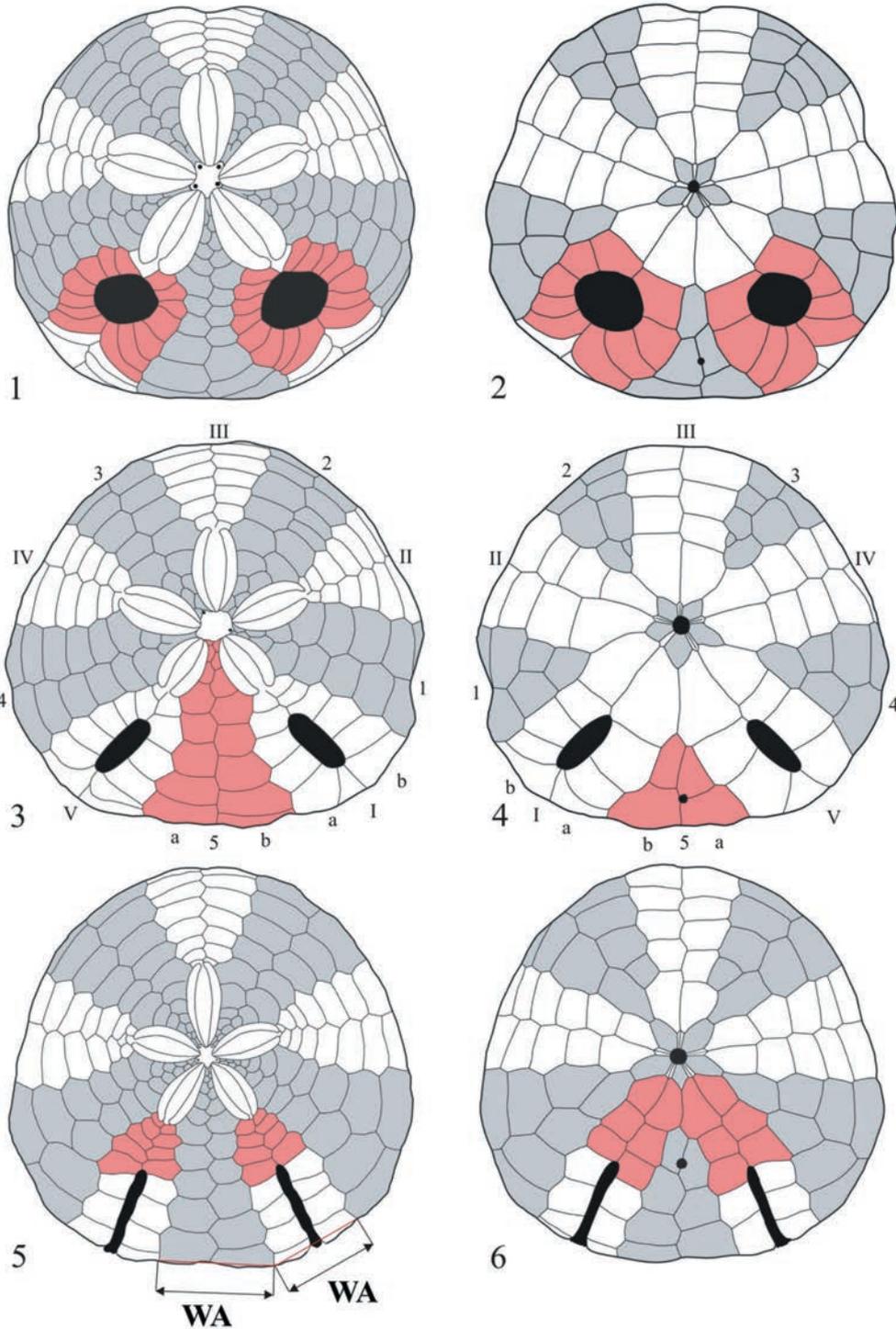


Plate 8. Examined features colored in reddish; interambulacra shaded gray. Figs. 1, 2. *Amphiope montezemoloi*, arrangement of plates surrounding lunules in oral and aboral face. Figs. 3, 4. *Echinodiscus* sp. 2, plate arrangement of interambulacum 5 on oral and aboral faces; numbering according to Loven's System. Fig. 5. *Sculpsitechinus auritus*, plates between notches and petal tips; measure of ambulacral and interambulacral areas at ambitus. Fig. 6. *S. auritus*, plates between basicoronals and notches.

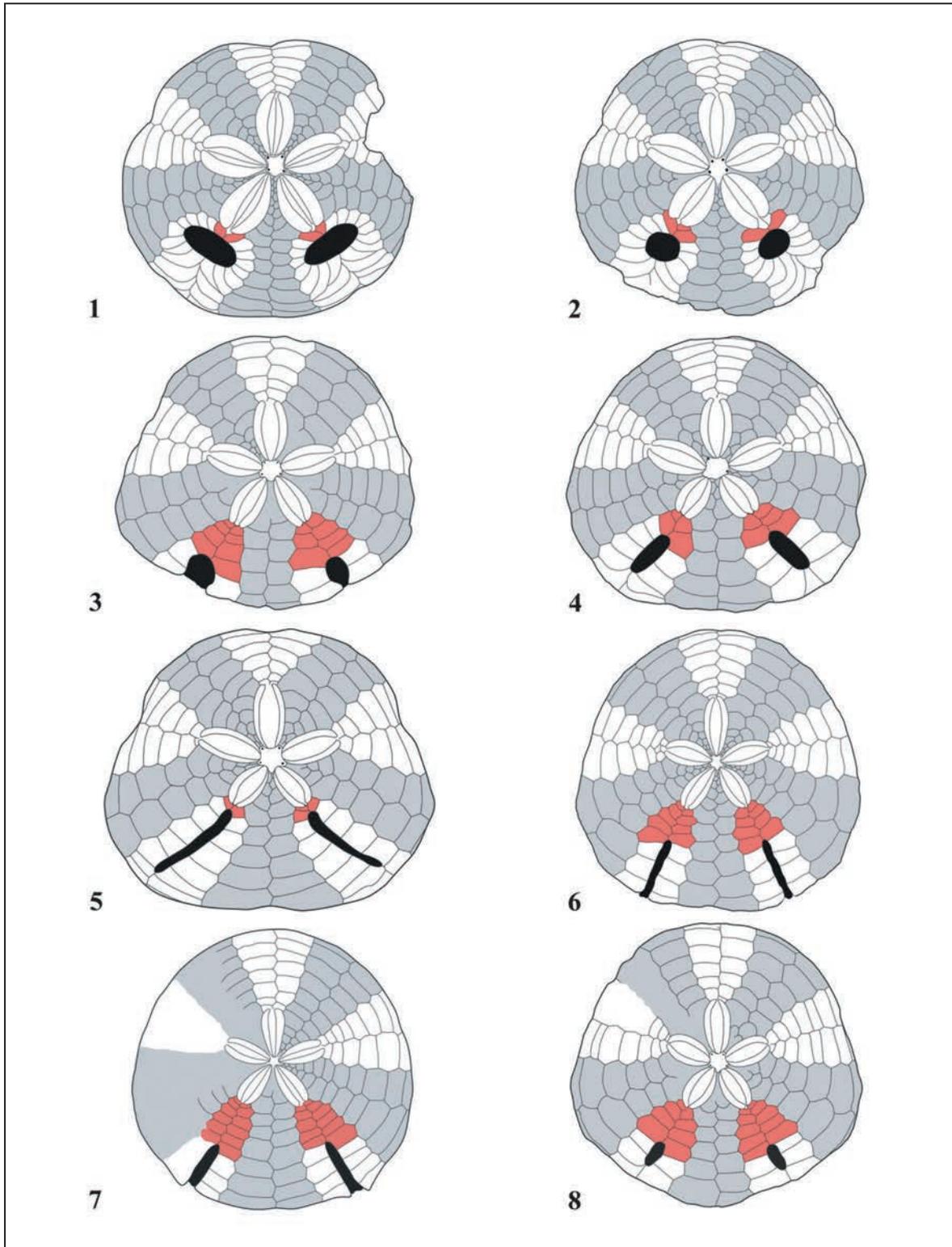


Plate 9. Comparison of number of plate couples between lunules and petal tips on aboral faces—examined features colored in reddish, interambulacral columns shaded gray. Fig. 1. *Amphiope nuragica*. Fig. 2. *Amphiope* sp. 2 from Bancali, Sardinia. Fig. 3. *Paraamphiope arcuata*. Fig. 4. *Echinodiscus* sp. 2. Fig. 5. *Echinodiscus bisperforatus*. Fig. 6. *Sculpsitechinus auritus*. Fig. 7. *Sculpsitechinus* sp. Fig. 8. *Sculpsitechinus tenuissimus*.

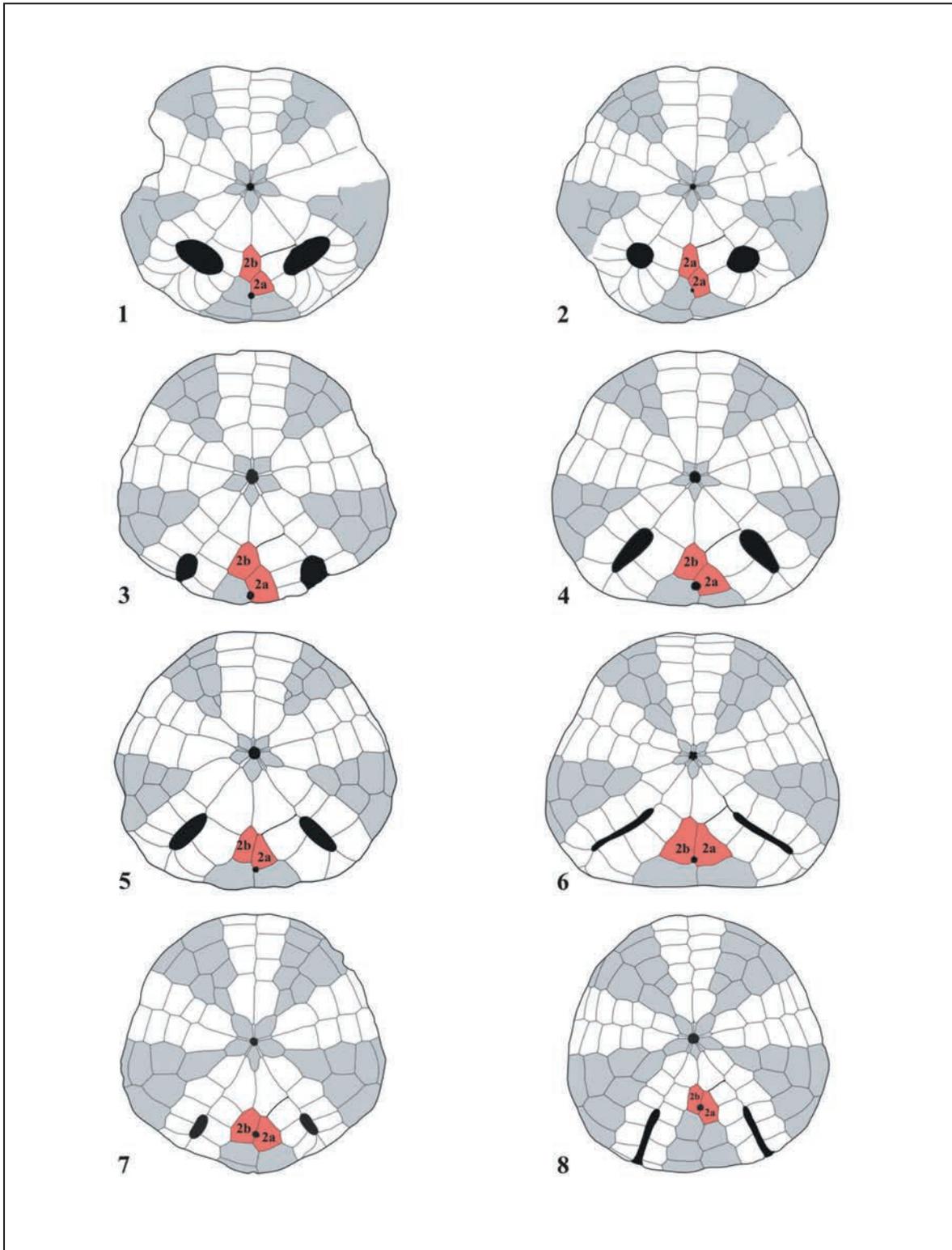


Plate 10. Comparison of number, shape and disposition of plates on oral interambulacrum 5 - examined features colored in reddish, other interambulacral columns shaded gray. Fig. 1. *Amphiope nuragica*. Fig. 2. *Amphiope* sp. 2 from Bancali, Sardinia. Fig. 3. *Paraamphiope arcuata*. Fig. 4. *Paraamphiope raimondii*. Fig. 5. *Echinodiscus* sp. 2. Fig. 6. *Echinodiscus bisperforatus*. Fig. 7. *Sculpsitechinus tenuissimus*. Fig. 8. *Sculpsitechinus auritus*.

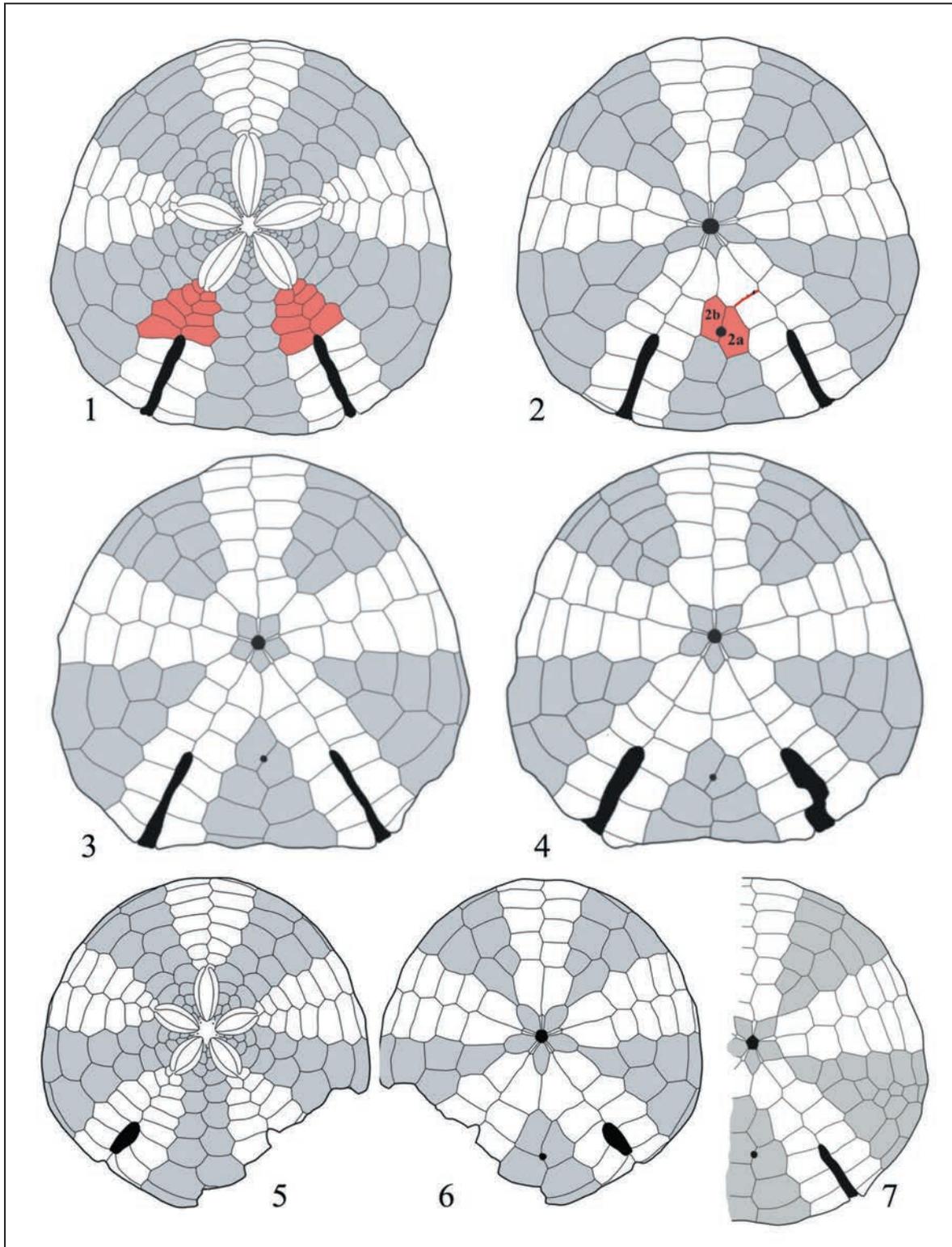


Plate 11. Plating features comparison in *Sculpsitechinus* species, interambulacral columns shaded gray. Fig. 1, 2. *Sculpsitechinus auritus*. Fig. 3, 4. *Sculpsitechinus* sp. 1 from the Philippines. Fig. 5, 6. *Sculpsitechinus tenuissimus* from Lembeh, Indonesia. Fig. 7. *Sculpsitechinus* sp. (in Agassiz, 1841). We can observe some common features: large number of plates between lunules/notches and the petal tips; high number of plates in the oral interambulacrum 5.

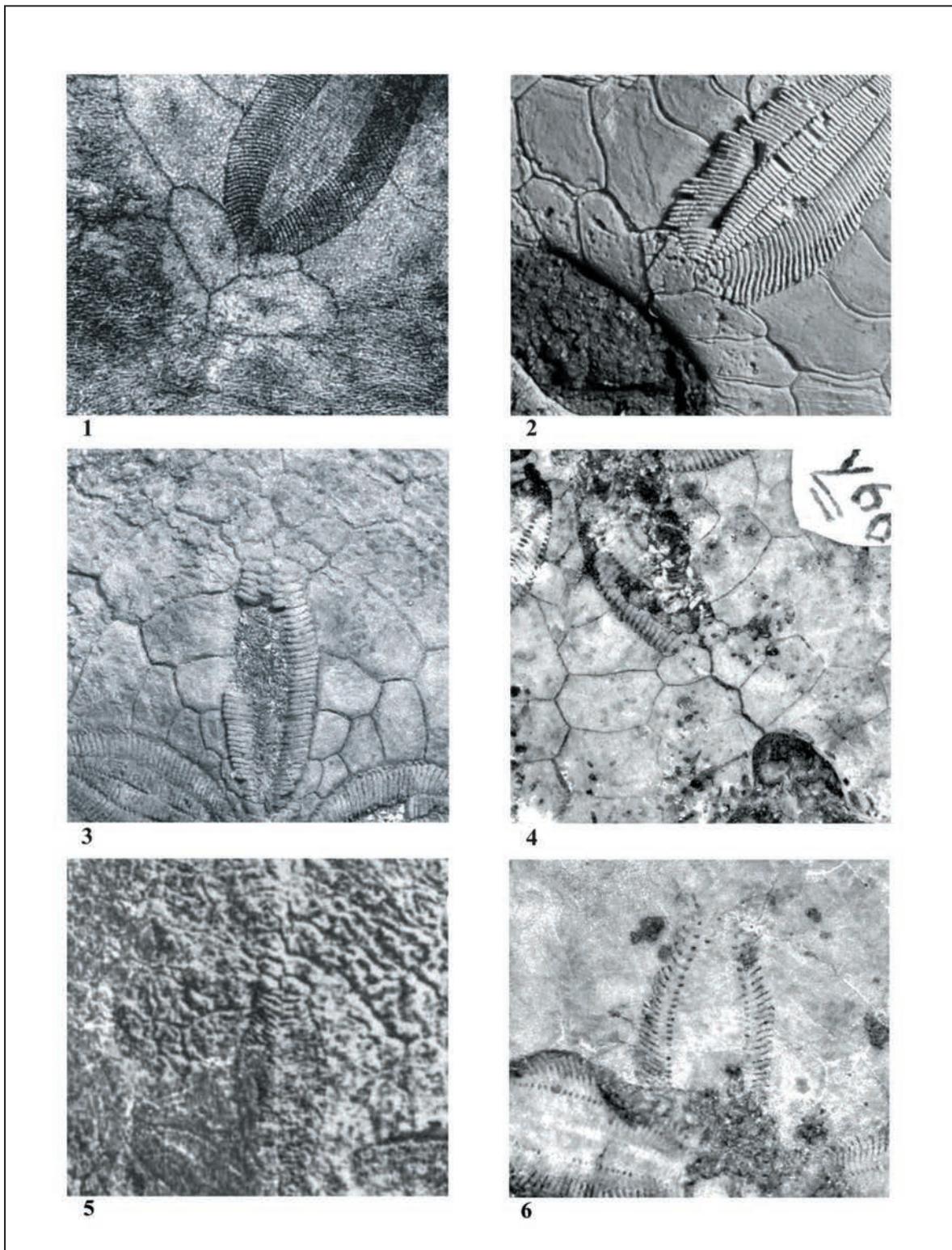


Plate 12. Petals open and petals closed in living and fossils species. Figs. 1. *Sculpsistechinus auritus* from Mangili: closed petal tip with ocluded plates. Figs. 2. *Amphiope nuragica*: closed petal tip with ocluded plates. Figs. 3, 5, 6. *Echinodiscus pedemontanus*: anterior odd petal open; 3 and 5 with gradual tip plate downsizing. Fig. 4. "*Echinodiscus*" *duffi*: posterior right petal tip open.

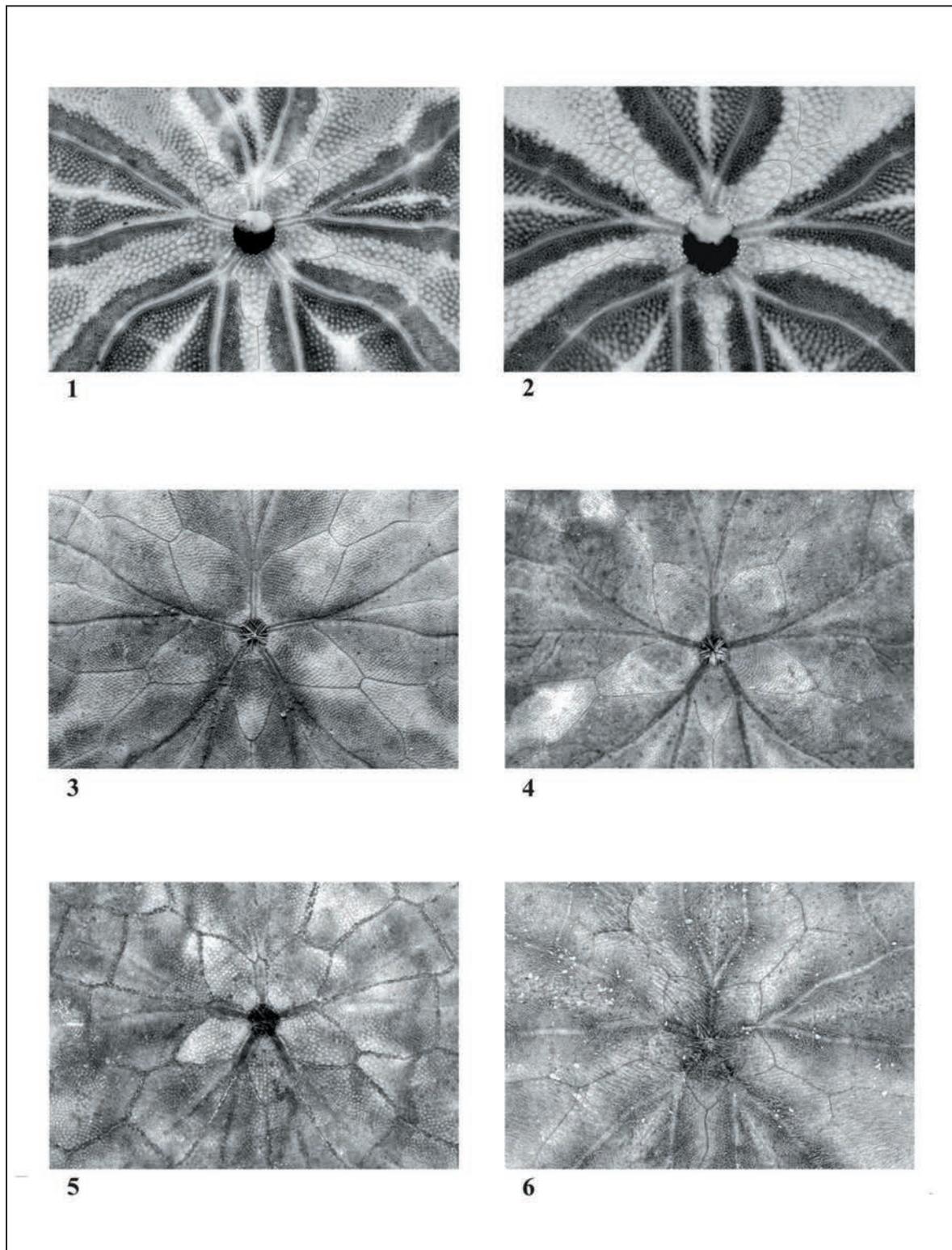


Plate 13. Random contact between basicoronals and related postbasicoronals interambulacral plates in *Echinodiscus* and *Sculp-sitechinus*. Figs. 1, 2. *E. bisperforatus* (South Africa). 1: interambulacra 2, 3 in contact; 1, 4, 5 disjoint; 2: disjoint. Figs. 3–5. *S. auritus* (Mangili): MAC.IVM110, interambulacra 1, 2, 3, 4 in contact; 5 disjoint; MAC.IVM115 4 in contact; MAC.IVM84, interambulacra 2, 3 in contact; 3, 4, 5 disjoint. Fig. 6. *S. sp. 1* (Philippines) MAC.IVM218: interambulacra all disjoint.

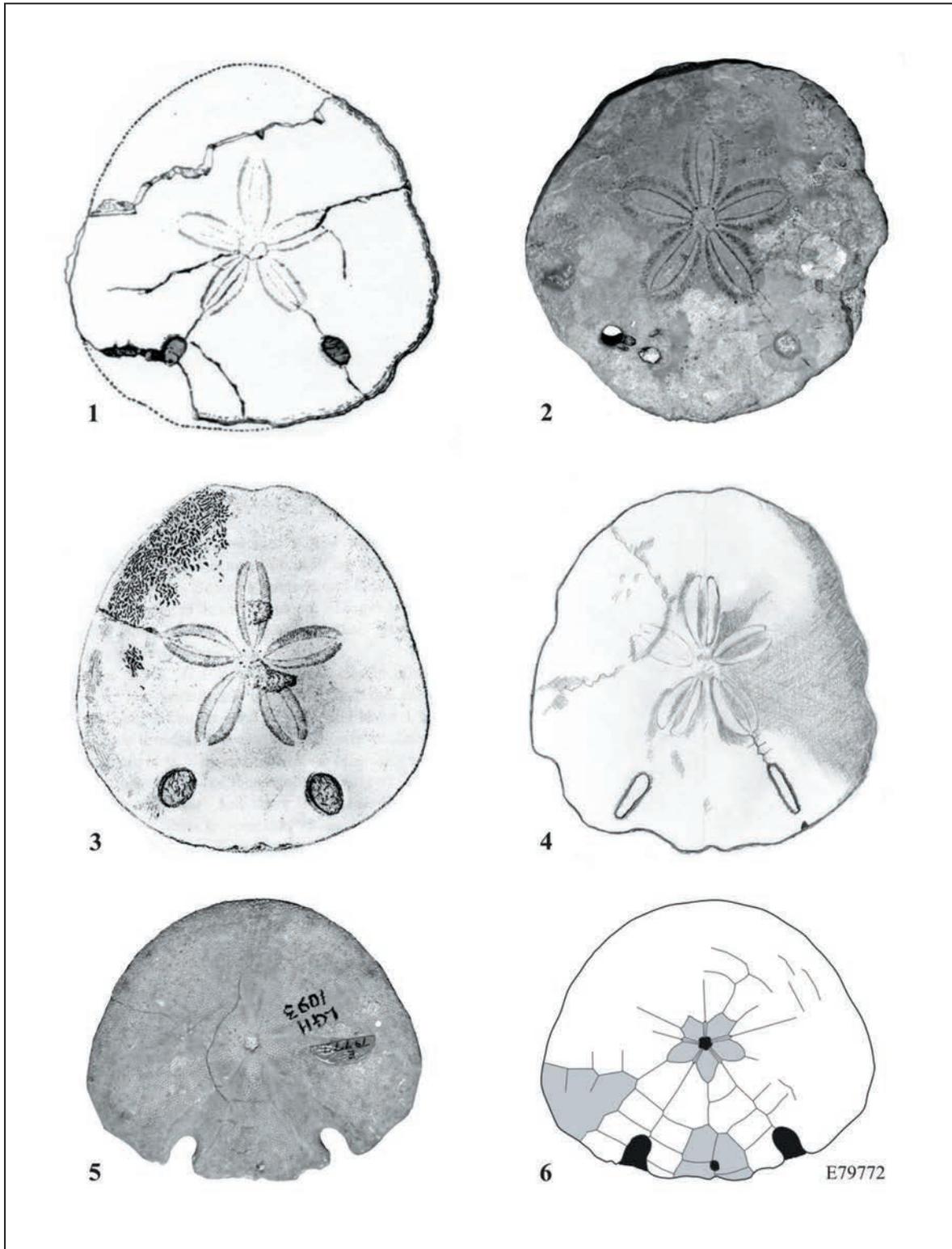


Plate 14. Other astriclypeids morphotypes. Fig. 1. Aboral face of "*Amphiope*" *boulei* (pl. 5, fig. 9). Fig. 2. Aboral face of "*A. cf. bioculata*" from Libya, specimen NHMUK E5788. Fig. 3. Aboral face of "*Echinodiscus*" *placenta* (Duncan & Sladen, 1883: pl. 52 fig. 1). Fig. 4. Aboral face of *Sculpsitechinus* sp. 2, in Lindley, 2001 (Fig. 7d). Fig. 5. Adoral face of "*Amphiope*" sp. from Libya, Miocene, NHMUK E79772. Fig. 6. Adoral plating pattern of "*Amphiope*" sp. from Libya, Miocene, NHMUK E79772.

Species	Pc posit.	Lunules or notches		Space (L3) and plates between lunules and (a) petals or (b) basicoronals			other
		L1	L2	L3	a	b	
<i>Paramphiope arcuata</i>	2a/3b	11,5	7	15	4-4	3-4	Lunules ellipsoidal in shape
<i>Paramphiope raimondii</i>	2a/3b	13	4	7	1-2	2-3	Lunules slit-like
<i>Echinodiscus pedemontanus</i>	2a/3b/3 a 3b/3a	15	6	8	3-4	2	Petals open
<i>Echinodiscus andamanensis</i>	2b/2a	14	5,4	10	2-4	2	Petals closed; $\beta = 75,5^\circ$; WA = 38% TL
<i>Echinodiscus truncates</i>	2b/2a/3 b	16	4	10			Petals closed; mean $\beta = 67^\circ$; WA = 38% TL
<i>Echinodiscus bisperforatus</i>	2b/2a 2b/2a/3 b	30- 34	3	3	1-2	2	Virtually closed petals; long slit-like lunules mean $\beta = 100^\circ$; WA = 48-50 % TL
<i>Sculpsitechinus</i> sp. (in L. Agassiz)	3b/3a	19	3	19	6-6	3-4	Posterior notches
<i>Sculpsitechinus tulearensis</i>	2a/2b	24	2	13	4-5	3-3	Posterior notches
<i>Sculpsitechinus tenuissimus</i>	2a/2b	12	4	16	4-6	2-3	posterior lunules; L11=11-26; $\beta = 66,5^\circ$; WA=32,5 TL

Table 14. Comparison between different species here studied. Data L1-3 in % TL.

III. SYSTEMATICS

In this chapter we will discuss the species and taxonomic groups that have been modified or proposed as a consequence of our observations. Others, such as *Amphiope* and *Astriclypeus* remain unaltered and are not considered / modified by us.

Family Astriclypeidae include the genera: *Astriclypeus* Verrill, 1867; *Amphiope* L. Agassiz, 1840; *Echinodiscus* Leske, 1778; *Paraamphiope* genus novum; *Sculpsitechinus* n. g.

Class ECHINOIDEA Leske, 1778
Subclass EUECHINOIDEA Bronn, 1860
IRREGULARIA Latreille, 1825
MICROSTOMATA Smith, 1984
NEOGNATHOSTOMATA Smith, 1981
Order CLYPEASTEROIDA L. Agassiz, 1835

Suborder SCUTELLINA Haekel, 1896
Infraorder SCUTELLIFORMES Haekel, 1896
Superfamily SCUTELLIDEA Gray, 1825
Family ASTRICLYPEIDAE Stefanini, 1912

Main characters of the family ASTRICLYPEIDAE

1. Main visceral central hollow, with floor reinforced by a network of thin trabeculae or by solid calcitic masses in apparently calloused form; peripheral buttressing developed as dense honey-combed meshwork of cellular structure;

2. Central or sub-central apical system with 4 gonopores;

3. Width of ambulacral and interambulacral zone at ambitus depends on the species or genera

4. Petals well developed and closed or nearly closed distally, sometimes open;

5. Small basicoronal circlet, with the interambulacral elements usually pointed, but not strongly

projected distally; all interambulacra disjointed or virtually disjointed on the oral surface;

6. Posterior interambulacral area always disjointed adorally and separated by enlarged first pair of post-basicoronal ambulacral plates;

7. Periproct oral open, along the perradial suture of the post-basicoronal plates in inter. 5;

8. Perradial lunules or notches in some or all ambulacra;

9. Food grooves well developed, bifurcated at the edge of the basicoronal cirlet and branched distally.

From Smith & Kroh (2011, accessed September 2013), as emended.

Genus *Echinodiscus* Leske, 1778

=*Echinoglycus* Leske, 1778, p. 197 (nomen nudum)
= *Lobophora* Agassiz, 1841, p. 64, not Curtis, 1825 in Smith & Kroh (2011).

=*Tretodiscus* Pomel, 1883, p. 71 (objective)

=*Tetrodiscus* Lambert & Thiery, 1921, p. 323 (nomen vanum) from Smith & Kroh (2011).

Species included

E. formosus Yoshiwara, 1901, Middle ?Eocene, Miocene, Taiwan

E. pedemontanus (Airaghi, 1899), Rupelian, Italy

E. chikuzenensis Nagao, 1928, Oligo-Miocene, Japan

E. yeliuensis Wang, 1982, Early Miocene, Taiwan

E. bisperforatus Leske, 1778, Pleistocene-Recent, Indo-Pacific

E. andamanensis n. sp., Recent, Indo-Pacific;

E. truncatus (L. Agassiz, 1841), Recent, Indo-Pacific

E. desori Duncan et Sladen, 1883, Miocene, India

Echinodiscus sp. 1, Rupelian, Italy

Echinodiscus sp. 2, Pleistocene-Holocene, Egypt

Other species attributed to this genus, that need to be revised

Echinodiscus placenta Duncan et Sladen, 1883, Miocene, India

Echinodiscus ellipticus Duncan et Sladen, 1883, Miocene, India

Echinodiscus ginauensis Clegg, 1933, Saudi Arabia and the Persian Gulf

Diagnostic features

1. Test sometimes slightly indented laterally in ambulacra II and IV; thin and sharp margin;

2. Main visceral central hollow with floor reinforced by a network of thin trabeculae;

3. Petals sometimes open; the posterior pair shorter than the rest, the anterior odd sometime being the longest;

4. Posterior ambulacra with axial ellipsoidal lunules, long slit-like lunules or notches;

5. Periproct open next to the rear margin on inter. 5;

6. Food grooves branched distally;

7. Angle between the lunules from 70 to 110°;

8. Width at ambitus of interambulacrum 5 from 36 to 53% TL;

9. Tube-feet extending into interambulacral zones;

10. Post-basicoronal plates 2a/2b, 3a/3b on inter. 5 large and paired, forming an obtuse triangle;

11. Only 2–4 plates present between the lunules and the tips of respective petals.

From Smith & Kroh (2011, accessed September 2013), as emended.

Echinodiscus is distinguishable from the other genera, by the first two couple of post-basicoronal plates in inter. 5 large and paired, whereas in *Amphiope* and in *Paraamphiope* n. g. they are staggered, with the first one elongated and in *Sculpsitechinus* they are smaller and only partially paired; furthermore, the contact of the first post-basicoronal plates in inter. 5 and the related ambulacral is meridoplacous in *Echinodiscus*, while in *Amphiope* and *Paraamphiope* these is amphiplacous. *Echinodiscus* is distinguished from *Sculpsitechinus* as having only 2–4 couples of plates between the lunules and the tips of respective petals, instead of 3–6, and by the periproct position, which is very close to the posterior margin (2,5–13% TL) while it is more distant in *Sculpsitechinus* (11–26% TL).

Echinodiscus andamanensis n. sp.

Plate 15 Figs. 1–5, Table 12.

SYNONYMY. The synonymy includes only the citations that certainty belong to this species.

1971, *Echinodiscus tenuissimus* L. Agassiz, 1847, Clark A.M. & Rowe F.W.E, pp. 144–145

- 1987, *Echinodiscus tenuissimus* L. Agassiz, 1847, Bussarawit S. & Hansen B. (n.v.)
 1991, *Echinodiscus tenuissimus* L. Agassiz, 1847, Warén A. & Crossland M.R., p. 106
 2004, *Echinodiscus tenuissimus* L. Agassiz, 1847, Puchakam S. & Sonchaeng P., p. 424, pl. 1
 2005, *Echinodiscus tenuissimus* L. Agassiz, 1847. Van der Steld b., Electronic Web Publ., accessed sept. 2013

EXAMINED MATERIAL. Holotype: specimen from Pak Meng Beach, Trang Province, Thailand, inventory n° PMBC 26346.1 TL 81 mm. Other specimens from Andaman coast of Thailand housed in the PMBC, Phuket, Thailand: PMBC.2842, TL = 66 mm, from Pak Meng Beach; PMBC.2843, TL = 66.2 mm and PMBC.2830, TL = 54.6 mm, from Noparat Tara Beach, Krabi Province; PMBC.2844, TL = 66.2 mm, from PMBC Jetty-South, Phuket Province. The series from Pak Meng Beach includes 5 specimens, inventory numbers 2842.1-5, TL 65.8–79.2 mm. 1 specimen from West side of Ko Yao Yai, Phuket, housed in the NHMD.Z n° ZMUC-ECH-1001, TL 37 mm (See also Warén & Crossland, 1991 figs. 10a, c); 1 specimen from “Thailand”, Recent (based on a illustration in “www. Echinoids NL”). In the latest specimen the TL is unknown, but the platings are well legible. The PMBC material was collected by S, Bussarawit and C. Nielsen, in 1975-1980, on sandy mud, at low tide and (PMBC jetty-South) on reef flat, sand.

DESCRIPTION. Small size, depressed test. Ambitus outline sub-rounded ($TW \approx 105 \div 110\%$ TL). Oral surface flat, peristome sub central. The inter. 5 has 2 post-basicoronal plates per column, the first two large and triangular, the second one larger, forming the complex a broad-based triangle; the width at the ambitus is $\approx 38\%$ TL. The periproct is very close to the rear edge ($L11 = 6.6\%$ TL) and small ($2 \div 3\%$ TL), and it opens along the suture between the first two post-basicoronal 2b/2a plates or between 2b/2a/3a, in the samples examined (Plate 15 Figs. 1–5). The peristome is round and large size (almost 5% of the TL); the basicoronal ambulacral circlet is small ($L13 = 10\%$ TL). The petals are closed, the odd petal is longer than the other; petalodium size 49% of TL. The lunules are short and axial ($L1 = 14\%$ TL), narrow ($L2 = 5.4\%$ TL) and with a β of 75.5°. Each lunule is separated from the corresponding petal tip by 2-3 couples of plates and surrounded by

3-5 couples of plates per column on the aboral face, and by 3–4 on the oral one. The apical disc is star-shaped and small in size ($\approx 8\text{--}10\%$ TL). The internal structure and the size of the Aristotle's lantern were not detected. However, the complete plating was detected (Plate 15 Figs. 3, 4). The number of plates per column is shown in tab. 6. The food grooves are simple (Plate 15 Fig. 5); the main food grooves run through the center of each ambulacral column, starting from long stretches parallel to the ambitus. The distribution of tuberculation is linked to the shape and distribution of the food grooves. Large tubercles can be found in the basicoronal interambulacral plates and along the sutures that lead to the post basicoronal plates. Large tubercles also cover the periphery of the post basicoronal interambulacral plates, moving up the ambitus where the tubercles are smaller. Medium sized tubercles also cover a band along the perradial ambulacra sutures and close to the lunules toward the stoma, and the periproct; the tuberculation is apparently absent along the main food grooves. On the aboral face the tuberculation is undifferentiated, evenly distributed, dense and small, all over the surface in all the specimens.

ETIMOLOGY. From Andamane coasts of Thailand, locus typicus.

DISTRIBUTION. Recent, Thailand coast of Andamane Sea, Noparat Tara Beach, Krabi Province; Pak Meng Beach, Trang Province; PMBC jetty-South, Phuket Province. The type locality is Trak Meng Beach, Trang Province, Thailand $7^{\circ}29'57.69''$ N, $98^{\circ}49'08.51''$ E, on sandy mud, low tide.

COMPARATIVE NOTES. *E. andamanensis* n. sp. differs from *E. pedemontanus* in that all of its petal are closed, the periproct is rounded in shape, instead of drop-shaped, and in that the periproct opens between plates 2a/2b, against 3b/3a, in oral interambulacrum 5; moreover, *E. andamanensis* n. sp. differs from *E. bisperforatus* due to the shape of the lunules, that are longer and twisted in the last one and due to the β angle that is 75.5° against 110°. *E. andamanensis* n. sp. have the WA at inter. 5 equal to 38% TL against 50% of *E. bisperforatus*. *E. andamanensis* n. sp. differs from *Echinodiscus* sp. 1 by the size of the stoma that is large ($\approx 4\%$ TL) while in *Echinodiscus* sp. 1 is very small ($<2.5\%$ TL) and by the position of the periproct, which lies between 2a/2b in inter. 5, instead between 3a/3b. Furthermore, *E. andamanensis* has 5–7 aboral

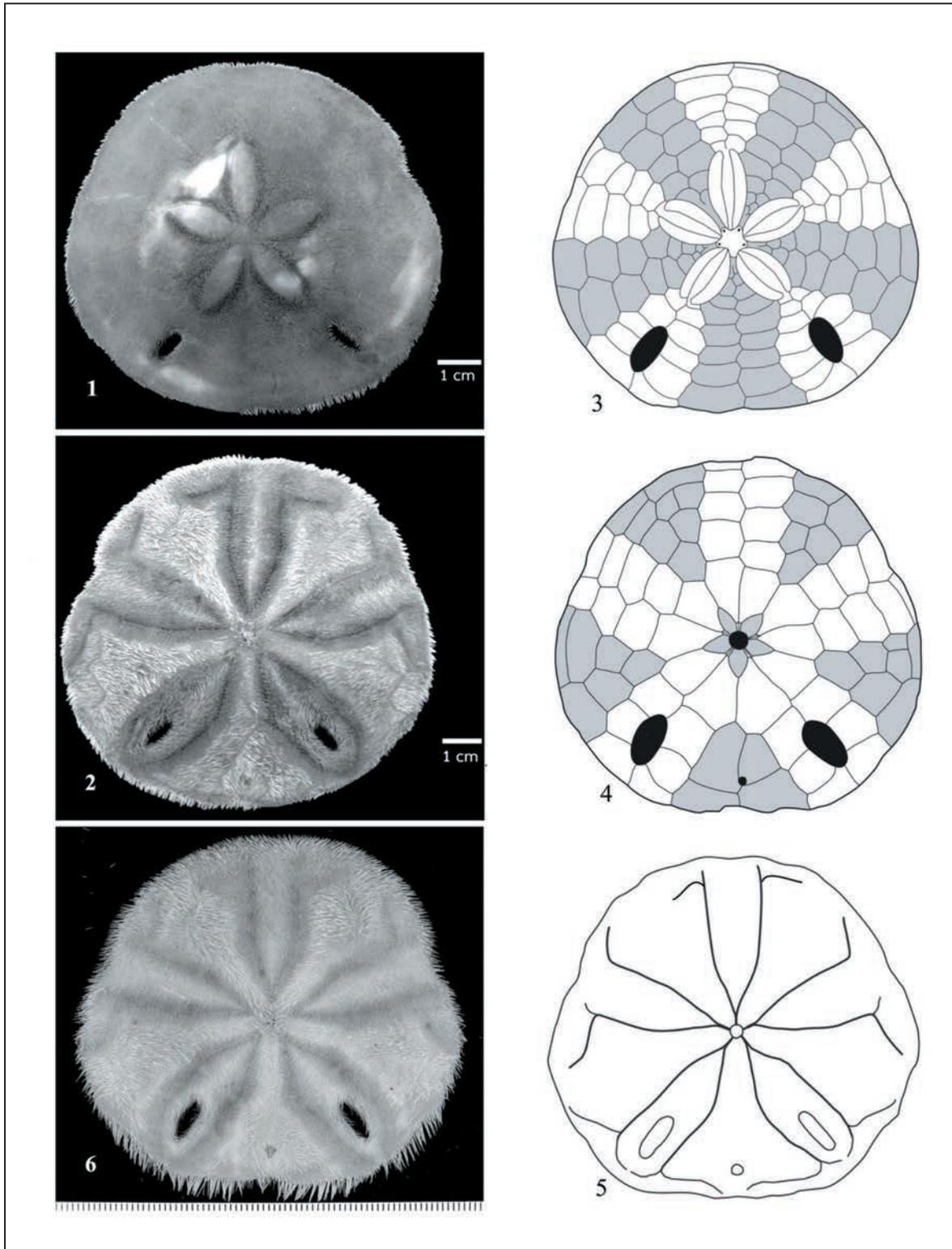


Plate 15. *Echinodiscus andamanensis* n. sp., Recent, Andaman coasts of Thailand. Figs. 1, 2. Aboral and adoral face of holotype PMBC.26346, from Pak Meng Beach. Figs. 3, 4. Aboral and oral plating pattern of specimen ZMUC-ECH-1001. Fig. 5. Food grooves scheme of specimen in Van Der Bas. Fig. 6. Oral face of PMBC.2643.1, from Noparat Tara Beach, in which are well visible the long coronal spines

couples of plates in the ambulacra I and V against 9-9. *E. andamanensis* n. sp. differs from *E. truncatus* in having the stoma much wider, spines much denser and longer (4.9 % TL against 3% TL) and simpler food grooves. Finally, *E. andamanensis* differs from *Echinodiscus* sp. 2 in having the periproct that opens between plates 2a/2b instead 2a/3b/3a.

Echinodiscus pedemontanus (Airaghi, 1899; pl. XXII, IV, fig. 4)

Plate 16 Figs. 1–8; Figs. 2a, b; Tables 3, 6, 8, 9

1899, *Amphiope pedemontana* Airaghi, p. 17, pl. VI, fig. 4a, b.

1901, *Amphiope pedemontana* Airaghi, p. 188, pl. XXII (IV), fig. 4.

TYPE SPECIMENS. The whole type-series, located at the Natural History Museum of Milan, was lost in the bombing during the last World War. The samples we studied are housed at the Museo di Storia Naturale “G. Doria” of Genoa (MSNDG) and one at the MAC, Cagliari. The sample inventoried with the number MSNDG.1218 is assigned as Neotype.

EXAMINED MATERIAL. Three specimens: MSNDG.25 from Pareto, MSNDG.1214 from Cairo Montenotte and MSNDG.1218 lacking indication of the locality; one specimen MAC.PL2014 from Merana (Alessandria Province). Illustrations of the samples described by Airaghi (1899 and 1901) were also examined.

EMENDED DIAGNOSIS. Species of medium-small size, depressed lateral profile, narrow and elongated axially lunules on the posterior ambulacra. Frontal odd petal slightly longer than the others and always open. In the oral face on inter. 5 there are only two pairs of post-basicoronal plates, with the first two large and paired.

DESCRIPTION. Small-medium sized, with more or less axially elongated lunules on posterior ambulacra. Depressed test (mean TH = 12% TL) with the highest point anterior to the apical disc. The margin is thin and uniform; ambitus rounded in outline and wider posteriorly. The frontal odd petal is slightly longer than the others and is open or almost open; the other one tends to be open, and the two rear ones are the shortest. Interporiferal and poriferal areas raised; sometime the poriferal zone is slightly

sunken, with the first ones 1 to 1.5 times larger than the others. The lunules are small (mean WI = 10.4), more elongated along the axis of the posterior ambulacra and narrow (mean SI = 0.37).

Only two post-basicoronal plates are present in each column on the oral inter. 5, with the first two plates being large and paired. The WA of inter. 5 at ambitus is, on average, 35% TL; on MAC.PL2014, the only one not deformed; β is 93°. The periproct is small, elongated and drop-shaped (wide 2.2% and long 3.5% of TL), close to the posterior test margin and open between plates 2a/3b/3a or 3b/3a. Internal structure and other features as for the genus.

DISTRIBUTION. Type locality and horizon. Val Bormida, Liguria and Piedmont. Molare Formation, Rupelian. Occurrence in Italy: Dego, Mioglia, Pareto, Squaneto, Santa Giustina, Giusvalla, Cairo Montenotte, Merana.

COMPARATIVE NOTES. *E. pedemontanus* differs from *E. bisperforatus*, *E. andamanensis* and *E. truncatus* in the shape of the front odd petal, which is always open, and the periproct position that opens more posteriorly, between the second two post-basicoronal plates; it also differ from *Echinodiscus* sp. 2 from Hurgada (Egypt) in the petals shape. *E. pedemontanus* differ from *E. bisperforatus* in the shape and length of the lunules; on the β angle that is 86° against 110°. Finally, *E. pedemontanus* have sub-equal petals and simpler food grooves, while *E. bisperforatus* have the front odd petal longer and the posterior petals always much shorter than the others and much complex food grooves.

***Echinodiscus* sp. 1**

Plate 17 Figs. 1–6; Fig. 2c; Tables 3, 6, 8, 9

EXAMINED MATERIAL. Two specimens: UNIGE.SM-VI-P-(5)-DN and UNIGE.SM-VI-DR and two large fragments: UNIGE.SM-DS and UNIGE.SM-VI-VI-DP.

DIAGNOSIS. Small-medium sized species, with a depressed lateral profile and axially elongated lunules in the posterior ambulacra. Petals sub-equal, large and closed, the frontal one a little longer than the others. In the oral face on the inter. 5, there are only two post-basicoronal plates per column, large and paired. In the rear margin there is a clear notch that arrives close to the periproct.

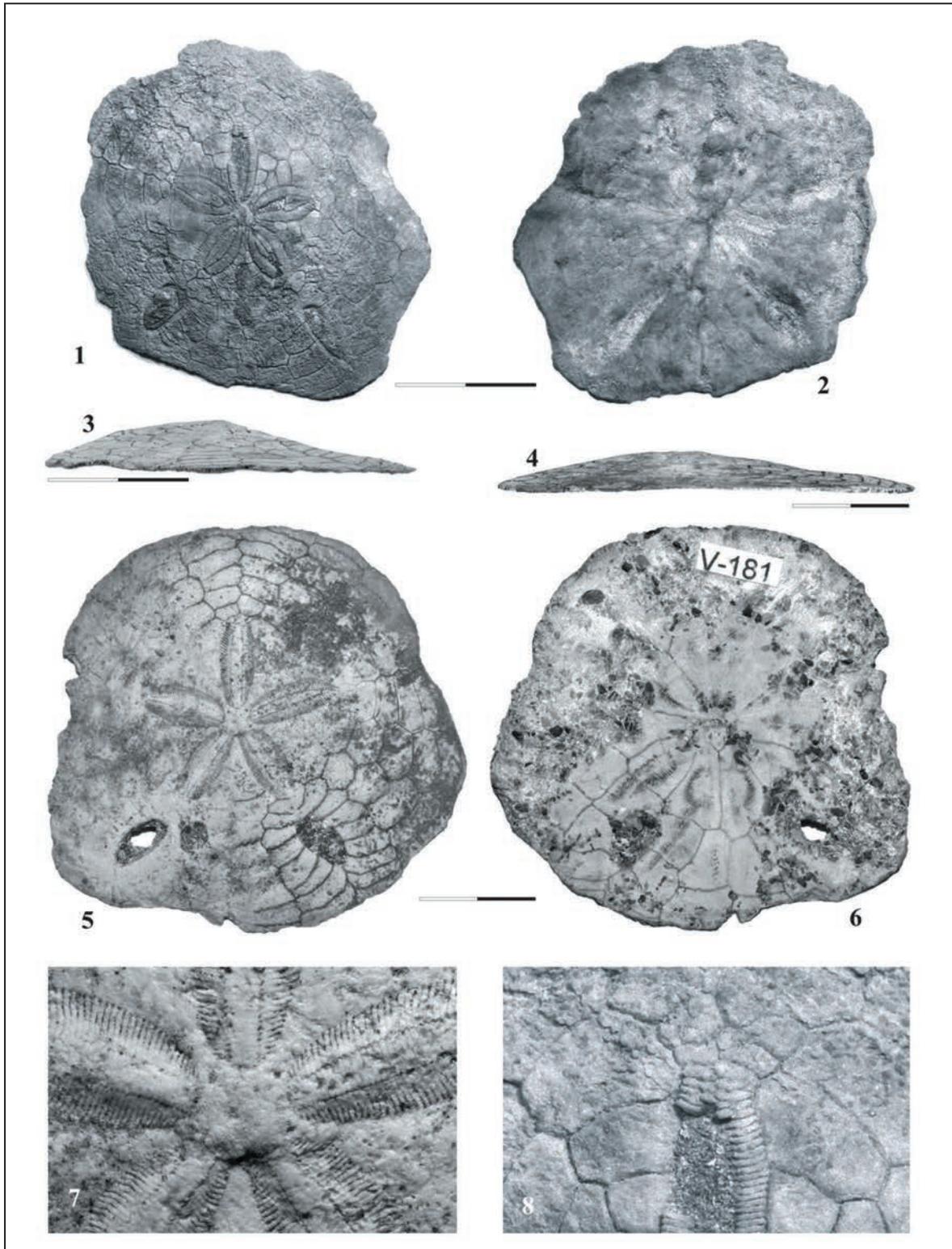


Plate 16. *Echinodiscus pedemontanus* from Liguria and Piedmont, Italy (Oligocene). Figs. 1–3. Aboral, adoral and antero (to the left)-posterior (to the right) lateral view of MSNDG 1218. Fig. 4. Antero (to the left)-posterior (to the right) lateral view of MAC.PL2014. Figs. 5, 6. Aboral and adoral view of MAC.PL2014. Fig. 7. Apical disc close-up of MAC.PL2014. Fig. 8. Magnification of open frontal odd petal in MSNDG 1218.

DESCRIPTION. Small-medium sized, with more or less axially elongated lunules in posterior ambulacra. Depressed test (TH = 10.5% TL) with the highest point anterior to the apical disc. Thin margin, anteriorly a little thicker than the rear. The ambulacra have sub-equal petals, closed, with poriferous and interporiferous zone similar in width. Small and narrow lunules, elongated along the axis of the posterior ambulacra. There are only two post-basical plates per column in inter. 5; the first two are large and paired. The periproct is small (width = 2.5% of the TL) and round; close to the posterior margin and open along the suture between 3b-3a. The internal structure and other features as for the genus.

DISTRIBUTION. Locality and horizon: Val Bormida, Liguria and Piedmont, Molare Formation, Rupelian. Occurrence: Pareto e Santa Giustina (Liguria) Italy.

COMPARATIVE NOTES. *Echinodiscus* sp. 1 differs from *E. pedemontanus* in having all the petal closed, by the periproct shape, sub-rounded instead of drop-shaped, and by the characteristic indentation on the posterior margin of the interambulacrum 5, absent in all other known *Echinodiscus*. *Echinodiscus* sp. 1 differs from *E. bisperforatus* in shape, length and angle of the lunules. In *Echinodiscus* sp. 1 β is 93° against 110° of *E. bisperforatus* and the WA at inter. 5 is only 35%, against 50% TL. *Echinodiscus* sp. 1 differs from *E. andamanensis* because in the last one the stoma is very large (> 5% of the TL) and by the position of the periproct, which lies between the plates 2a/2b in the inter. 5. Furthermore, *E. andamanensis* has 5-7 aboral couples of plates in the ambulacra I and V against 9-9. *Echinodiscus* sp. 1 differs from *E. truncatus* in having the periproct that open between the plates 3b-3a, while in *E. truncatus* it opens between plates 2b/2a/3b.

REMARKS. The specimen is inventoried as UNIGE.SM VI (P5) DN, and consists of a small-medium sized specimen (TL = 76 mm, TW = 104% TL, TH 8 mm), with both faces visible.

***Echinodiscus* sp. 2**

Plate 18 Figs. 1-3, 6; Plate 8 Figs. 3, 4; Tables 9, 12

EXAMINED MATERIAL. 1 specimen, MAC.PL 1850, TL = 21 mm.

DESCRIPTION. Small size echinoid, very flat test and thin ambitus, with rounded to sub-rounded outline. In the inter. 5 there are two plates per column, paired and wide. The β angle is 80°, the axial lunules are narrow; the periproct opens between plates 2a/3a/3b. The anterior odd petal are the longest and the two posterior pair are shorter. Internal structure not detected.

DISTRIBUTION. Locality and horizon: Pleistocene-Holocene from Hurghada, Red Sea, Egypt.

REMARKS. *Echinodiscus* sp. 2 differs from *E. pedemontanus* in that all of its petal are closed, the periproct is rounded in shape, instead of drop-shaped; *Echinodiscus* sp. 2 differs from *E. bisperforatus* by the shape and size of the lunules, that are longer and twisted in the last one and due to the β angle that is 80° against 110°. *Echinodiscus* sp. 2 differ from *Echinodiscus* sp. 1 by the size of the stoma that is very large (> 5% TL) while in *Echinodiscus* sp. 1 is very small (<2.5% TL) and by the position of the periproct, which lies between 2a/2b on oral interambulacrum 5, instead between 3a/3b. *Echinodiscus* sp. 2 differs from *E. truncatus* in having the stoma much wider and simpler food grooves.

***Echinodiscus truncatus* (L. Agassiz, 1841)**

p. 66; pl. 11, figs. 11-16

Plate 18 Figs. 4-6; Figs. 4a, b, Figs. 3, 4; Tables 9, 12

1841, *Lobophora truncata* L. Agassiz, pp. 66-67, pl., 11, fig. 11-16

1855, *Echinodiscus truncatus* Gray, p. 20 (n.v),

1872, *Echinodiscus truncatus* Gray, Gray, p. 122 (n.v)

1921, *Amphiope (Tetradiscus) laevis* Klein (Melita), Lambert J. & Thiéry P., p. 323

1948, *Echinodiscus bisperforatus truncatus* (L. Agassiz), Mortensen, pp. 410-411, pl. 71, figs., 6, 18

1914, *Echinodiscus bisperforatus* var. *truncatus* Clark H. L., p. 42

1925, *Echinodiscus bisperforatus* var. *truncatus* (L. Agassiz, 1841) Clark H.L., p. 171

1981, *Echinodiscus bisperforatus truncatus* (L. Agassiz, 1841) Dollfus R. & Roman J., p. 102, data (n.v. 1855-1872 taken from Kroh, A., 2012)

EXAMINED MATERIAL. 2 specimens from Changi East coast, Singapore, in the Fantin collection: 137,

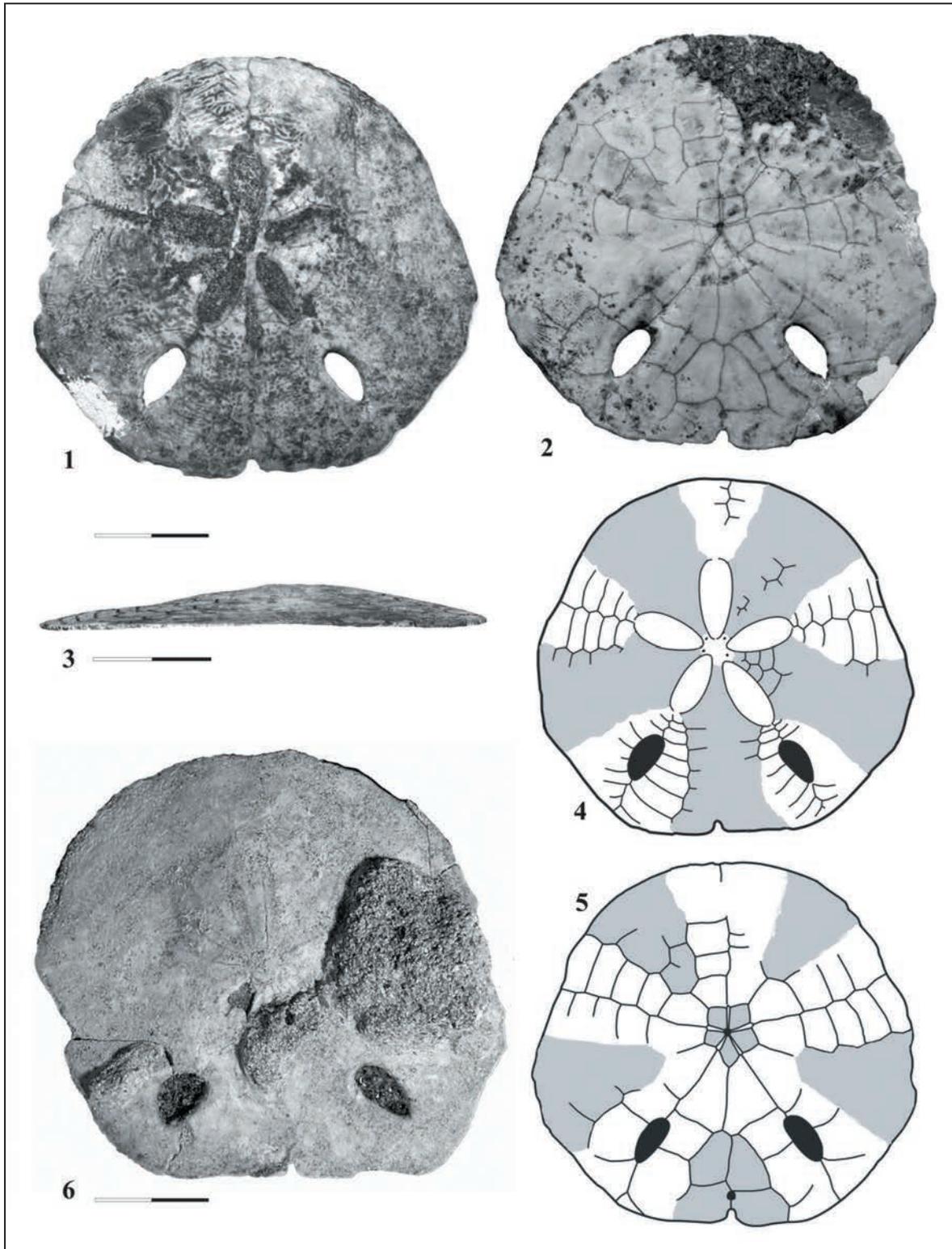


Plate 17. *Echinodiscus* sp. 1 from Liguria Italy (Oligocene). Figs. 1–3. Aboral, adoral and antero (to the left)-posterior (to the right) lateral view of UNIGE.SM VI (P5) DN. Figs. 4, 5. Aboral and adoral plate pattern of UNIGE.SM VI (P5). Fig. 6. Aboral view of UNIGE.SM-VI-DR. Figs. 2, 5. Despite the large deformations and distortions of lunules and shell, the generic characters remain intact and legible in the plate pattern of oral interambulacrum 5.

137A, TL = 51 and 60 mm (Plate 18 Figs. 4–6); three specimens from Kampong Pasir Ris, North East, Singapore; based on pictures from Ria Tan (web site www.wildsingapore.com, 2014); named S.1-3, TL unknown, but complete of spines.

DESCRIPTION. Small-medium size echinoid, flat test and thin ambitus with sub-rounded outline truncated at the posterior edge. The apical disc is eccentric forward (L4 = 57% TL; L 13 small (mean = 14% TL). In the inter. 5 there are two plates per column, paired and wide. β is 67° on average; the WA vary from 37 to 40% TL. The lunules are axial and slit-like in shape; SI vary from 0.19 to 0.28 (mean = 0.22) and WI is 8.68 on average. The periproct is small and opens between plates 2b/2a/3b, with L11 on average 10% TL. The petals are sub-equal in size and PL is about 50% TL long. The food grooves are finely branched in all the ambulacra (Plate 4 Fig. 4). The primary spines are short (about 3% TL) and sparse; the tuberculation is visible in Plate 18 Figs. 3, 5.

DISTRIBUTION. Locality and horizon: Recent, Singapore.

COMPARATIVE NOTES. *E. truncatus* differs from *E. andamanensis* n. sp. in having the stoma smaller, spines much sparse and shorter (3% TL against 4.9% TL) and much branched food grooves; *E. truncatus* differs from *E. pedemontanus* in that all of its petals are close and the periproct is rounded in shape, instead of drop-shaped; *E. truncatus* differs from *E. bisperforatus* by the shape of the lunules, that are longer and twisted in the last one and due to the β angle that is about 67° against 110°; *E. truncatus* differs from *Echinodiscus* sp. 1 by the size of the stoma that is very small (<2.5% TL) while in *Echinodiscus* sp. 1 is very large (> 5% TL) and by the position of the periproct, which lies between 2b/2a/3b in oral interambulacrum 5, instead between 3a/3b. *E. truncatus* differs from *Echinodiscus* sp. 2 in having the periproct that opens between plates 2b/2a/3b instead 2a/3b/3a.

REMARKS. Agassiz L. (1841: 66), named these species *Lobophora truncata* because the ambital outline truncated at the posterior margin; among other features this species showed well food grooves, more branched than in *E. bisperforatus*. In addition, the lunules are shorter and a bit larger than in *E. bisperforatus* (formerly *Lobophora bifora*), The specimen

described by L. Agassiz was deposited at the “Museum of Paris” but where it came from is unknown.

Clark H.L. (1914) cites seven specimens from New Caledonia and two from Penang (Malaysia), but we believe that the New Caledonia's specimens belong to *E. tenuissimus* group. In fact, the information in our possession, says that in New Caledonia there are not *E. bisperforatus* and *E. truncatus*, but only echinoids belonging from the *Sculpsitehinus tenuissimus* group (formerly *E. tenuissimus*). As distinctive features, Clark H.L. (1914) mentions short lunules and short petals.

The same author (p. 171) confirms that he has observed several specimens from New Caledonia and from Penang (Malaysia), but he “doubts” that these correspond to “*E. tenuissimus*”, and says that these specimens “would look like” to *E. truncatus*.

Dollfus & Roman (1981) consider *E. truncatus* a variety of *E. bisperforatus* and cite (p. 102) Singapore as locality where the described specimens came from. All this shows how much uncertainty there is in the recognition of certain species without the use of structural characteristics.

Paraamphiope n. gen.

TYPE SPECIES. *Paraamphiope raimondii* n. sp.; the holotype is housed in the Department of Animal Biology and Ecology, University of Cagliari (UNICA).

DESCRIPTION. Diagnostic features:

1. Sub pentagonal visceral hollow width almost 47% TL;
2. Main visceral central hollow with wall reinforced by a network of thin trabeculae;
3. Petalodium small in size (from 42 to 47% TL); petals well developed and almost closed distally;
4. Posterior axial ambulacral lunules ellipsoidal or narrow slits;
5. 3 to 4 pairs of plates between petals and lunules;
6. Periproct open less than 13% TL from the posterior margin;
7. The first two plates in inter. 5 must be staggered with the 2b in amphiplacous contact with the post basicoronal ambulacral plates;
8. Food grooves very branched distally near the rear edge;

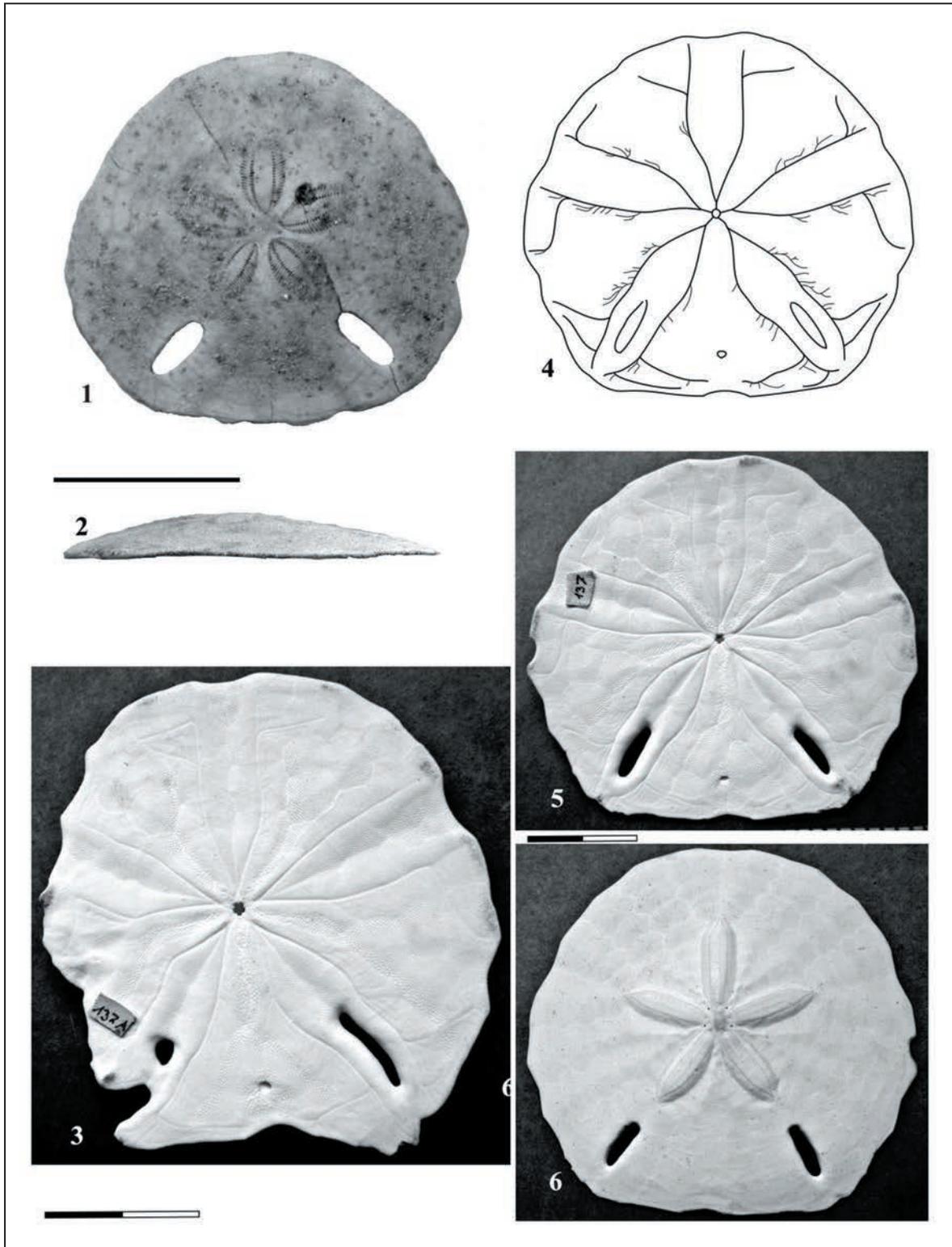


Plate 18. Fossils and living *Echinodiscus* species. Figs. 1, 2. *Echinodiscus* sp. 2, aboral and antero (to the left)-posterior (to the right) lateral view of MAC.PL1850, from Hurgada, Egypt. Fig. 3. *Echinodiscus truncatus*, aboral face of malformed individual (specimen 137A from Fantin collection), Recent, Singapore. Fig. 4. Food groovers scheme of *E. truncatus* from Singapore. Figs. 5, 6. *E. truncatus*, oral and aboral view of specimen 137, from Fantin collection, Recent, Singapore.

9. width at ambitus at inter. 5 zone, measuring almost 36% TL;

10. β angle about 88°;

11. Tube-feet extending into interambulacral zones.

ETIMOLOGY. Para = affinity with the relate genus *Amphiope*

DISTRIBUTION. From Libya and Indonesia, Miocene to Recent.

REMARKS. *Paraamphiope* n. g. differs from *Echinodiscus* in having the first two post-basicoronal plates of inter. 5 which are staggered whereas they are always large and paired in the second; moreover, in *Paraamphiope* n. g. the contact by post-basicoronal ambulacral plates in inter. 5 is amphiplacous, as in *Amphiope*, while this is meridoplacous in *Echinodiscus*. *Paraamphiope* n. g. differs from *Amphiope* in that has axial lunules separated by 3 to 4 couples of plates from the respective posterior petals, in the latter they are rounded or transverse and separated from respective petals tip by only 1-2 couples of plates; *Paraamphiope* n. g. has very branched food grooves in the posterior part of the test, in *Amphiope* they are very simple and in *Sculpsitechinus* these are highly branched and developed on the entire adoral surface. *Paraamphiope* have a petalodium long 42–46% TL, against 45–60% of *Amphiope* and 30–45% TL of *Sculpsitechinus*. *Paraamphiope* n. g. differs from *Sculpsitechinus* by the position of the periproct that is close to the rear margin (2.5–13% TL) against 11–26% TL.

This genus includes the following species:

P. raimondii n. sp., Recent, Indonesia (Borneo)

P. arcuata (Fuchs, 1882), Miocene, Egypt and Libya

Paraamphiope raimondii n. sp.

Plate 19 Figs. 1–7; Tables 9, 12

EXAMINED MATERIAL. Holotype, MAC.IVM 206, TL 53 mm housed in the Department of Animal Biology and Ecology (UNICA), Cagliari, Italy.

DIAGNOSIS. Small-medium sized species, with a low side profile and slit-like lunules axially elongated in the posterior ambulacra. Petals closed distally, with the front odd longer than the other and

the posterior ones slight shorter. In the oral inter. 5 there are 2 post-basicoronal plates in column "a" and 2 in column "b", with the first two ones staggered; between the petals and the notches there are 3 or 4 couples of plates, and the periproct opens along the suture between plates 2a/3b.

DESCRIPTION. Small-medium sized echinoid (TL 53 mm), with depressed test (TH = 11% TL) with the higher point anterior to the apical disc and a thin margin, rounded in outline. Petaloid medium size (42% TL); petals closed, with the frontal odd longer than the other. Poriferous zone flat, interporiferous ones slightly raised, with interporiferous size ranging from 1.5 to 2 those poriferous. Lunules axially, more long than large (L1 = 20 mm; L2 = 6.6 mm) and surrounded by 4 couple of plates on the aboral side and by 3 in the oral one. In the inter. 5 there are 2 couples of post-basicoronal plates, the first two 2b and 2a staggered and the 2b in amphiplacous contact with the first ambulacral postbasicoronal plates; in this interambulacrum the WA is 36% TL.

The periproct is small (3% TL) and sharply rounded, close the posterior margin (7% of TL) and open along the suture 2a/3b. Main visceral central hollow with wall reinforced by a network of thin trabeculae; peripheral buttressing developed as dense honeycombed meshwork of cellular structure; Aristotle's lantern width almost 27% of TL and large but short caecum cavity. The food grooves are very branched posteriorly; tubercolation well differentiated adorally, dense and poorly differentiated aborally (see Plate 19). Other data in relate Tables.

ETIMOLOGY. From the name of S. Raimondi, the collector that have donated the specimen to the museum.

DISTRIBUTION. Type locality and horizon: Recent, Indonesia (Borneo). Occurrence: Recent, Indonesia (Borneo).

COMPARATIVE NOTES. *P. raimondii* n. sp. differs from *P. arcuata* in the shape of the lunules and in the shorter distance of the lunules from the petals tip. Moreover, in the oral side of *P. arcuata*, the lunules open after two couples of post-basicoronal plates in ambulacra I and V, while in *P. raimondii* lunules open after only one couples of plates. Finally, the tubercles are absent or scarce along the perradial sutures in *P. raimondii* and are always present in *P. arcuata*.

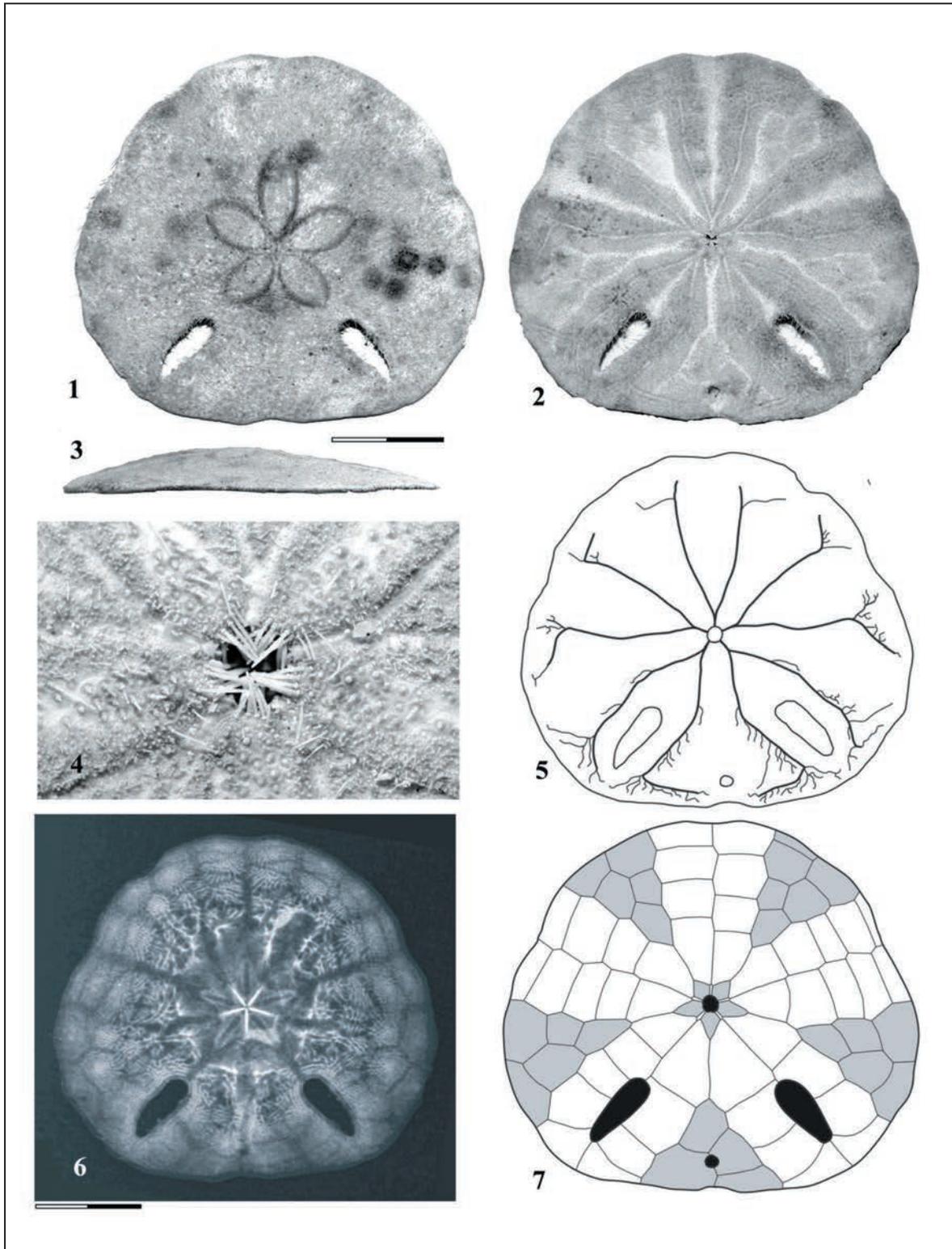


Plate 19. *Paraamphiope raimondii* n. sp., Recent, Indonesia. Figs. 1–3. Aboral, adoral and antero (to the left)-posterior (to the right) lateral view of MAC.IVM206. Fig. 4. Close-up of spines and tuberculation in the oral area. Fig. 5. Scheme of food grooves, more branched posteriorly. Fig. 6. Radiograph in supero-inferior projection with well visible support system and a large Aristotle's lantern. Fig. 7. Oral plate pattern.

Paraamphiope arcuata (Fuchs, 1882)

Plate 20 Figs. 1–6; Tables 6, 9

1882, *Amphiope arcuata* Fuchs, p. 311899, *Amphiope arcuata* Fuchs, Fourtau R., p. 6981911, *Amphiope arcuata* Fuchs, Gregory, p. 6671914, *Amphiope truncata* Fuchs, 1882, Cottreau, p. 551920, *Amphiope arcuata* Fuchs, Furtau, p. 401920, *Amphiope arcuata* Fuchs, Migliorini, p. 153

EXAMINED MATERIAL. The material studied by us is labeled as Miocene, Libyan desert (locality not specified), housed in the NHMUK in London, with code E1671-2, E1674-6, TL 35 ÷ 79 mm.

DIAGNOSIS. Small-medium sized species, with a low side profile and ovoid lunules axially elongated in the posterior ambulacra. Petals closed distally, sub-equal in size. In the oral face of the inter. 5 there are 2 post-basicoronal plates in column "a" and 2 (sometimes also a small part of the fourth plate is visible) in column "b", with the first two staggered; between the petals tip and the lunules there are 3 or 4 couples of plates, and the periproct opens between plates 2a/3b.

DESCRIPTION. Size small-medium (in our sample max TL = 79 mm) as wide as long. Test depressed (TH = 6 ÷ 12% TL). The highest part of the test lies on the apical disc, which is sub-central. The ambitus outline is subrounded to subtrapezoidal; the adoral surface is flat or slightly plano-concave with the inner point near the peristome, which is sub-central. There are 2 post-basicoronal plates in column "a" and 2–3 in column "b", in which the 2b is wide and elongated (like as in *Amphiope*) and are in amphiplacous contact with the relate post-basicoronal ambulacrals. The periproct is small (2–3% TL) and opens between the post-basicoronal plates 2a/3b on inter 5; L11 varies from 4 to 14 % TL. The peristome is round and measure from 3.5% to 5.5 TL.

The petals are just closed in larger specimens, but the frontal odd seems open in the smaller specimen. The Petalodium is of medium size (42 ÷ 47 % TL). The lunules are very small and ellipsoidal shaped. The β angles ranges between 88° to 96°. Each lunule is separated from the corresponding petal by 4–5 couples of plates and surrounded by

4–4 couples of plates on the aboral side, against 3–4 couples on the adoral one.

Apical disc with a small (\approx 6% TL) star-shaped madreporite, with 4 genital pores, all open also in the smaller individuals. Internal structure and size of Aristotle's lantern were not detected.

The main food grooves are simple and run through the center of each column in the ambulacra, starting from small branches parallel to the ambitus or from the ambitus itself (in E76164). Short secondary branches grow along the grooves on the posterior ambulacra and near the lunules and the periproct. Tubercolation is poorly differentiated on the oral face; tubercles are large on the basicoronal interambulacral plates and on the post-basicoronal ambulacral ones. In the interambulacra the tubercles diminished in size farther from the center; large tubercles surround the periproct. The tubercolation covers with small tubercles also major food grooves. On the aboral face the tubercolation is undifferentiated, evenly distributed, dense and petite, over the entire surface.

DISTRIBUTION. Libya, Miocene. Locality and horizon: Syouah, Gebel Ndefer, Egypt (the Holotype is housed in the Naturhistorisches Museum of Vienna) and Libyan desert (Tobruca area), Middle Miocene.

COMPARATIVE NOTES. Morphologically, *P. arcuata* differs from "*Amphiope*" *truncata* Fuchs, 1882, in its smaller size, smaller petalodium, lunules outline much more ovoids and the food grooves less branched distally; *P. arcuata* differs from *P. raimondii* n. sp. by the shape of the lunules and by the longest distance of the lunules from the petal tips. Moreover, the tubercles are always present along the perradial sutures while in *P. raimondii* are absent or scarcely.

REMARKS. Under careful observation of the specimen E76164, the rear part of the test seems incomplete and for this reason the measurements and plating are biased in this way. It is unclear whether this anomaly occurred before or during the process of fossilization.

The illustrations of the type species provided by Fuchs (1882: 31, pl. XI, figs. 4-6) correspond, from a morphological point of view, to the specimens studied by us. Cottreau (1914) puts this species in synonymy with *A. truncata* Fuchs, 1882 and *A. fuchsi* Fourtau, from the Middle Miocene of Egypt, then,

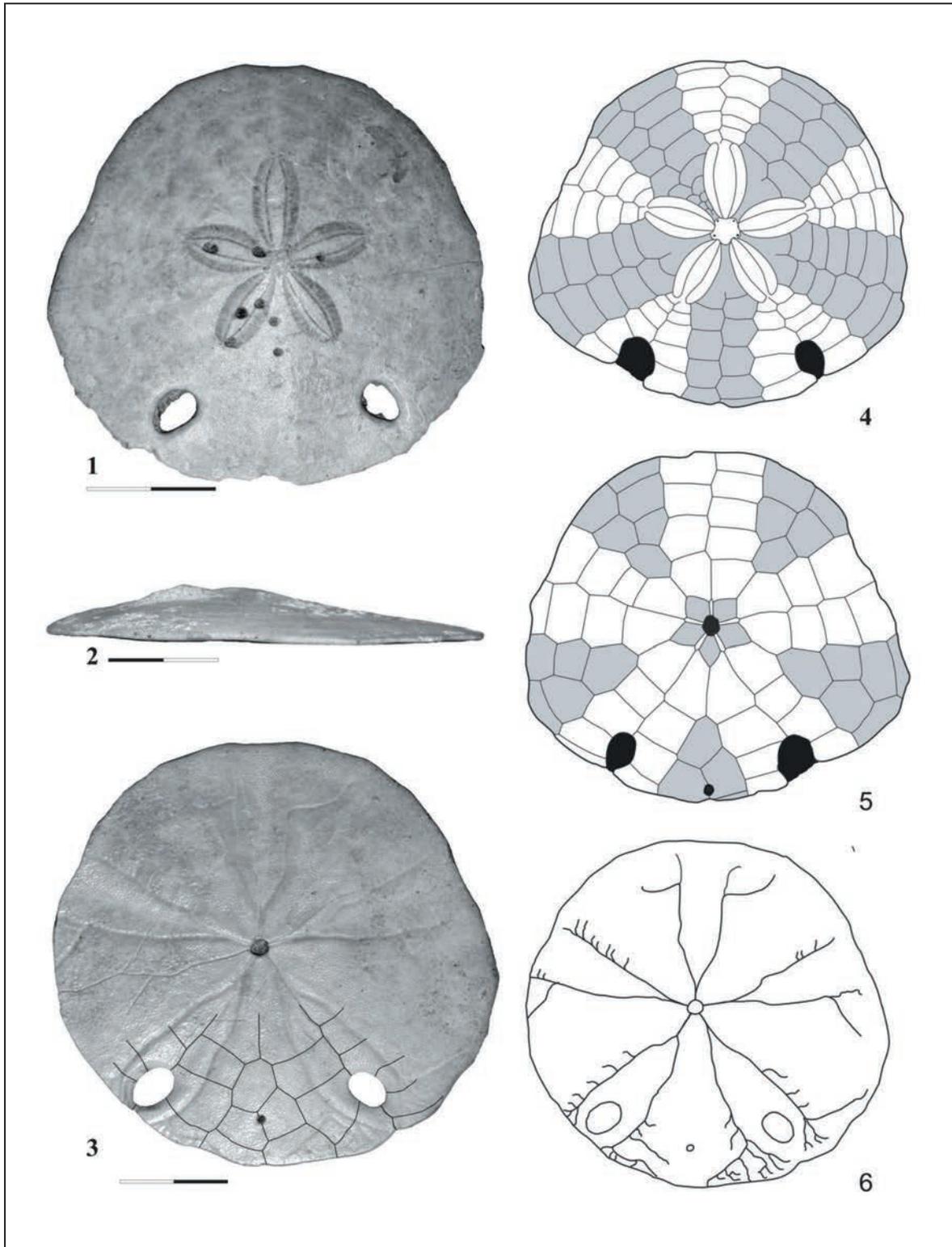


Plate 20. *Paraamphiope arcuata* from Libya (Miocene). Fig. 1. Aboral view of NHMUK.E76162. Figs. 2, 3. Antero (to the left)-posterior (to the right) lateral and adoral view of NHMUK.E76161. Fig. 4, 5. Plate pattern of aboral and adoral face of NHMUK.E76164. Fig. 6. Food grooves scheme of NHMUK.E76161. In this example it is evident the great outline variability, in particular in the rear of the ambitus, due (Figs. 4, 5), perhaps, to defects in fossilisation.

in figure 23 he illustrates *A. arcuata* as type. However, the scheme of the plates of the other nominal species has never been published, and therefore we believe that they should remain a separate species.

***Sculpsitechinus* n. gen.**

TYPE SPECIES. *Sculpsitechinus auritus* (Leske, 1778) = *Echinodiscus auritus* Leske, 1778.

As Neotype are assigned specimen MAC.IVM109 and is housed in the Department of Animal Biology and Ecology, University of Cagliari (UNICA).

DESCRIPTION. Diagnostic features:

1. Subcircular or vaguely polygonal visceral hollow, with the floor reinforced by a network of ribs;
2. Petalodium small, PL about 30–48% of TL; petals always closed distally;
3. Pentastellate basicoronal cirlet, with the interambulacral plates that can be elongated distally, usually separated from the post-basicoronal ones;
4. Posterior ambulacra with axial notches or lunules; the lunules shape may vary from ellipsoidal to narrow slits like, which may be open to the ambitus;
5. 3 to 6 couples of plates are present between petals tip and lunules/notches;
6. Periproct far from the rear margin almost $13 \div 26\%$ of TL;
7. 3 or 4 post-basicoronal plates per column in inter. 5, with the first two partially paired and normally in meridoplacous contact with the relate ambulacra;
8. Food grooves very branched and spread over all the oral surface;
9. Width at inter. 5 zone at ambitus about 30–38% of TL;
10. β angle within 48° to 70° ;
11. Tube-feet extending into interambulacral zones.

ETIMOLOGY. *Sculpsit* = carved: the name derives from the rear notches that characterized the species *Echinodiscus auritus* Leske, 1778, transferred here to *Sculpsitechinus auritus* (Leske, 1778).

DISTRIBUTION. From Indian Ocean, Red Sea, Persian Gulf to West-Pacific. Time span: from Middle Miocene to Recent.

COMPARATIVE NOTES. *Sculpsitechinus* n. gen. differs from *Amphiope* and *Echinodiscus* in that it has 3 to 6 pairs of plates between the posterior petals tip and the respective lunules, whereas there are only 1–2 in *Amphiope* and 2–4 in *Echinodiscus*; also the first two post-basicoronal plates in inter. 5 are relatively small and only partially coupled, in *Amphiope* and *Paraamphiope* they are always staggered, with the first one longer, and in *Echinodiscus* they are always large and paired. *Sculpsitechinus* n. gen. differs from the other genera also by the position of the periproct that is far from the rear margin (13–26% TL), while in the other ones this distance ranges from 2.5 to 13% of the TL. Furthermore, *Sculpsitechinus* n. g. differs from *Amphiope* also in having a smaller petalodium (30–47% against 45–60%). *Sculpsitechinus* n. g. differs from *Echinodiscus* by the smaller width of inter. 5 at the ambitus (30–38 against 35–54), and the lower angle between the lunules ($\beta = 54^\circ$ – 70° against 70° – 117°). Finally, *Sculpsitechinus* n. g. differs from *Amphiope* and *Echinodiscus* by the food grooves highly branched on the whole adoral surface.

REMARKS. This genus includes the following species:

S. auritus (L. Agassiz, 1838); Recent; Tulear, Madagascar, Red Sea, Indian Ocean and West Pacific.

S. tenuissimus (L. Agassiz, 1847) Recent; Lembeh, North Sulawesi and Waigeo, West Papua (Indonesia); New Caledonia, Papua New Guinea and Palau, Micronesia.

Sculpsitechinus sp. 1; Recent; Bohol and Oslob islands, Philippines.

Sculpsitechinus sp. 2, Middle Miocene; Papua New Guinea.

***Sculpsitechinus auritus* (Leske, 1778)**

Plate 21 Figs. 1–7; Tables 6, 9, 11, 12 (see also Table 3 in Stara & Fois D., 2014)

1778, *Echinodiscus auritus*, Leske N.G., p. 138

1778, *Echinodiscus inauritus* Leske N.G., p. 138

1816, *Scutella bifissa* Lamarck J.B.P.A., p. 10

1817, *Scutella bifissa* Savigny, pl. 7 fig. 3 (n.v)

1826, *Scutella bifissa* Lamarck, Auduin, p. 210 (n.v)

1841, *Lobophora aurita* L. Agassiz, pp. 70–71, pl. 14, figs. 3, 7

- 1892, *Echinodiscus auritus* Leske, Boutan L., p. 29, 46, 47
- 1893, *Echinodiscus auritus* Leske, de Loriol P, p. 375
- 1894, *Echinodiscus auritus* Leske, Mazzetti G, pp. 222, 225–226 (n.v)
- 1899, *Echinodiscus auritus* Leske, Fourtau R, pag. 540
- 1904, *Tetrodiscus auritus* Fourtau, pag. 425, 444 (n.v)
- 1914, *Amphiope (Tetrodiscus) aurita* Leske, Fourtau R, p. 88 (n.v.)
- 1948, *Echinodiscus auritus* Leske, Mortensen T., pp. 400–406
- 1955, *Echinodiscus auritus* Leske, Tortonese E., p. 38
- 1971, *Echinodiscus auritus* Leske, Clark A.M. & Rowe F.W.E., p. 144
- 1971, *Echinodiscus auritus* Leske, James D.B. & Pearce J.S., p. 99
- 1981, *Echinodiscus auritus* Leske, Dollfus R. & Roman J., pp. 97–99
- 2014, *Echinodiscus auritus* Leske, Stara & Fois M.

EXAMINED MATERIAL. Neotype: MAC.IVM.109, TL 125 mm, Recent, from Mangili, Tulear Province, Madagascar. Housed in the Department of Animal Biology and Ecology (UNICA), Cagliari, Italy. 31 specimens from Mangili, Tulear Province, Madagascar, caught in back-barrier lagoon, \approx 5 to 8 m in deep, in sandy-mud, MAC.IVM82 - 113–1 TL = 74 ÷ 140 mm, housed in the Museo di Storia Naturale Aquilegia, Cagliari and in the Department of Animal Biology and Ecology (UNICA), Cagliari, Italy.

DIAGNOSIS. Medium sized species, with a low side profile and axially elongated notches in the posterior ambulacra. Petals closed distally, in a small petalodium. In the oral interambulacrum 5 there are 3 post-basicoronal plates in column “a” and 4 in column “b”, with the first two partially coupled; between the petals tips and the notches there are 4 - 5 couples of plates, and the periproct opens along the suture between plates 2b/2a in interambulacrum 5.

DESCRIPTION. Medium-sized echinoid with a almost polygonal ambital outline; the posterior margin line, sited between the two notches (like a tail), is always irregular and often very asymmetric.

Although in smaller individuals a rounded outline seems to prevail, the larger individuals present clearly truncate lines; however the ambitus outline can vary greatly. The adoral face is flat or slightly plano-concave. The periproct is small and far from the posterior margin (L11 = 18–24% TL). The plating structure is reported in Plate 23.

In this samples the Aristotle’s lantern measures about 15% TL. The petalodium is medium size (PL = 35–40% TL) and the petals are sub-equal, twice as long as the width and always closed (L5 = 18%; L7 and L9 = 17% TL); the poriferous areas are 1.2 to 1.5 times wider than the poriferous ones. The apical disc measures 6% TL. Only one pair of post-basicoronal ambulacral plates occlude the interambulacrum 5. The notches are surrounded by 4-5 couples of plates on the oral face and by 4-5 on the aboral one. Between the petal tip and the beginning of the notch there are 6 couples of plates per column. β is approximately 55° and WA at interambulacrum 5 is on average 32% TL. In the oral side of the interambulacrum the periproct opens between post-basicoronal plates 2b-2a. The stoma is pentagonal, with a diameter of 4% TL; L13 = 11% TL. The basicoronal interambulacral plates are all irregular, with some in contact and others disjointed. The tuberculation is dense, made up of medium sized tubercles, poorly differentiated and extended over the entire aboral surface. The tubercles are larger around the periproct and the smaller ones are found particularly along the main food grooves. On the aboral face the tuberculation is undifferentiated, thick and petite, evenly distributed over the entire surface. The food grooves are very branched out over the entire oral surface.

DISTRIBUTION. Tulear, Madagascar; Indian Ocean, Red Sea, Persian Gulf, Oceania West-Pacific Ocean. Recent.

COMPARATIVE NOTES. *S. auritus* differs from *S. tenuissimus* and from *Sculpsitechinus* sp. 2, by having notches against lunules. *S. auritus* differs from *Sculpsitechinus* sp. 1, in having smaller Aristotle’s lantern and greater size.

REMARKS. To establish this species, Leske (1778: 202), did not mention the locality where the specimens studied come from and neither the museum in which these specimen has been deposited. The author, however, has not even provided an illustration of the sample that he described.

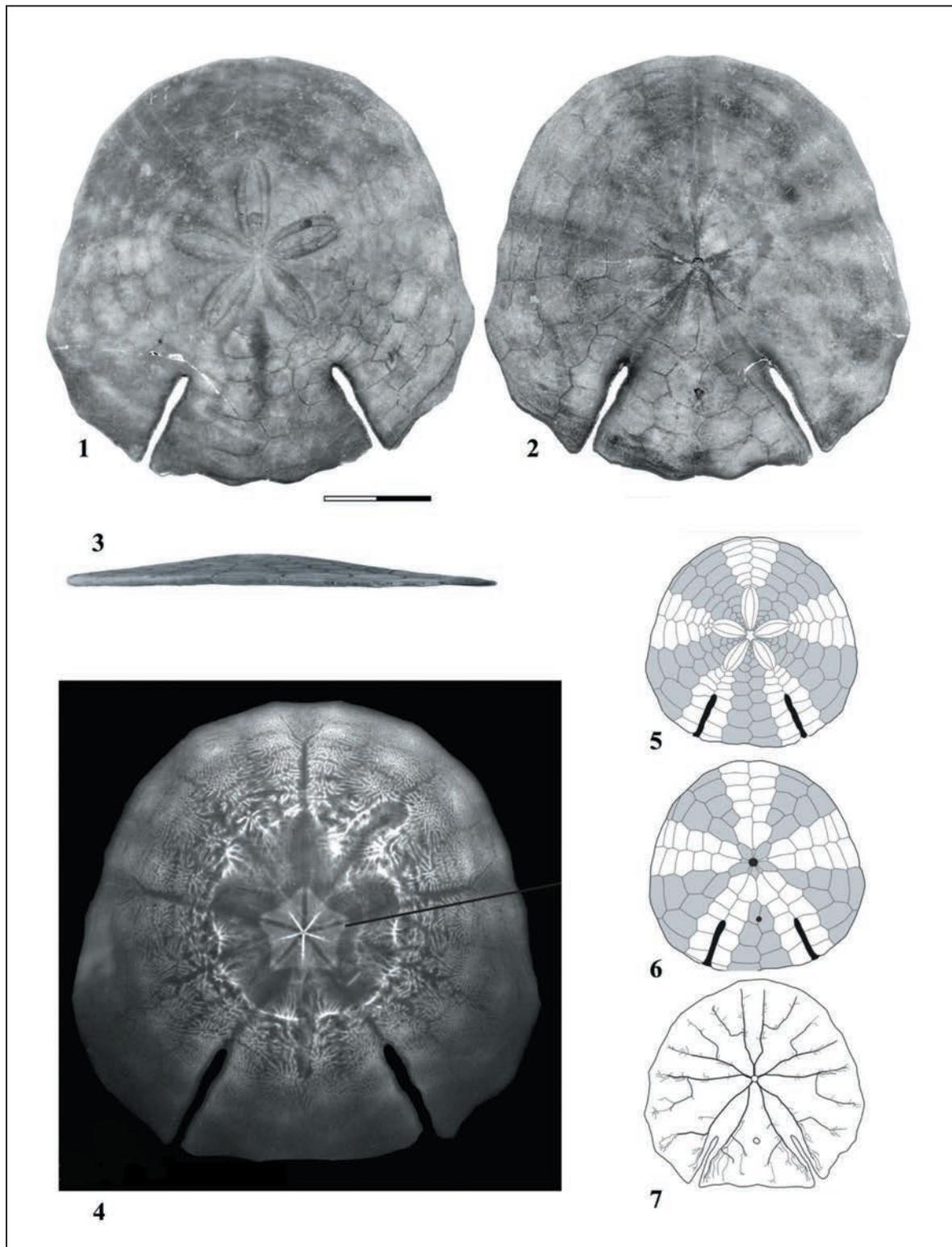


Plate 21. *Sculpseitechinus auritus*, Recent, Mangili, Madagascar. Figs. 1–3. Aboral, adoral and antero (to the left)-posterior (to the right) lateral view of MAC.IVM109. Fig. 4. Radiograph taken in super-inferior position of MAC.IVM109, in which is visible the small Aristotle's lantern. Figs. 5, 6. Plate pattern of aboral and adoral faces of MAC.IVM110. Fig. 7. Well branched food grooves scheme.

Despite our historical research, followed by a information request to the Natural History Museum in Leipzig, the city where Leske has worked for long time, we could not find the type specimens. Kindly, R. Schiller from the Museum of Natural History in Leipzig, communicated us (June, 17. 2014) that are not found in their museum specimens of the Leske's collection. Thanks to R. Schiller, R. Wolf, from the Zoologic Collection of the University of Leipzig has informed us that some of his old collections were dispersed in several other museums in Germany but they do not possess these samples. Our historical research will be continued but, being necessary to know some features that are not described by the first author, as the test plate structure, we felt it opportune to name as Neotype a specimen of *Sculpsitechinus auritus* (former *Echinodiscus* cf. *auritus* in Stara & Fois M., 2014) from Mangili, Madagascar.

Sculpsitechinus tenuissimus (L. Agassiz, 1847)
Plates 22, 23; Figs. 9a–c; Tables 6, 9, 12

- 1847, *Echinodiscus tenuissima* (L. Agassiz & Desor E.,)
1847, *Lobophora tenuissima* L. Agassiz & Desor E., p. 78
1861, *Lobophora deplanchei* Michelin (n.v.)
1863, *Lobophora texta* A. Agassiz, p. 359
1872–74, *Echinodiscus laevis* A. Agassiz (n.v.)
1881, *Echinodiscus biforis* Pfeffer (n.v.)
1948, *Echinodiscus bisperforatus* var. *truncatus*,
Mortensen T., pp. 409, 411, 413
1971, *E. tenuissimus* Agassiz, 1847, Clark A.M. &
Rowe F.W.E, p. 148
1986, *E. tenuissimus* Agassiz, 1847 De Ridder C.
(n.v.)
Data (n.v. 1861-1881 taken from Kroh, A., 2014)

EXAMINED MATERIAL. The Type material is not traceable in the Museum of Natural History of Paris where it was housed (see Agassiz & Desor, 1847). For these reasons we had to establish a Neotype.

Neotype: one specimen from Lembah Channel, North Sulawesi, Indonesia, MAC.IVM207, TL 50 mm (Plate 21 Figs. 1, 2, housed in the Department of Animal Biology and Ecology (UNICA), Cagliari, Italy.

Two specimens from Lembah Channel, North

Sulawesi, Indonesia, MAC.IVM207-208, and two from Fantin Collection TL = 50–60 mm; one specimen from New Caledonia, NHMUK.1981.11.2.25, TL 112 mm, TH 10.5 mm, one specimen from Palau, Micronesia, NHMUK.59.7.1.14, TL 120 mm, TH 11 mm. We have also considered a specimen from “New Caledonia” by literature in: Dollfuss & Roman (1981, table 33 figs. 5, 6), TL 121 mm; and one by personal communications and photos by F. Hattemberger collection, TL 68 mm, collected at the depth of 2 meter in a sandy beach from Noumea, Baie des Citrons, New Caledonia.

DIAGNOSIS. Medium sized species, elongated (in the specimens of New Caledonia and Palau) with a maximum width very rear of the center (mean TW = 97% TL), profile low, small and ellipsoidal-shaped to slit-like lunules. Petalodium highly variable (30 to 38% TL) smaller in the samples of New Caledonia and in those of North Sulawesi, the greater one in the specimen from Palau. In the oral face of the inter. 5 there are 2–3 post-basicoronal plates in column “a” and 3 in column “b”, with 2a and 2b partially paired; between the petals and the lunules there are 4-5 couples of plates.

DESCRIPTION. Medium sized; small, narrow and elongated ambulacral lunules (L1 = 12% and L2 = 4% TL, with WI = 7.7 and SI = 0.33) and with a narrower angle β (67°). Depressed test (\approx 9% TL), with the most highly point anterior to the apical disc. Thin margin, more thick anteriorly. Sub-equal petals, closed distally, with the front one slightly longer than the others; interporiferous zone wider 1–1.5 times of the poriferous ones. In the inter. 5 there are 2-3 post-basicoronal plates in column “a” and 3 in column “b”, with the first two partially coupled. The WA at the inter. 5 is 31% TL, one of the lowest among *Sculpsitechinus*. The periproct is small (2.5% TL), round shaped, far from the posterior margin (11 to 18% TL) and open between plates 2b/2a or 2b/3a/3b in inter. 5. The peristome is sub-pentagonal and small (3.5% TL), sub-central. Other features as for the genus. For any other data see the relate tables and plates.

DISTRIBUTION. Lembah Channel, North Sulawesi; Waigeo, West Papua (Indonesia); New Caledonia, Papua New Guinea and Palau Sibuan, (Micronesia and Melanesia) and perhaps Japan. Recent.

COMPARATIVE NOTES. *S. tenuissimus* differs from *S. auritus* and from *Sculpsitechinus* sp. 1 in that it has lunules instead notches. *S. tenuissimus* differ from *Sculpsitechinus* sp. 2 by the SI index that is greater (0.33) against 0.18 of *Sculpsitechinus* sp. 2. The data, however, is not sufficient to separate with certainty this species, because the oral plate structure of *Sculpsitechinus* sp. 1 is still unknown.

REMARKS. As already mentioned in the paragraph on *Echinodiscus andamanensis* n. sp., not having been published the plating of the type species *Echinodiscus tenuissimus*, under this name are included several morphotypes based on the test and lunules shape, coming also from very different geographical areas. However, the description of the type species made by Agassiz & Desor (1847: 78) is really laconic "species very flat, with small lunules, corresponding to the ambulacra pair posterior" and the sample deposited at the time in the "Museum of Paris", is now wanting (pers. comm. Sylvain Charbonnier, June 03.2014). Agassiz & Desor (1847) mentions the geographical origin (Waigiou), which corresponds to New Britannia (Indonesia). In the zonation resulted from our observations, in this area only *Sculpsitechinus* species are present. It seems clear, therefore, the need to appoint a neotype from the closest geographical area.

Sculpsitechinus sp. 1

Plates 1, 2; Table 1 in Stara & Sanciu (2014)

EXAMINED MATERIAL. 12 specimens, Recent, MAC IVM 81; MAC.IVM206 - MAC.IVM215; MAC.IVM233, housed in the MAC, Cagliari, Italy.

5 specimens from Oslob (TL 131 ÷ 154 mm), 5 specimens from Cebu (TL 152 to 173 mm); two examples of generic origin "Philippines" (TL 121 and 152 mm).

DIAGNOSIS. Large sized specie (up to 173 mm), with low side profile (mean TH = 12% TL), narrow and elongated ambulacral notches open on the posterior margin. Sub-equal petals, closed distally, with the frontal odd petal sometimes slightly longer than the other ones. In the oral face of the inter. 5 there are 3 post- basicoronal plates in column "a" and 4 in column "b", with the first two partially coupled

and the periproct that opens between the plates 2a/2b. Between the petals tip and the beginning of the notches there are 4 or 5 couples of plates.

DESCRIPTION. Large in size (in the studied sample TL 121 ÷ 173 mm), with more or less axially elongated ambulacral notches open on the posterior margin. Depressed test with the highest point anterior to the apical disc. Thin margin, more thick anteriorly. The petals are closed, sub-equal, with the frontal odd one a little longer than the other; poriferous zone flat or slightly sunken, interporiferous ones slightly raised, with interporiferous areas 1.5 to 2 larger than the poriferous ones. Notches varying in length from 18 to 27% of TL and are more or less narrow. The WA at inter. 5 is on average 33% TL and the β angle is on average 57°. The periproct is small (2.5% TL), rounded in shape, far from the posterior margin (16–24% TL) and always open along the suture 2b/2a. The internal structure consists of a central visceral hollow and a peripheral support structure. The hollow is sub-rounded to polygonal shaped and its size corresponds to the petalodium length (PL \approx 42% TL), the floor is thin and reinforced by a structure made by a network of thin trabeculae. The system of pillars and buttresses is similar to the *S. auritus*. the Aristotle's lantern is very large (20–24% of TL in specimen 140 mm long). For descriptive statistics see Stara & Fois M. (2014).

DISTRIBUTION. Island of Talibon (Bohol) and Island of Oslob (Cebu), Philippines. Recent.

COMPARATIVE NOTES. *Sculpsitechinus* sp. 1 differs from *S. auritus* by a larger Aristotle's lantern that measures 20–24% TL against 15–18% TL in a specimens 140 mm long. *Sculpsitechinus* sp. 1 differs from *S. tenuissimus* by a less number of couples of plates between petals tip and lunules/notches, which are 3–4 against 5–6 and have notches instead lunules.

Sculpsitechinus sp. 2

Plate 14 Fig. 4

Based on the illustration in Lindley (2001:128, fig. 7d.

2001, *Echinodiscus bisperforatus* Leske, 1778. Lindley, p. 128.

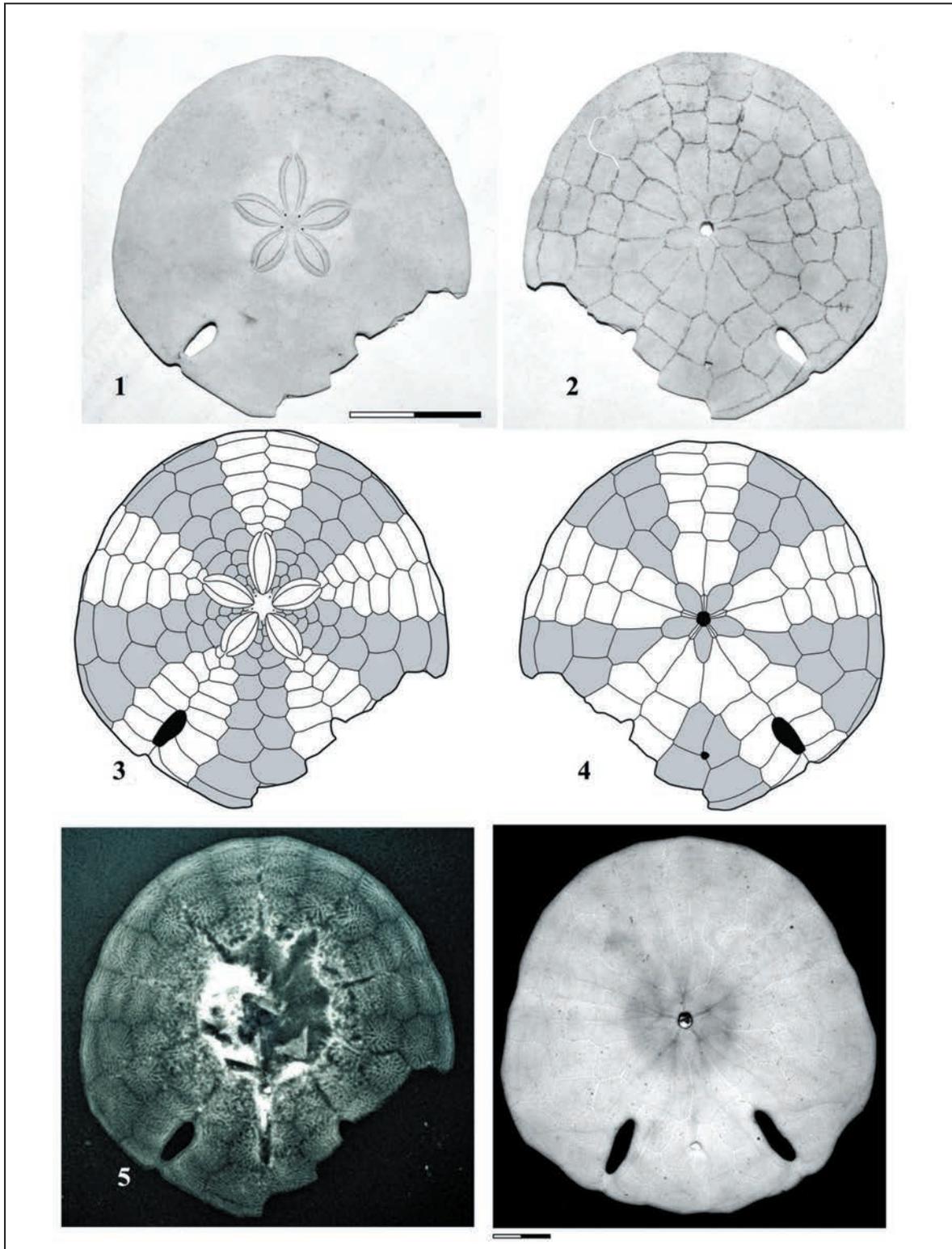


Plate 22. *Sculpitechinus tenuissimus*, Recent, Lembeh (Indonesia) and New Caledonia. Figs. 1, 2. Aboral and adoral view of MAC.IVM207 from Lembeh, North Sulawesi, Indonesia. Figs. 3, 4. Plate pattern of aboral and adoral faces of MAC.IVM207. Fig. 5. Radiograph taken in supero-inferior position of MAC.IVM207; are visible the parts of the small Aristotle's lantern. Fig. 6. Aboral view of well preserved specimen from New Caledonia (F. Hattemberg collection).

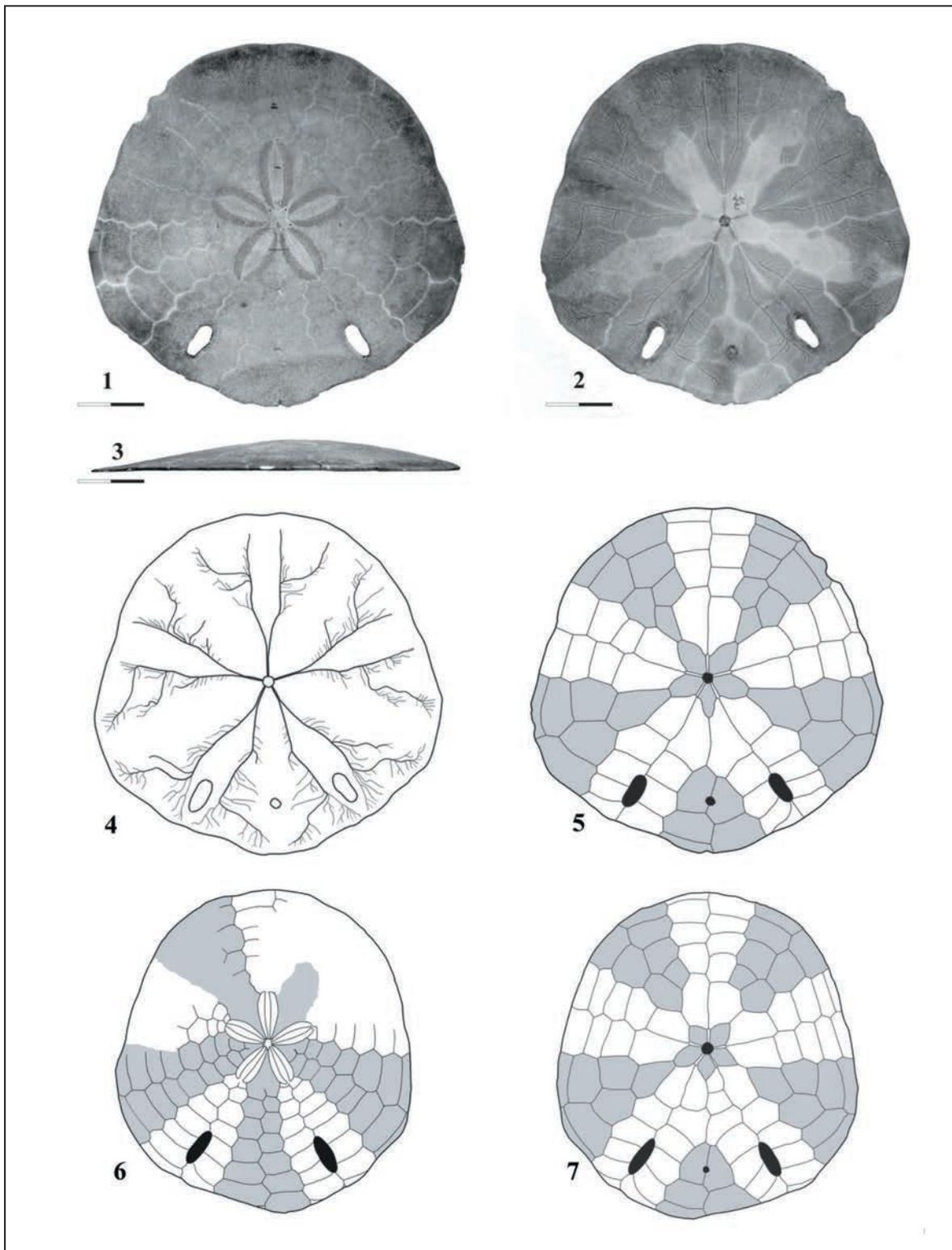


Plate 23. *Sculpsitechinus tenuissimus*, other example from New Caledonia. Figs. 1-3. Aboral, adoral and antero (to the left)-posterior (to the right) lateral view of NHMUK.1981.11.2.25. Fig. 4. Food grooves very branched scheme of NHMUK.1981.11.2.25. Fig. 5. Plate pattern of aboral face of NHMUK.1981.11.2.25. Figs. 6, 7. Aboral and adoral plate pattern from figs. 5-6, Pl. 33 in Dolfuss & Roman (1981).

EXAMINED MATERIAL. One specimen TL = 70 mm; TW = 65 mm, housed in the Department of Geology, Australian National University of Canberra; code ANU 60549.

DESCRIPTION. Test depressed of medium size, discoidal with anterior semi-circular outline, truncated posteriorly. Central apical system not well legible. Petals straight, narrow, distinctly closed distally; PL medium (43% TL); poriferous areas slightly less than the width of interporiferous ones. Axial, narrow Lunules in the posterior ambulacra. Tuberculation not legible.

Given its general shape, its large distance separating the lunule from the respective petals tips, and given the small β angle, this echinoid appears very near to *S. tenuissimus*.

Lindley (2001) accost this form to *E. truncatus* "lunule length relative to test radius or petal length as a diagnostic character. The possession of closed posterior lunules of a similar length to petals clearly indicates assignment of the Aseki specimen to *Echinodiscus bisperforatus* Leske, 1778. *E. tenuissimus* (L. Agassiz, 1847), a similar species in many respects, possesses lunules shorter than petals. Although Mortensen (1948: 409) observed that the length of lunules varies very considerably within this species, it is useful to note that the lunules of the Aseki specimen are at most about as long the petals, a diagnostic character of var. *truncatus* (L. Agassiz, 1841)".

Besides, the size of the lunules (L1 = L2 = 15% TL and 2.8% TL and SI = 0.18) is different from that of *S. tenuissimus*, in which L1 = 12% TL and L2 = 4% TL, with an SI = 0.33. The data, however, is not sufficient to separate with certainty this species from *S. tenuissimus*. In fact, the features of the oral face and of the plate structure are unknown.

DISTRIBUTION. Langimar Beds, Middle Miocene, Aseki Village (Morobe Province), Papua New Guinea.

REMARKS. Based on its geological age, we believe that it is an ancestral species of *S. tenuissimus* and *S. auritus* currently living in the same regions. However, in the absence of further details such species is left in open nomenclature: *Sculpsitechinus* sp. 2.

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