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MONOGRAPH

The echinoid genus *Amphiope* L. Agassiz, 1840 (Echinoidea Astriclypeidae) in the Oligo-Miocene of Sardinia (Italy)

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ABSTRACT The records of the genus *Amphiope* Agassiz, 1840 (Astriclypeidae) from Sardinia are revised on the basis of 110 specimens, collected from 15 localities of Oligo-Miocene age. Since the morphological characters stated in the literature to distinguish the species of *Amphiope* described in this region cannot provide a clear separation between them, analyses of the plate patterns and of the internal test structure are introduced as taxonomic tools useful for species-level taxonomy in this genus. Five different species of *Amphiope* are identified. Three of the six species erected on the basis of fossil material from Sardinia are confirmed as valid: *Amphiope lovisatoi* Cotteau, 1895, *A. montezemoloi* Lovisato, 1911 and *A. nuragica* (Comaschi Caria, 1955). Two additional species are left in open nomenclature. The morphological descriptions and the stratigraphical distributions are updated and improved.

KEY WORDS Echinoidea; *Amphiope*; Oligo-Miocene; Sardinia; Mediterranean.

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INTRODUCTION

The genus *Amphiope* L. Agassiz, 1840 (Echinoidea Astriclypeidae) is known from the Oligocene and Miocene of Central and Southern Europe, Northern Africa, Angola, Middle East, India (Smith & Kroh, 2011).

It is well represented also in the Oligo-Miocene of Sardinia (Fig. 1) since ten species of *Amphiope* were recorded in the literature (Table 1), six of which were erected as new taxa on the basis of Oligo-Miocene fossils from this region: *A. lovisatoi* Cotteau, 1895, *A. dessii* Lovisato in Cotteau, 1895, *A. montezemoloi* Lovisato, 1911, *A. pallavicinoi* Lovisato, 1914, *A. calvii* Lovisato, 1914 and *A. nuragica* (Comaschi Caria, 1955). *A. montezemoloi* was subsequently placed into synonymy with *A. bioculata* (des Moulins, 1837), the type-species of the genus, by Comaschi Caria (1955), Philippe (1998) and Kroh (2005); the last author considered also *A. lovisatoi* as synonymous with *A. bioculata*. Since the type-specimens belonging to Lovisato's collection, at that time housed at the "Regio Museo Mineralogico e Geologico di Cagliari", were lost in 1943 (Comaschi Caria, 1955), this work is based mainly on new material collected from the respective type-localities and on the holotype of *A. nuragica*, still available to study at the "Dipartimento di Scienze Chimiche e Geologiche, Università di Cagliari".

The genus *Amphiope* accounts for more than 40 species, most of which are nominal species in need of revision, due to high intraspecific variation and

Figure 1. Regions of Italy in which *Amphiope* has been recorded in the literature (dark grey). Enlarged area (Sardinia): finding localities examined in this study (black circlets), or recorded in the literature (grey squares). Province of Sassari: 1 = Porto Torres; 2 = La Crucca; 3 = Bancali; 4 = San Giorgio; 5 = Sedini; 6 = Monte Oria Pizzinnu; 7 = Billiu and Monte Sa Loca, near Chiaramonti; 8 = San Matteo, near Ploaghe; 9 = Ardara; 10 = Bessude; 11 = Bonnanaro; 12 = Monte Zarau, near Torralba; 13 = Bonorva. Province of Oristano: 14 = Nuraghe Caiu, near Villa Sant'Antonio; 15 = Laconi; 16 = Bruncu Muntravigu and Tanca Sierra, near Senis; 17 = Duidduru and Genoni (Nuoro); 18 = Monte Is Casteddus, near Isili; 21 = Santadi and Sa Lisporra, at Capo Frasca. Province of Cagliari: 19 = Cuccuru Tuvullao; 20 = Strintu 'e Melonis and Nurri; 23 = Monte S. Michele; 24 = Capo S. Elia and Bonaria. Medio Campidano province: 22 = Monte Arcuentu.

poor species definition (Smith & Kroh, 2011). The complex taxonomy of this genus has been traditionally based on the external morphological features, mainly test outline, size and shape of lunules and petals. Structural characters, largely used in the taxonomy of other clypeastroids (Durham, 1955; Lohavanijaya, 1965; Mooi, 1989; Kroh, 2005; Jansen & Mooi, 2011), were almost overlooked in earlier studies dealing with *Amphiope* and, although several species of *Amphiope* have been described in the literature, important features for species-level taxonomy, such as oral plating, were poorly illustrated or omitted completely.

During a preliminary investigation we attempted to find out whether the specimens from Sardinia might be attributed to already known species, but a particular difficulty was found in the use of the external characters alone, because comparison with taxa whose structural characters are unknown remained uncertain. This paper presents the results of further studies based on a large and well preserved fossil sample, to bring light into the problem of classification of *Amphiope*. The main purpose is a modern revision of Sardinian occurrences of *Amphiope*, using morphological and morphometric analyses, with emphasis on the plate patterns and the internal test support system.

Geological setting

The geology and palaeoecology of the Sardinian *Amphiope*-bearing localities cited in this study were described by Stara et al. (2012) and Mancosu & Nebelsick (2013). In the following a brief summary is given of the type localities of the three species revised from this region.

Central Sardinia (Marmilla). Three main marine sedimentary cycles have been recognized in the Sardinian Basin, from late Oligocene to early Messinian (Assorgia et al., 1997; Funedda et al., 2000; Carmignani et al., 2001). The *Amphiope*-bearing deposits in Central Sardinia belong to the first cycle, extending from the late Oligocene to the late Burdigalian. The Cenozoic sequence starts with the late Oligocene-early Aquitanian Ussana Formation (Pecorini & Cherchi, 1969), consisting mainly of sediments of continental origin. The Ussana Formation is partly heteropic with and is followed by the Nurallao formation, late Chattian-early Burdigalian (Serrano et al., 1997), which consists of the "Conglomerato di Duidduru" member, made of coarse clastics from transitional (deltaic) environments (Sowerbutts & Underhill, 1998) and the littoral marine deposits of the Arenarie di Serralonga member, late Oligocene-early Aquitanian (Assorgia et al., 1997; Barca et al., 2005), which yielded the *Amphiope* specimens examined from this area. The Nurallao Formation is partially heteropic with and followed by the Calcari di Villagreca, dated to the late Oligocene-early Burdigalian, and by the Marmilla Formation, dated to the Aquitanian (Cherchi et al., 2008). The material studied from this area was collected from eight localities: Villa Sant'Antonio, Bruncu Muntravigu, Tanca Sierra, Duidduru,

Recorded species	Cited by	Locality (Province)
A. bioculata (des Moulins, 1837)	Lambert (1907)	Capo S.Elia (Cagliari)
	Comaschi Caria (1955, 1972)	Cuccuru Tuvullao (Cagliari)
	Barca et al. (2000)	Thiesi (Sassari)
	Spano et al. (2002)	Capo Frasca (Oristano)
A. hollandei Cotteau, 1877	Cotteau (1895)	Castelsardo (Sassari), Capo S. Elia and Monte S. Michele (Cagliari), Santadi (Oristano)
	Lovisato (1911, 1914)	Capo Frasca (Oristano), Nurri (Nuoro), Torralba (Sassari)
A. lovisatoi Cotteau, 1895 *	Cotteau (1895)	Billiu* near Chiaramonti (Sassari)
	Comaschi Caria (1955, 1972)	Cuccuru Tuvullao (Cagliari)
A. dessii Cotteau, 1895 *	Cotteau (1895)	Nurri* (Nuoro)
	Lovisato (1914)	Bessude (Sassari)
	Comaschi Caria (1955, 1972)	Cuccuru Tuvullao (Cagliari)
A. montezemoloi Lovisato, 1911 *	Lovisato (1911)	San Giorgio* near Sassari
A. deydieri Lambert, 1912	Comaschi Caria (1955, 1972)	Cuccuru Tuvullao (Cagliari)
A. transversivora Lambert, 1912	Comaschi Caria (1955, 1972)	Cuccuru Tuvullao (Cagliari)
A. calvii Lovisato, 1914 *	Lovisato (1914)	San Matteo* near Ploaghe (Sassari)
A. pallavicinoi Lovisato, 1914 *	Lovisato (1914)	Monte Zarau* near Torralba (Sassari)
	Comaschi Caria (1955, 1972)	Cuccuru Tuvullao (Cagliari)
Amphiope sp.	Lovisato (1914)	Nulvi and Bonorva (Sassari); Monte Arcuentu (Oristano), Sant'Antonio Ruinas (actually Villa S. Antonio), Laconi, Genoni, Capo S. Elia and Monte S. Michele (Cagliari).
A. nuragica (Comaschi Caria, 1955) *	Comaschi Caria (1955, 1972)	Cuccuru Tuvullao* (Cagliari)
Amphiope sp.	Stara et al., 2012	Cuccuru Tuvullao, Monte is Casteddus and Isili (Cagliari); Nuraghe Caiu, Bruncu Montravigu and Tanca Sierra (Oristano); Duidduru (Nuoro); Bancali; La Crucca; Porto Torres; Ardara; Chiaramonti and Bonnanaro (Sassari)

Table 1. Records of *Amphiope* from Sardinia reported in the literature. An asterisk marks the species firstly described on the basis of material collected from this region.

Genoni, Isili, Cuccuru Tuvullao and Capo Frasca (see Fig. 1).

- Cuccuru Tuvullao (n. 19 in Fig. 1). The type-locality of *A. nuragica* (Comaschi Caria, 1955) is located 1.5 km NE of Nuragus (Cagliari). *Amphiope* occur in high numbers in a medium to coarse-grained volcanoclastic sandstone (herein named C. Tuvullao I), 2-2.5 m thick, corresponding to the "Facies B" of Mancosu & Nebelsick, 2013; Fig. 2). *Amphiope* is the most abundant taxon, followed by *Parascutella* sp., reworked balanids and bivalves. Seven species of *Amphiope* were cited by Comaschi Caria (1955) in this layer, including *A. nuragica*. The echinoids are denuded, commonly fragmented in the shape of pie-slices. Loosely packed or dispersed specimens are both in life position and upside down, their long axes being more or less parallel to the stratal surfaces. This sand dollar deposit is assigned to a shoreface environment and represents a multiple in situ reworking accumulation (Mancosu & Nebelsick, 2013).

Fragments and rare complete specimens of *Amphiope* occur also at the base of the overlying richly fossiliferous fine mudstone (herein named C. Tuvullao II), corresponding to the "Facies C" of Mancosu & Nebelsick (2013); Fig. 2). The fossil content is dominated by gastropods, belonging to the genus *Turritella* Lamarck, 1799, and by the bivalve *Panopea* Ménard, 1807.

Northern Sardinia. Seven *Amphiope*-bearing localities were sampled in the Sassari province: Porto

Torres, La Crucca, Bancali, San Giorgio, Chiaramonti, Ardara and Bonnanaro. These deposits belong to the second Cenozoic sedimentary cycle, late Burdigalian-early Langhian (Mancosu & Nebelsick, 2013). At the base, the lacustrine and fluviodeltaic sediments of the Oppia Nuova formation (Funedda et al., 2000) are overlain by the Calcari di Mores Formation, consisting of bioclastic limestones and poorly cemented sands of shallow water origin (Mazzei & Oggiano, 1990; Funedda et al., 2000). The Calcari di Mores Formation is followed by the Marne di Borutta Formation, which represents a deeper shelf facies.

- Chiaramonti (n. 7 in Fig. 1). Billiu, the type-locality of *A. lovisatoi*, rests along the main road from Ploaghe, close to Chiaramonti. The specimens examined in this paper were collected from the section studied by Stara et al. (2012) cropping out at Monte Sa Loca, less than 1 km far from Billiu: it is 9 m thick and extends laterally for some 40 m. The main *Amphiope*-bearing layer corresponds to the "Facies C" of Mancosu & Nebelsick (2013; Fig. 4), dated to the lower part (late Burdigalian) of the Calcari di Mores Formation, and represents the lateral extension of the strato-type of Billiu. It consists of very coarse, poorly sorted, massive sandstone, about 1 m-thick, with carbonate cement, which, though discontinuous, can be traced over the entire length of the outcrop. The dense accumulation of well-preserved echinoids of Facies C is considered to represent an autochthonous assemblage in a shoreface environment (Mancosu & Nebelsick, 2013). *Amphiope* prevails by far, followed in abundance by *Agassizia* Yoshiyasu, 1987, *Parascutella* Durham, 1953, *Echinolampas* Gray, 1825 and small bivalves, and is represented almost exclusively by complete tests (80%) with subordinate fragmented tests.

- San Giorgio (n. 4 in Fig. 1). The type locality of *A. montezemoloi* was never cited again since its original description. It has been traced by one of the authors (P.S.) following the indication of Lovisato (1911; 1914), along the Sassari-Alghero railroad, 1.5 km far from the abandoned rail-station of San Giorgio towards Olmedo. The *Amphiope*-bearing outcrop consists of a coarse-grained sand-stone and extends for a few square meters, only. *Amphiope* is mainly represented by fragmented specimens in chaotic position.

MATERIAL AND METHODS

The studied material consists of 110 specimens, preserved as whole coronas deprived of the spines, and several fragmented individuals, from 15 Miocene Sardinian localities (Fig. 1). Most of them are

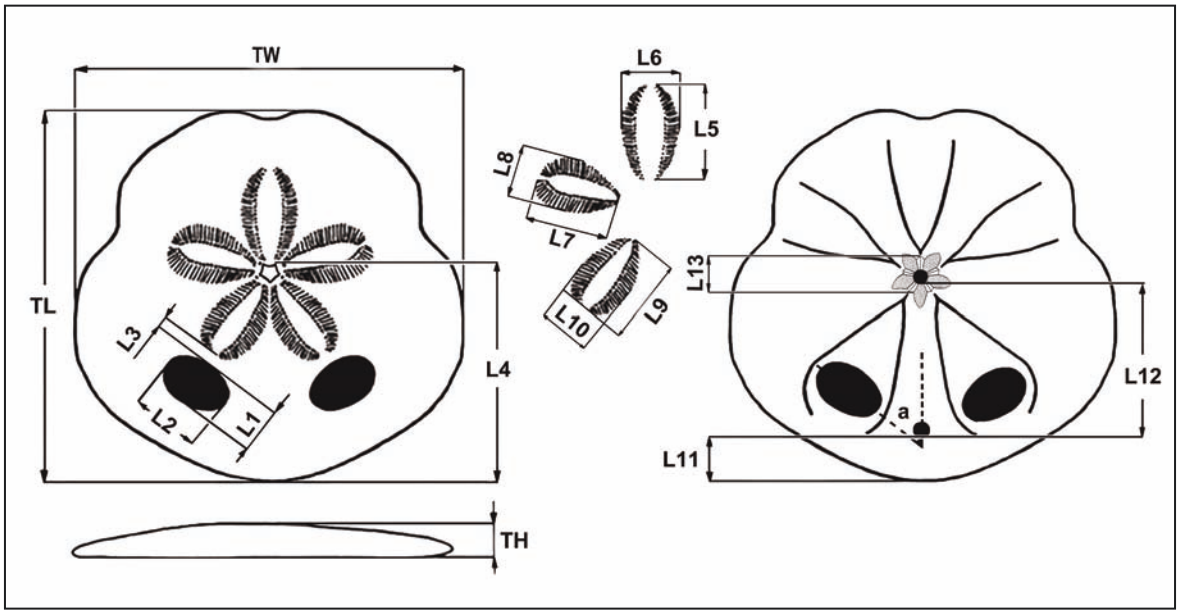

Figure 2. *Amphiope*: scheme of the biometric parameters measured in the studied specimens.

housed at the Museo di Storia Naturale "Aquilegia" of Cagliari (MAC code): 95 specimens were collected by one of the authors (P.S.), 12 specimens were donated by private collectors. Three additional specimens have been examined in the Dipartimento di Scienze Chimiche e Geologiche, Università di Cagliari (UNICA); they include the holotype of *A. nuragica* (code 9CC.8-10504) and two specimens classified as "*A. calvii*" (code 3CC) and "*A. dessii*" (code 6CC-10503) by Comaschi Caria (1955; pl. 1 and pl. 7, respectively).The other specimens from Cuccuru Tuvullao described by Comaschi Caria (1955) have not been traced at the UNICA. The measurements of ten lost specimens, reported by Lovisato (1911; 1914) and Comaschi Caria (1955), were used in the statistical biometrical analyses; since some data were lacking, they were taken from the figures given by Comaschi Caria (1955: pl. 2, figs. 1, 2, pl. 3, figs. 1, 2, pl. 4, figs. 1, 2, pl. 5, figs. 1, 2, pl. 6, figs. 1, 2, pl. 8, figs. 1, 2, pl. 9, figs. 1, 2, pl. 13, fig. 1; 1972: pl. 44. figs. 3-4).

According to Lovisato (1911; 1914) the specimens he provided for study to other echinologists, including the type series used by Cotteau (1895) to erect *A. lovisatoi* and *A. dessii*, returned back to his collection at that time stored in the "Regio Museo Mineralogico e Geologico di Cagliari". All those specimens, as well as the type material of the other species based on fossils from Sardinia, with the exception of *A. nuragica*, were lost in 1943 during the 2nd World War (fide Comaschi Caria, 1955).

The internal structure was studied by sectioning the test, and by X-ray; 5 specimens from Bancali, 3 from C. Tuvullao, 2 from Bonnanaro and 2 from Chiaramonti were used for this purpose.

Morphological abbreviations (Fig. 2) -α = angle between the axes of the two posterior petals; TL = test lenght; TW = test width; TH = test height; L1-L2 = lunule length and width, respectively; L3 = distance posterior petal tip from the corresponding lunule; L4 = distance 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 posterior border of periproct and of the test; L12 = distance between the posterior border of the peristome and of the periproct; L13 = antero-posterior diameter of the basicoronal circlet. Measurements of L1 to L10 were taken from the left side of the test, where possible. Systematic palaeontology follows Kroh & Smith (2010).

Broken edges were indicated by dotted lines in drawings, heavier lines indicate unbroken ambitus. Plates were numbered according to Lovén's system (CIT; compare Plate 1 Fig. 3b), interambulacral plates were shaded in grey.

Geographic coordinates on the World Geodetic System of 1984, WGS84.

Biometric analyses were carried out and data analyzed using the software PAST -version 1.97 (2010) (Hammer & Harper, 2010; Hammer et al., 2001), to help interpret the samples collected from eight Sardinian localities. The original values of the metric parameters were divided by TL to exclude the effect of size, as suggested by Durham (1955), Lohavanijaya (1965) and Pereira (2010). Principal component analysis (PCA) is based on 71 specimens [8 from Bancali, 4 from Bonnanaro, 34 from Chiaramonti, and 25 from C.Tuvullao (22 from layer I and 3 from layer II)]. The analysis utilizes 11 variables: TW/TL, TH/TL, L1/TL, L2/TL, L3/TL, L4/TL, L5/TL, L6/TL, L9/TL and L10/TL. Univariate and bivariate analyses were based on a data set taken from 79 specimens: 9 from Bancali, 38 from Chiaramonti and 28 from C.Tuvullao (25 from layer I and 3 from layer II) and 4 from Bonnanaro-San Giorgio.

RESULTS: MORPHOLOGICAL FEATURES OF *AMPHIOPE* FROM SARDINIA

Lunules. Though a large variability is present in the outline, lunules are commonly large-sized and subcircular (Plate 4 Fig. 14c) to broad elliptical (Plate 4 Fig. 14b) at Bancali, Ardara, Villa S. Antonio, Bonnanaro and San Giorgio. Similar shaped, but smaller, lunules occur at Porto Torres and La Crucca, whereas they are mainly broad elliptical (Plate 1 Figs. 1, 2) at Chiaramonti and narrow-elliptical at C. Tuvullao (Plate 2 Figs. 13b–d). Specimens from different localities bearing similar-shaped lunules often have different external test characters and/or internal structure, so that test and lunules features are not univocally linked. Lunules may be different even in a single specimen (e.g. Plate 1 Fig. 3a).

Plate structure. A number of constant structural features are recognized in the studied material:

- Interambulacral columns are always disjunct adorally, plate 2b and sometime both plates 2a and 2b being separated from the basicoronals by enlarged first ambulacral post-basicoronal plates.

- Oral interambulacra 1, 4, 5 are meridoplacous, whereas interambulacra 2 and 3 may be either amphiplacous or, more frequently, meridoplacous.

- The first post-basicoronal plates are the longest of the series, both in ambulacral and interambulacral columns. In interambulacrum 5, the plate 2b is more elongate than 2a.

- There always is a higher number of plates aborally than adorally in each column.

- There is almost the same number of plates in each column of interambulacra 1, 4, 5 and ambulacra I and V: 14–15, seldom 16, plates in the specimens of Bancali and Chiaramonti, whereas they are more numerous (16-20) at C. Tuvullao. The same condition occurs in interambulacra 2 and 3, and in ambulacra II, III and IV: 14–16 plates in each column at C. Tuvullao I, 12-14 at Bancali and only 10–13 at Chiaramonti.

- Lunules walls have vertical sutures (Pl. 4 Fig. 8) corresponding to the *Echinodiscus*-type ("cross linked" sutures, sensu Mooi, 1989). Adorally, lunules begin to open in correspondence of the second pair of post-basicoronal plates, whereas 1–2 couples of plates separate lunules from the petal tips, aborally. Plates encircling lunules are more numerous on the aboral side (6–9) than adorally (3–5).

The composition of the oral interambulacrum 5 is characteristic (Table 2): at C. Tuvullao I the normal condition is 3 (33% of cases; Plate 2 Fig. 1b) to 4 plates (67%) in column 5b, whereas in all the other samples there are only 2 post-basicoronal plates in column 5a and 3 in 5b (Plate. 4 Figs. 11, 12).

Also the position of the periproct is highly characteristic (Table 2): the specimens of C. Tuvullao II have the periproct far from the posterior test margin and bounded by the first pair of post-basicoronal plates 2a/2b (Plate 3 Figs. 9b, 10b). At Bancali, Bonnanaro and San Giorgio the periproct is invariably associated with plates 2a/3b (Plate 3 Figs. 2a, b; Plate 4 Figs. 11, 12), usually positioned halfway along the suture. This is the most frequent condition also at Chiaramonti, but at this locality the periproct opens more distally, near the outer edge of plates 2a/3b towards plate 3a (Plate 1 Fig. 3b), or just at the conjunction point 2a/3b/3a (9 cases of 27; Plate 1 Fig 4b), sometimes even between 3a/3b (3 cases). At C. Tuvullao I the periproct is commonly found (21 cases of 41 = 51%) at the conjunction point 2a/3a/3b (Plate 2 Figs. 1b, 2b) or more distally (22%; Plate 2 Fig. 3).

The interambulacral basicoronal circlet is very variable in shape and size, even at the same locality. The ambulacral circlet is more homogeneous: the mean value of L13 is 11.3% TL at Bancali and 10.8% at C. Tuvullao I; it is smaller at Chiaramonti, Bonnanaro and San Giorgio.

Locality	Position of the periproct								Plates present in the interambulacrum 5 adorally			
	2b/2a	2b/2a/3b	2a/3b	2a/3b/3a	3b/3a	3a/4b	3b/3a/4b	3b/4a/4b	3a/4b	4a/4b	4a/5b	5a/5b
Ardara	-	-	2	-	-	-	-	-	1	-	-	-
Bancali	-	-	9	-	-	-	-	-	7	2	-	-
Bonnanaro	-	-	3	1	-	-	-	-	2	1	-	-
Chiaramonti	-	-	14	9	3	1	-	-	19	5	-	-
C.Tuvullao (I)	-	-	11	21	5	1	2	1	-	12	21	3
C.Tuvullao (II)	2	1	-	-	-	-	-	-	2	1	-	-
La Crucca	-	-	3	-	-	-	-	-	-	-	-	-
Porto Torres	-	-	1	-	-	-	-	-	-	1	-	-
Senis	-	-	1	-	-	-	-	-	-	-	-	-

Table 2. Plates present in the interambulacrum 5 adorally and position of the periproct in the examined samples of *Amphiope* from Sardinia.

INTERNAL TEST STRUCTURE. It consists of a well developed peripheral ballast system surrounding a central cavity with domed ceiling. The extension of the central cavity roughly corresponds to the petaloid area; adorally, it does not extend beyond the distal border of the first pair of post-basicoronal ambulacral plates, in all samples. In the specimens of Chiaramonti the central cavity has an almost flat floor and is bordered by thin transversely elongate straight walls delimiting a sub-pentagonal area (Plate 1 Fig. 8). At Bancali, Bonnanaro and San Giorgio the first pillars of the radiating interambulacral buttresses (Plate 3 Fig. 5a, Plate 4 Fig. 7) are stronger and get closer to the centre, thus forming an almost "starring" outline (Plate 4 Fig. 15). At C. Tuvullao I the floor of the interambulacra begin to thicken close to the peristome and gradually rise towards the first pillars of the radial supports (Plate 2 Fig. 11); the central cavity has a rough sub-circular outline, with floor and ceiling thicker than in the specimens from Bancali and much thicker than those from Chiaramonti, Bonnanaro and San Giorgio (Plate 3 Fig. 7). The convexity present on the external surface of the petals contributes to strengthen the ceiling. In the specimens from C. Tuvullao I the whole petal surface is convex whereas only the interporiferous areas are convex at the other localities.

The lantern muscle attachment structures always consist of five fused interradial pegs (Plate 1 Fig. 8). The peripheral ballast system is made of a series of sub-cylindrical pillars and walls extending from the ceiling to the floor and crossed by cavities. Towards the ambitus it becomes very dense, almost massive, and crossed by micro-canals, in all the examined samples.

On the whole, the support system is strongly developed in the specimens of C. Tuvullao I and II, whereas it is lighter and more complex at Bancali and much lighter at Bonnanaro, San Giorgio and Chiaramonti.

RESULTS OF BIOMETRIC ANALYSES

The PCA analysis resulted in three components accounting for more than 70% of the total variance in the data set. The first (PC1) explains 35.5% of the variance; the ratios TW/TL and TH/TL enter the heaviest loading into PC1. The second component (PC2) is mainly controlled by L4/TL, the third (PC3) by the lunule dimension variables. On the whole, the PCA scatterplot (Fig. 4) shows large overlaps in the distributions of specimens from the different localities in multivariate space, delimited by convex hulls. Only the samples from C. Tuvullao I and Bonnanaro are clearly separate from that of C. Tuvullao II. According to the PCA analysis results, the specimens from C. Tuvullao I and II present higher test and lunules with lower values of L1 and higher values of L2.

Descriptive statistics resulting from the univariate analysis are reported in Table 3. The bivariate plots confirm that the specimens from C. Tuvullao II have much higher test (Fig. 3), the length of the frontal ambulacrum and the distance of the periproct from the posterior test margin have more elevate values than those from layer I, the apical disc is more centrally located. The sample from C. Tuvullao I has higher tests and more transversely elongated lunules than those from the other localities (Fig. 5), with the exception of C. Tuvullao II. The specimens from Chiaramonti and Bonnanaro-San Giorgio have a very low test (Fig. 3). At Chiaramonti the frontal petal has almost the same length of the posterior petals (mean L9 = 95.1% L5), whereas it is slightly longer at C. Tuvullao I, Bancali, Bonnanaro (mean of L9 ranging from 86.6 to 88.8% L5), and much longer at C. Tuvullao II (mean L9 = 79.1% L5, only).

On the whole, the statistical analyses indicate the presence of five different morphotaxa in the studied material, corresponding to the samples from C. Tuvullao I, C. Tuvullao II, Bonnanaro-San Giorgio, Chiaramonti, Bancali.

DISCUSSION

The material under study indicates a large variability of the morphological characters stated to separate the species of *Amphiope* recorded from Sardinia, mainly consisting of the external test features: test outline, size and shape of lunules and petals (Cotteau, 1877, 1895; Lovisato, 1911, 1914; Cottreau, 1914; Comaschi Caria, 1955, 1972; Philippe, 1998).

Using these "diagnostic" characters, Comaschi Caria (1955) recognized seven species at C. Tuvullao I.

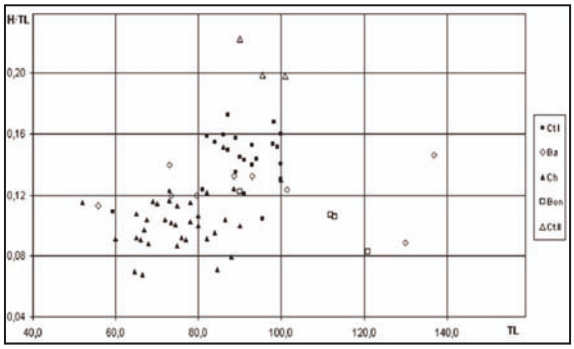

Figure 3. *Amphiope* from five Sardinian localities: bivariate plot of test height (values of H divided by TL) against test length (TL, in mm). Legend: Ba = Bancali; Bon = Bonnanaro; Ch = Chiaramonti; Ct I and Ct II = Cuccuru Tuvullao, layer I and layer II, respectively.

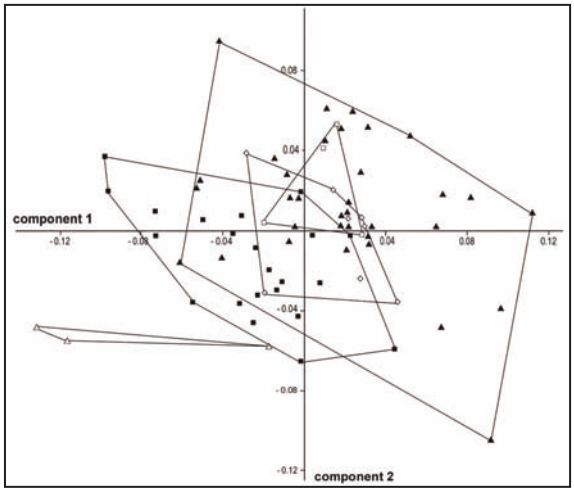

Figure 4. Scatter diagram of PCA analysis based on specimens of *Amphiope* from five Sardinian localities. The legend is reported in figure 3.

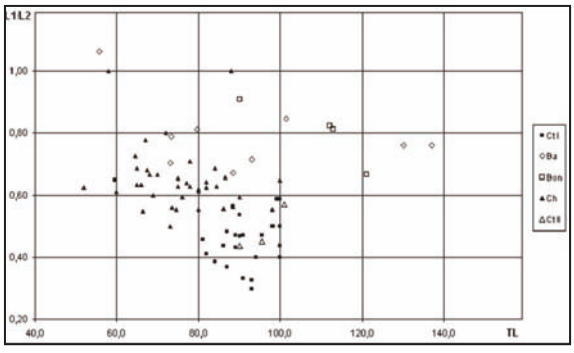

Figure 5. *Amphiope* from five Sardinian localities: bivariate plot of L1/L2 ratio against the test length (TL, in mm). The legend is reported in figure 3.

However, intermediate cases are present in the sample studied from this locality. On the other hand, basing on the recent interpretation of *A. bioculata* by Philippe (1998) as a taxon with large morphological variability and stratigraphical distribution, the examined material from Sardinia should be attributed to a single species. The specimens bearing the "diagnostic" characters of *A. lovisatoi*, *A. pallavicinoi* and *A. calvii* could be included in the variability range of "population B" of *A. bioculata* described by Philippe (1998; fig. 15 b, e; pl. 16, fig. 6). The same case occurs with the *A. transversivora-A. deydieri-A. hollandei* group, which is close to "population A" (Philippe 1998; fig. 14 d-f; pl. 16, fig. 4), and with *A. montezemoloi*, apparently corresponding to "population D" (Philippe 1998; fig. 17d, pl. 16, fig. 5).

The results of the biometric analyses clearly show a number of significant differences and point to the occurrence of at least five different morphotaxa in the studied sample.

To tackle the uncertainty, the analysis of the structural features is introduced in the taxonomy of *Amphiope*. The plate patterns and the inner test structure have already been utilized in the classification of other clypeasteroid genera (Durham, 1955; Lohavanijaya, 1965; Mooi, 1989; Jansen & Mooi, 2011). The arrangement of the plates in echinoids is fixed early in ontogeny and the basic pattern does not change during further growth in most forms, especially in scutelliform echinoids in which the plates forming the sharp ambitus are of special form and prevent plate translocation from the aboral to the oral side during later growth (Kroh, pers. comm., 2012). The taxonomic potential of the plate structure has been recently tested by Stara & Sanciu (2014) in *Echinodiscus* Leske, 1778, a genus closely related to *Amphiope*. The results indicate that the position of the periproct, the shape and the number of plates in the oral interambulacrum 5 clearly separate *E. auritus* Leske, 1778 from the other extant species of *Echinodiscus*. These features are expected to provide a taxonomic potential also in *Amphiope*. Indeed, structural features are well preserved in the studied material from Sardinia and show a low variability; additionally, the structural differences identified between the Sardinian samples match with the diversities indicated by the morphometric analyses.

Basing on the external test morphology, the study of the structural characters and the statistic biometric analyses, the specimens from Chiaramonti (Pl. 1) are assigned to *A. lovisatoi* since they were collected from the type locality of this species and they are consistent with the original description and illustration given by Cotteau (1895) and Lovisato (1914): test very low with sharp margin and rather broad, transversely elongated elliptical lunules. The sample from this locality is clearly separated from the others by the combination of structural characters: only two post-basicoronal plates present in the oral interambulacral column 5a, periproct located in the posterior part of the suture between plates 2a/3b, internal structure very light with thin shell and subpentagonal central cavity.

Well-preserved material recently collected from San Giorgio, the type-locality of *A. montezemoloi* Lovisato, 1911, and Bonnanaro, corresponds to the original description of this species: large-sized and anteriorly constricted test, with broad subcircular lunules (Plate 3 Figs. 3a, b). *A. montezemoloi* differs statistically from *A. lovisatoi* by a much larger test. Additionally, the specimens from Chiaramonti have smaller and more elongate lunules, the frontal petal almost as long as the others, the internal structure is lighter and the central cavity is subpentagonal not starring as in *A. montezemoloi*.

The holotype of *A. nuragica* (Plate 2 Figs. 1a, b) has four post-basicoronal plates in the oral interambulacral column 5b, three in column 5a, and the periproct is located at the conjunction of plates 2a/3a/3b. Comparison with the specimens collected from the type-layer (C. Tuvullao I) with the holotype is entirely consistent. No significant statistical differences were observed between the specimens with the periproct close to the conjunction point 2a, 3a, 3b and those with the periproct more posteriorly located. The characteristic and strong internal test structure is present in all the specimens from this bed. Thus, the whole sample from C. Tuvullao I is assigned to *A. nuragica* (Comaschi Caria, 1955). The combination of the peculiar structural features distinguishes *A. nuragica* from all the other Sardinian examined samples.

The specimens from C. Tuvullao II stand apart from all the others from Sardinia by much higher test, apical system more centrally located, frontal petal much longer than the posteriors and the periproct bounded by the first pair of post-basicoronal plates. Due to the scarcity of the available material these specimens are assigned to *Amphiope* sp. 1, and left in open nomenclature.

The specimens of Bancali (Plate 4 Figs. 1–3), though rather similar to those from San Giorgio-Bonnanaro, differ statistically from *A. montezemoloi* by more elevate test, larger ambulacral basicoronal circlet and smaller lunules, and by a stronger internal structure. The same differences separate them from *A. lovisatoi*; additionally, the specimens from Chiaramonti are smaller and the periproct, though bounded by plates 2a/3b as well as in the sample of Bancali, is closer to the conjunction point 2a/3b/3a. Though the studied sample looks like well differentiated, additional well-preserved material is needed to corroborate the observed differences and to confirm the occurrence of a distinct species. Therefore, the specimens from Bancali are assigned to *Amphiope* sp. 2.

Only scant and poorly preserved material is currently available from the type-localities of *A. dessii* Lovisato in Cotteau, 1895, *A. pallavicinoi* Lovisato, 1914 and *A. calvii* Lovisato, 1914. The oral plating as well as the internal support arrangement of those species were not reported in the original descriptions and cannot be made out from illustrated specimens. Cotteau (1895) attributed a test fragment from Sardinia to *A. hollandei* Cotteau, 1877. Other Miocene specimens from Sardinia were attributed to this species (Lovisato, 1911; 1914). Since all that material was lost (fide Comaschi Caria, 1955) the occurrence of *A. hollandei* in Sardinia is not confirmed.

Most of the *Amphiope* species described in the literature lack primary data on the plating patterns and the internal test structure and are therefore not completely documented in terms of their morphology. This is the case also for the type-species of *Amphiope*: the type locality and stratum of the specimen "*variété 3*" of *Scutella bifora* (see Lamarck, 1816) on which des Moulins (1837) based the diagnosis of *Amphiope bioculata*, are unknown; des Moulins tentatively proposed "*terrain tertiaires*" of Suze la Rousse in the Rhône Basin and Bordeaux (France) as type-localities for that specimen. No well preserved specimens from these localities have been traced in public institutions (Philippe, 1998; pers. comm. B. Martin Garin, March 2013) and the plate patterns could not be taken from figures re-

ported in the literature (Lambert, 1912). Philippe (1998), when studying *Amphiope* from the Rhône Basin, described also specimens from the Serravallian of Suze la Rousse, but he could not describe the plate patterns since they were not preserved.

As a consequence, the structural features of the type-species, as well as of most of the earlier described species of *Amphiope*, are still uncertain/unknown thus preventing a reliable comparison with the material under study, based on these important characters.

SYSTEMATIC PALAEONTOLOGY

Family ASTRICLYPEIDAE Stefanini, 1912

Genus ***Amphiope*** L. Agassiz, 1840

TYPE SPECIES. *Scutella bioculata* des Moulins, 1837, by subsequent designation of Lambert (1907, p. 49).

EMENDED DIAGNOSIS. (Partially modified from Smith & Kroh, 2011). Test low with sharp margin. Internal support well developed, consisting of pillars and walls crossed by cavities. Towards ambitus, peripheral ballast system very dense, almost massive and crossed by micro-canals. Apical disc monobasal, sub-central or slightly anterior to centre, with four gonopores. Petals well developed; short (about half radial length of test) and almost closed distally. All five petals similar in length. Ovate lunules or notches present in the posterior ambulacra. Oral side flat or slightly concave. Interambulacra on the oral surface narrower than the ambulacra, even at their widest point. Interambulacra 1, 4 and 5 always meridoplacous adorally, the interambulacral zones being separated by enlarged first post-basicoronal ambulacral plates. Interambulacra 2, 3 may be either amphiplacous or meridoplacous adorally. Basicoronal circlet pentastellate with interambulacral plates forming the points. Peristome small, subcentral or slightly anteriorly located. Periproct circular, small, opening between the first, the second or the third pair of post-basicoronal interambulacral plates. Two to five post-basicoronal plates present in the interambulacrum 5 adorally. Food grooves well developed, bifurcating at the edge of the basicoronal plate; they do not reach the margin.

Posterior pair of food grooves running around the lunules; finer distal branches well developed. Ambulacra a little wider than interambulacra at ambitus. Tuberculation dense, made of very small, perforate and crenulate tubercles, larger on the oral face than aborally.

DISTRIBUTION. Oligocene and Miocene. Central and Southern Europe, North Africa, Middle East, India, Angola (Smith & Kroh, 2011).
Sardinian species included:

- *Amphiope lovisatoi* Cotteau, 1895. Late Burdigalian.
- *Amphiope montezemolo*i Lovisato, 1911. Late Burdigalian-early Langhian.
- *Amphiope nuragica* (Comaschi Caria, 1955). Late Chattian-early Aquitanian.
- *Amphiope* sp. 1. Late Chattian-early Aquitanian.
- *Amphiope* sp. 2. Late Burdigalian-early Langhian.

REMARKS. Both *Amphiope* and *Echinodiscus* Leske, 1778 show two lunules in the posterior ambulacra. *Echinodiscus* differs in having axially elongated, slit-like lunules or notches and posterior petals shorter than the others.

Amphiope lovisatoi Cotteau, 1895
Plate 1 Figs. 1–8; Plate 3 Fig. 7b

1895 *Amphiope Lovisatoi* Cotteau - Cotteau p. 16 pl. 3, fig. 15
1914 *Amphiope Lovisatoi* Cotteau - Lovisato, p. 118, pl. 2, figs. 6a-b
Non 1955 *Amphiope lovisatoi* Cotteau - Comaschi Caria, p. 9, pls. 9, 11, 12.

TYPE-LOCALITY AND HORIZON. Chiaramonti (Sassari). The type-layer described by Lovisato (1914) corresponds to the "Facies C" of Mancosu & Nebelsick (2013; Fig. 4), attributed to the lower part of the Calcari di Mores Formation, dated to the late Burdigalian.

TYPE MATERIAL. Cotteau (1895) did not detail the composition of the type-series provided by Lovisato, nor designated a holotype. All those specimens, as well as the others from Chiaramonti belonging to the Lovisato's collection, were lost in 1943 (fide Comaschi Caria, 1955). They could not be traced by the authors at UNICA. A neotype is proposed herein, to clarify the diagnostic char-

acters of this nominal taxon which cannot be extracted from published descriptions and illustrations of the lost type. Additionally, *A. lovisatoi* has been synonymised with other species of *Amphiope*, and the structure features firstly described in this paper are not visible in the illustration provided by Cotteau (1895) and Comaschi Caria (1955).

Neotype: MAC.PL1706 (Pl. 1 Figs.1a-c and 5a-b), a specimen with both faces well preserved (TL = 73, TW = 77.5, TH = 8.5 mm). It was recovered at Monte Sa Loca (40°44'55.15" N, 8°49'59.20" E), from the main *Amphiope*-bearing bed (Facies C of Mancosu & Nebelsick, 2013), which represents the lateral extension of the type-layer cropping out at Billiu (Stara et al., 2012). Billiu is less than1 km far from Monte Sa Loca, both are located in the suburbs of Chiaramonti. The road-cut of Billiu currently yields only scarce and poorly preserved fossil material, whereas at Sa Loca abundant and well preserved material is available to study.

Examined material. The studied sample from the type-locality consists of 61 complete tests (MAC code: PL1301-3, PL1317, PL1413, PL1418-20, PL1422-4, PL1427, PL1429, PL1567-70, PL1572-80, PL1583, PL1585-7, PL1692-99, PL1700-1707, PL1709-1714, PL1715-18, PL1720-23, PL1726) and 7 test fragments.

Revised diagnosis. Middle-sized species of *Amphiope* with low test, sharp margin and broad, transversely elongated elliptical lunules. A low number of plates is present in each ambulacral and interambulacral columns, only two post-basicoronal plates occur in the interambulacral column 5a adorally. Periproct bounded by plates 2a/3b, rather close to the posterior test edge. Internal structure very light, with thin shell and subpentagonal central cavity.

Description. Middle sized test (mean TL= 76 mm). Outline sub-circular to anteriorly constricted, usually slightly transversely elongated, posteriorly rounded (Plate 1 Fig. 1) or subtruncate (Plate 1 Fig. 3a). Maximal width located subcentrally. Test very low (mean TH = 10.2% TL), with maximum height positioned anteriorly. Marginal indentations well developed in ambulacra II and IV (Plate 1 Figs. 1, 2). Shallow notches may occur also in ambulacra I, III, V and interambulacra 1 and 4. Test edge sharp.

Ambulacra. Frontal and posterior petals similar in length. Poriferous zones depressed; interporiferous zones slightly raised. Interporiferous area larger than the corresponding poriferous one. Lunules transversely elongate and broad elliptical (Plate 1 Figs. 1, 2 and 7d); the shape-variability includes also rare small subcircular (Plate 1 Fig. 7c) and narrow elliptical (Plate 1 Fig. 7a) lunules. Ambulacra slightly depressed adorally, along their central suture. Ambulacral basicoronal circlet small.

Interambulacra. Only 14–16 plates in each column of interambulacra 1, 4, 5 and ambulacra I and V; 10–13 plates in interambulacra 2 and 3, as well as in ambulacra II, III and IV. Adorally, only two, sometimes a small part of the third, post-basicoronal plates in the interambulacral column 5a adorally, three of them in column 5b (Plate 1 Figs. 3b, 4b, 5b).

Periproct. Commonly found in the distal half of the suture 2a/3b (Plate 1 Figs. 3b, 5b).

Internal structure. Reduced, with spaces between elements larger than the calcite elements comprising the buttress system (Plate 1 Fig. 6). Central cavity bordered by five transversely elongate straight walls, delimiting a sub-pentagonal area (Plate 1 Fig. 8). Peripheral ballast system very dense, almost massive towards the ambitus.

Other features as for the genus. See Table 3 for descriptive statistics.

Remarks. Most of the "diagnostic" features stated for *A. lovisatoi* by Cotteau (1895) and Lovisato (1914) are very variable in the studied sample from Chiaramonti and cannot provide a clear separation from the other Sardinian species. Some specimens do not correspond to "posteriorly rounded test" (e.g. Plate 2 Fig. 3a), or to "deep notches in the margin" (e.g. Plate 2 Fig. 4a), as stated for this species. Only "test middle-sized and depressed" and "sharp margin" are confirmed as valid distinctive characters by this study.

A. lovisatoi was synonymised with *A. bioculata* by Kroh (2005), however, the figured specimen from Austria differs from the Sardinian fossils by much higher test (TH = 20% TL) and by the frontal petal, which is clearly longer than the posterior paired petals (L9/L5 = 0.80 in the Austrian specimen, against 0.95 in the sample of Chiaramonti).

Comaschi Caria (1955) cited this species at C. Tuvullao. However all the specimens from that locality bearing external features similar to those of *A. lovisatoi* had very different plate patterns and

much stronger internal structure, corresponding to that of *A. nuragica*.

OCCURRENCE IN SARDINIA. Chiaramonti, Calcari di Mores Formation, late Burdigalian.

Amphiope montezemoloi Lovisato, 1911
Plate 3 Figs. 1–6, 7a

1911. *Amphiope Montezemoloi* Lovisato - Lovisato, p. 43, pl. 6, figs. 1a, b
1928. *Amphiope montezemoloi* Lovisato - Lambert [36], p. 23, pl. 8, fig. 4
1955. *Echinodiscus* (*Amphiope*) *bioculata* var. *montezemoloi* Comaschi Caria - Comaschi Caria, p. 184, pls. 14, 15
1972. *Amphiope bioculata* des Moulins - Comaschi Caria, p. 42.

TYPE-LOCALITY AND HORIZON. Near the abandoned railway station of San Giorgio (Sassari) towards Olmedo. The *Amphiope*-bearing outcrop, belongs to the Calcari di Mores Formation, late Burdigalian-early Langhian (Carmignani et al., 2001).

TYPE MATERIAL. Lovisato (1911) did not designated a holotype nor detailed the composition of the type-series. According to Comaschi Caria (1955) all those specimens were lost; they were not traced by the authors at the UNICA. The validity of *A. montezemoloi* is still debated, since it has been synonymised with other *Amphiope* species, and the plate patterns were not described. Thus, a neotype is herein designated.

Neotype: MAC code PL1827 (Plate 3 Fig. 1a, b). It consists of a large complete specimen with oral structure partially visible (TL = 116, TW = 133, TH = 10, L11 = 14 mm). It comes from Stazione di San Giorgio, Sassari, the type locality of this species (40°41'13.68" N, 8°27'03.41" E), from the Calcari di Mores Formation.

EXAMINED MATERIAL. The studied material includes also 2 large test fragments from the type-locality (PL1828-9) and 3 specimens (PL1674-6) from Bonnanaro (Sassari).

REVISED DIAGNOSIS. Large sized species with low lateral profile and very large, subcircular to slightly transversely elongate, lunules. Frontal petal longer than the others. In the oral interambulacrum 5, plate 2b very elongate and only 2 post-basicoronal plates present in column 5a. Ambulacral basicoronal circlet very small. Internal structure reduced, central cavity with starring outline.

DESCRIPTION. Large sized test with transversely elongate and anteriorly restricted outline. Test very low (mean TH = 9.8% TL), almost flattened adapically. Margin posteriorly sharp, anteriorly more rounded and 3–3.5 mm thick.

Ambulacra. Frontal petal longer than the posteriors. Poriferous zones depressed; interporiferous zones slightly raised. Lunules very large, subcircular to broad elliptical with moderately transversely elongate outline. Ambulacra slightly depressed adorally along their central suture.

Interambulacra. The first post-basicoronal plate (2b) in the oral interambulacrum 5 is very elongate (Plate 3 Figs. 2a, b) and plate 2a is close to the posterior margin. Three post-basicoronal plates are present in column 5b, only two plates in column 5a.

Periproct. Small (mean diameter = 1.7% TL), rather close to the posterior test margin and located along the suture 2a-3b.

Internal structure. Rather complex but reduced, with thin shell and large spaces between the calcite elements comprising the buttress system (Plate 3 Figs. 5a, c). Central cavity large (Plate 3 Figs. 4, 7b) with flat and thin floor. On the ceiling, the interporiferous areas of the petals are convex, the poriferous areas slightly concave. Peripheral ballast system dense towards the ambitus.

Other features as for the genus. See Table 3 for descriptive statistics.

REMARKS. Large-sized test and broad subcircular to elliptical lunules (Lovisato, 1911) are confirmed by this study as distinctive features of *A. montezemoloi*. The other "diagnostic" characters stated in the original description cannot provide a clear separation from the other examined species.

In particular, the "irregularities on the aboral surface" described by Lovisato (1911) were not observed in any specimen. The apical disc is "eccentric towards the anterior test edge", but the measures of the two specimens reported by Lovisato (1911), as well as the mean of L4 in the examined sample of *A. montezemoloi*, almost correspond to those of *A. lovisatoi* and *Amphiope* sp. 2 (see Table 3).

A. montezemoloi was placed into synonymy with *A. bioculata* by Comaschi Caria (1955), Philippe (1998) and Kroh (2005). However, since at present a comparison with *A. bioculata* based on the structural characters is not possible, the separation between the two is herein maintained.

Occurrence in Sardinia. San Giorgio and Bonnanaro (Sassari), Calcari di Mores Formation, late Burdigalian-early Langhian.

Amphiope nuragica (Comaschi Caria, 1955)
Plate 2 Figs. 1–13

1955. *Echinodiscus* (*Amphiope*) *nuragica* Comaschi Caria - Comaschi Caria, p. 186, pl. 1
1955. *Echinodiscus* (*Amphiope*) *deydieri* Lambert - Comaschi Caria, p. 186, pls. 2-3
1955. *Echinodiscus* (*Amphiope*) *transversivora* Lambert - Comaschi Caria, p. 187, pl. 4
1955. *Echinodiscus* (*Amphiope*) *pallavicinoi* Lovisato - Comaschi Caria, p. 188, pls. 5-6, pl. 13, fig. 2
1955. *Echinodiscus* (*Amphiope*) *calvii* Lovisato - Comaschi Caria, p. 188, pls. 7-8, pl. 13, fig. 1
1955. *Echinodiscus* (*Amphiope*) *lovisatoi* Cotteau - Comaschi Caria, p. 189, pl. 9; Pl. 11, fig. 2, pl. 12
1955. *Echinodiscus* (*Amphiope*) *dessii* Lovisato - Comaschi Caria, p. 190, pl. 10, pl. 11, fig. 1.

Type material. Holotype (UNICA code 9CC.8-10504; Plate 2 Figs. 1a, b and 9). TL = 106, TW = 107, TH = 16 mm. It was the sole specimen attributed to this species by Comaschi Caria (1955).

Type-locality and horizon. Layer I of Cuccuru Tuvullao (Cagliari; 39°47'18.88" N, 9°26'55.54" E), corresponding to facies "B" of Mancosu & Nebelsick (2013), Nurallao formation, Arenarie di Serralonga member, late Chattian-early Aquitanian.

Examined material. Two additional whole tests from C. Tuvullao I (UNICA, code 3CC and 6CC-10503). Nineteen specimens and 66 large test fragments from the same layer are housed at the MAC (PL1590-1, PL1678-80, PL1684, PL1727, PL1820, PL1829; PL1835-1844).

Revised diagnosis. Test high, with narrow and transversely elongate lunules. Petal surface convex, including the poriferous areas. High number of plates in ambulacral and interambulacral columns. Three to four post-basicoronal plates in each column of the oral interambulacrum 5. Periproct close to the conjunction of plates 2a/2b/3a, or more posteriorly located. Internal support system strongly developed, with thick shell and roundish outline of the central cavity.

Description. Medium to large sized test. Outline subcircular in the holotype, but more frequently transversely elongate and restricted anteriorly (Pl. 2 Figs. 5-7). Maximal width located subcentrally. Test high (mean TH = 14.2% TL). Marginal indentations slightly developed in ambulacra II and IV, shallow notches may occur also in ambulacra I, III, V and interambulacra 1 and 4. A shallow but distinct anal notch may be present. Posterior edge thin, the anterior margin is thicker.

Ambulacra. Petals almost closed distally (Plate 2 Fig. 12), the frontal one slightly longer than the others. Maximal petal width about one half to two-thirds of petal length. External petal surface slightly raised and convex, including the interporiferous zones. Angle between the axis of posterior petals large: mean $\alpha = 76°$, against a mean of 71° at the other localities. A transversely elongate lunule is present in each posterior ambulacrum. Shape and size of lunules variable (Pl. 2, Figs. 13a–d). They are commonly narrow (Plate 2 Fig. 13b) to rather broad elliptical (Plate 2 Fig. 13a), seldom subpolygonal (Plate 2 Fig. 7). A small protuberance is present along the internal margin of the lunules in the holotype and in another specimens (Plate 2 Figs. 1, 3). Ambulacra slightly depressed adorally along their central suture. Ambulacral basicoronal circlet rather large.

Interambulacra. There are 16–20 plates in each column of interambulacra 1, 4, 5, as well as in ambulacra I and V; 14–16 plates in interambulacra 2 and 3 and in ambulacra II, III and IV. Adorally, at least 3, frequently also 4, post-basicoronal plates present in each column of the interambulacral column 5a adorally (Plate 2 Fig. 1b, 3, 4).

Peristome. Small (mean diameter = 3.3% TL).

Periproct. It opens along the distal half of the suture 2a/3b, close to the conjunction point 2a/3b/3a (as in the holotype, compare Plate 2 Fig.

1b, 2b) or more posteriorly located (Plate 2 Fig. 3). It is close to the posterior test edge (mean L11 = 9.1 % TL).

Internal structure. Well developed, with thick shell and spaces between elements narrower than the elements comprising the buttress system (Plate 2 Fig. 11). The floor of the central cavity in the interambulacra begins to thicken close to the peristome and gradually rises, extending radially towards the first pillars of the radial supports (Plate 3 Fig. 7c). Central cavity with a rough sub-circular outline.

Other features as for the genus. See Table 3 for descriptive statistics.

REMARKS. The noticeable test height (TH = 14.2% TL), the periproct close to the posterior edge (L11 = 9.1% TL) and the characteristic shape and proportion of lunules, stated by Comaschi Caria (1955) for *A. nuragica*, are confirmed by this study as valid distinctive characters. The other "diagnostic" features are variable in the studied sample and cannot provide a clear separation from the other examined species. In particular, irregularities in the lunules outline, as the prominences described by Comaschi Caria (1955), occur randomly in other species (Plate 1 Fig. 7e; Plate 2 Figs. 1, 3) and have no taxonomic value. The morphology and the plate patterns of two specimens assigned by Comaschi Caria (1955) to *A. dessii* and *A. calvii* (UNICA, code 6CC-10503 and 3CC, respectively), correspond to those of *A. nuragica* and are therefore assigned to this species. The same case occurs with specimens bearing external features corresponding to *A. deydieri*, *A. transversivora*, *A. pallavicinoi*, *A. calvii* and *A. lovisatoi*, all species recorded from this locality by Comaschi Caria (1955); additionally they are not statistically separable from the others from C. Tuvullao I.

OCCURRENCE IN SARDINIA. Cuccuru Tuvullao (Cagliari), Nurallao formation, Arenarie di Serralonga member, late Chattian-early Aquitanian.

Amphiope sp. 1
Plate 3 Figs. 8–10

EXAMINED MATERIAL AND HORIZON. 3 specimens (MAC code PL1681, PL1685 and PL1834) and 1 test fragment (PL1684), from layer II of C.Tuvullao (Cagliari, 39°47'18.88"N, 9°26'55.54"E), corresponding to facies "C" of Mancosu & Nebelsick (2013), Nurallao formation, Arenarie di Serralonga member, late Chattian-early Aquitanian.

DESCRIPTION. Middle to large sized test with thick margin. Outline transversely elongate and slightly anteriorly restricted. Maximal width located subcentrally. Test very high (mean TH = 20.7% TL), with maximal height slightly anterior of the apical disc (Plate 3 Fig. 8c). Marginal indentations slightly developed in ambulacra II, III and IV. Faint notches may occur also along the posterior test edge, in ambulacra I and V and interambulacra 1 and 4.

Ambulacra. Frontal petal distinctly longer than the posteriors (mean L9 = 79.1% L5). Maximal petal width about one half to two-thirds of petal length. Poriferous zones depressed; interporiferous zones slightly raised. Lunules transversely elongate, narrow elliptical and close to the tips of the posterior petals (mean L3 = 4.6% TL). Ambulacra slightly depressed adorally along their central suture. Ambulacral basicoronal circlet small.

Interambulacra. Adorally, only two, maximum three, post-basicoronal plates are present in each column of interambulacrum 5 (Plate 3 Figs. 9b, 10b).

Periproct. Bounded by the first pair of post-basicoronal plates 2a/2b (Plate 3 Figs. 9b, 10b) and far from the posterior test margin (mean L11 = 13.8% TL).

Other features as for the genus. See Table 3 for descriptive statistics.

REMARKS. The specimens from C. Tuvullao II stand apart from all the others examined from Sardinia by their much higher test, more centrally located apical disc, frontal ambulacrum much longer than the posterior ones and lunules closer to the tips of the posterior petals.

In addition, it differs from *A. nuragica* by the presence of only three post-basicoronal plates in each column of interambulacrum 5 adorally and the periproct bounded by the first pair of post-basicoronal plates.

The plate patterns in oral interambulacrum 5 correspond to the drawings of *A. bioculata* reported by Durham (1955), Kroh (2005) and Pereira (2010), but the attribution of those schemes to the type-species

is doubtful since they were not based on topo-typic material. Besides, the specimens of C. Tuvullao II differ by more transversely elongate lunules.

Occurrence in Sardinia. Cuccuru Tuvullao (Cagliari), Nurallao formation, Arenarie di Serralonga member, late Chattian-early Aquitanian.

Amphiope sp. 2

Plate 4 Figs. 1–15

Examined material. Ten complete specimens (MAC PL343, PL547-553, PL1665, PL1836) and ten fragments from Bancali (Sassari, 40°43'55.66"N, 8°26'55.54" E), collected in a bioclastic sandstone at "outcrop 2" described by Stara et al. (2012), attributed to the Calcari di Mores Formation, late Burdigalian-early Langhian.

Description. Middle to very large sized test, with rather thin margin. The test width reached up to 133 mm in complete specimens, but some fragments points to complete test with length up to about 170 mm. Outline slightly transversely elongate and restricted anteriorly (Plate 4 Figs. 1–3). Maximal width located subcentrally. Maximum test height slightly anterior of the apical disc (Plate 4 Figs. 4–6). Marginal indentations well developed in ambulacra II and IV, faint indentations may occur also in ambulacra I, III and V and interambulacra 1 and 4. Oral side flat or slightly concave. Food groves well developed (Plate 4 Figs. 2, 3), bifurcating at the edge of the basicoronal circle. Posterior pair of food grooves running around the lunules, not reaching the margin; finer distal branches well developed.

Apical system. Distinctly anterior to centre (mean L4 = 59.7% TL).

Ambulacra. Frontal petal slightly longer than the others.Maximal petal width about one half to two-thirds of petal length. Poriferous zones depressed; surface of the interporiferous zones slightly convex. A broad and slightly transversely elongate lunule is present in each posterior ambulacrum. Lunules commonly subcircular (Plate 4 Figs. 14c, d) to broad elliptical (Plate 4 Fig. 14e). Ambulacra slightly depressed adorally along their central suture. Ambulacral basicoronal circlet rather large (mean L13 = 11.3% TL).

Interambulacra. There are 14–16 plates in each column of interambulacra 1, 4, 5 and ambulacra I and V, 12-14 plates in interambulacra 2 and 3 and in ambulacra II, III and IV. Only 3–4 post-basicoronal plates present in each column of oral interambulacrum 5 (Plate 4 Figs. 11, 12).

Peristome. Small (mean diameter = 2.8 % TL).

Periproct. Small (mean diameter = 2% TL), located between the second pair of post-basicoronal plates (Plate 4 Figs. 11, 12) and rather far from the posterior test margin.

Internal structure. Well developed, with rather thick shell wall and spaces between elements narrower than the elements comprising the buttress system. Central cavity with almost starring outline and interambulacral radial supports extending towards the centre.

Other features as for the genus. See Table 3 for descriptive statistics.

Remarks. *Amphiope* sp. 2 differs statistically from *A. montezemoloi* by more elevate test, larger ambulacral basicoronal circlet and smaller lunules; it has also a stronger internal structure. The same differences separate *Amphiope* sp. 2 from *A. lovisatoi*; additionally, the specimens from Chiaramonti are smaller and the periproct, though bounded by plates 2a/3b as well as in the sample of Bancali, is closer to the conjunction point 2a/3b/3a.

The closely related specimens from Ardara (Sassari) likely belong to this species, though a larger sample from this locality is needed to confirm this hypothesis.

Occurrence. Bancali, probably also Ardara, (Sassari), Calcari di Mores Formation, Late Burdigalian-early Langhian.

STRATIGRAPHICAL DISTRIBUTION AND EVOLUTIVE TRENDS

The genus *Amphiope* is represented in Sardinia by forms with rounded or transversely elongate lunules, only. The first records of *Amphiope* with axial lunules are dated to the middle Oligocene of the Gulf of Biscay, Val Bormida (Piedmont, Italy) and Libya, whereas *Amphiope* with transverse lunules appeared in the late Oligocene-early Miocene in the area between the Gulf of Biscay and the intra-AlCaPeKA Basin (Stara & Rizzo, 2013). At that

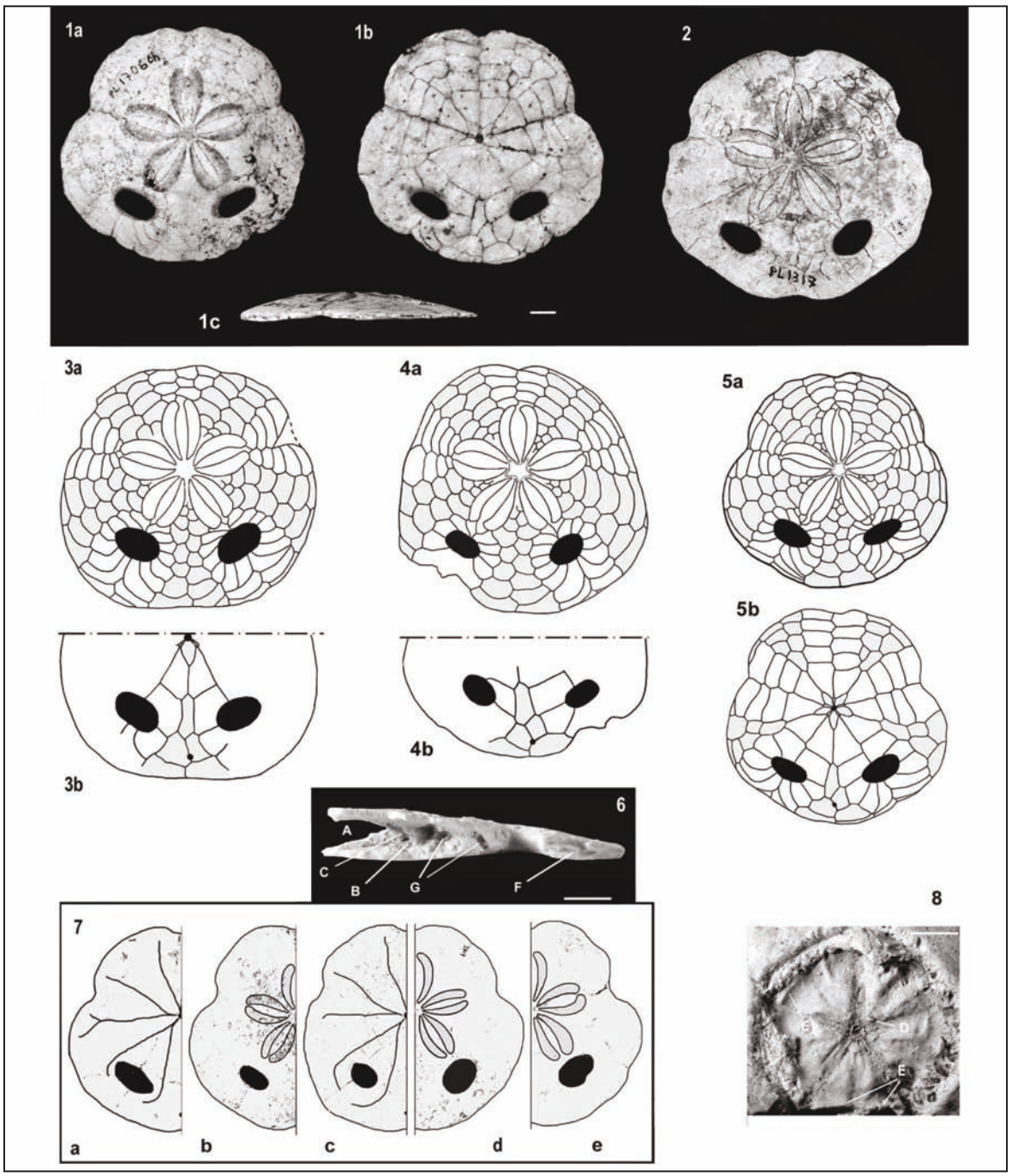

Plate 1. *Amphiope lovisatoi* Cotteau, 1895, Calcari di Mores Formation, late Burdigalian, Chiaramonti (Sassari). Figs. 1a–c Neotype (PL1706, TL = 73 mm), aboral (a), oral (b) and antero (to the left)-posterior (to the right) lateral view (c). Fig. 2. Aboral view of PL1317 (MAC code), TL = 82 mm. Figs. 3a, b. Plate patterns of PL1704 (TL = 82 mm); a) aboral side, b) oral side. Figs. 4a, b. Plate structure of PL1574 (TL = 80 mm); a) aboral side, b) oral side. Figs. 5a, b. Plate patterns of PL1706 (TL = 73 mm); a) aboral side, b) oral side. Fig. 6. Internal structure: cross-section along the radial axis of ambulacrum I. Figs. 7a-e. Variation range of test outline and lunules shape. All specimens in aboral view, if not otherwise specified. a) PL1308 (oral view; TL = 78 mm). b) PL1312 (TL = 76.2 mm). c) PL1311 (oral view; TL = 85 mm). d) PL1306 (TL = 89 mm). e) PL1303 (TL = 83.5 mm). Fig. 8. Internal view of oral surface, with almost flat floor and straight walls (E) delimiting the subpentagonal outline of the central cavity. In Figs. 6 and 8: A = central cavity, B = first peripheral elements (pillars or walls), C = radial cavity of the interambulacrum 5 leading to the periproct, D = lantern supports, E = straight walls at the periphery of the central cavity, F = massive peripheral support system, G = small cavities. Scale bar equals 1 cm.

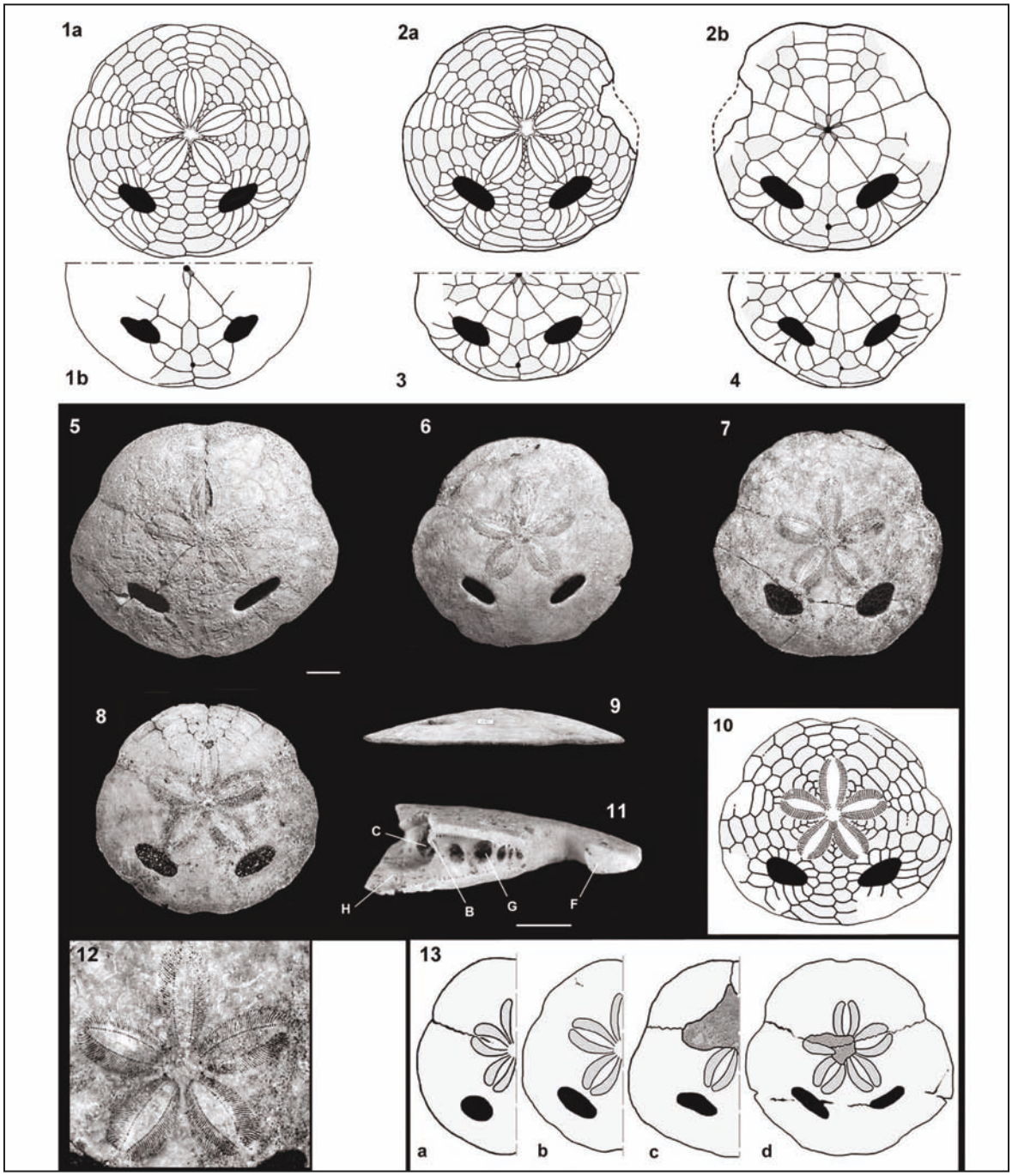

Plate 2. *Amphiope nuragica* (Comaschi Caria, 1955), Nurallao formation, late Chattian-early Aquitanian, Cuccuru Tuvullao (Cagliari). Figs. 1-4, 10 Plate structure drawings with interambulacral plates shaded grey. 1) Holotype (UNICA code 9CC.8; TL = 100 mm), aboral (1a) and oral (1b) views. 2) PL1680 (TL = 100 mm), aboral (2a) and oral (2b) views. 3) PL1591 (TL = 81 mm), oral view. 4) PL1684 (TL = 91 mm), oral view. 10) PL1835 (TL = 89 mm), aboral view. Fig. 5. PL1836 (TL = 93 mm), aboral view. Fig. 6. PL1835 (TL = 89 mm), aboral view. Fig. 7. PL1837 (TL = 88.5 mm), aboral view. Fig. 8. PL1838 (TL = 82 mm), aboral view. Fig. 9. Antero (to the right)-posterior (to the left) lateral view of PL1820 (TL = 98.2 mm). Fig. 11. Close up view of a cross-section through the radial axis of the ambulacrum I. B = first peripheral elements (pillars), C = radial cavity of the interambulacrum 5 leading to the periproct, F = massive peripheral support system, G = small cavities, H = floor of the central cavity. Fig. 12. Close up of the petals (PL1835, TL = 89 mm). Figs. 13a-d. Variability of test outline and lunules shape. All specimens in aboral view. a) PL1839 (TL = 59.4 mm), b) PL1838 (TL = 82 mm), c) PL1840 (TL = 83.6 mm), d) PL1841 (TL = 98.2 mm). Scale bar equals 1 cm.

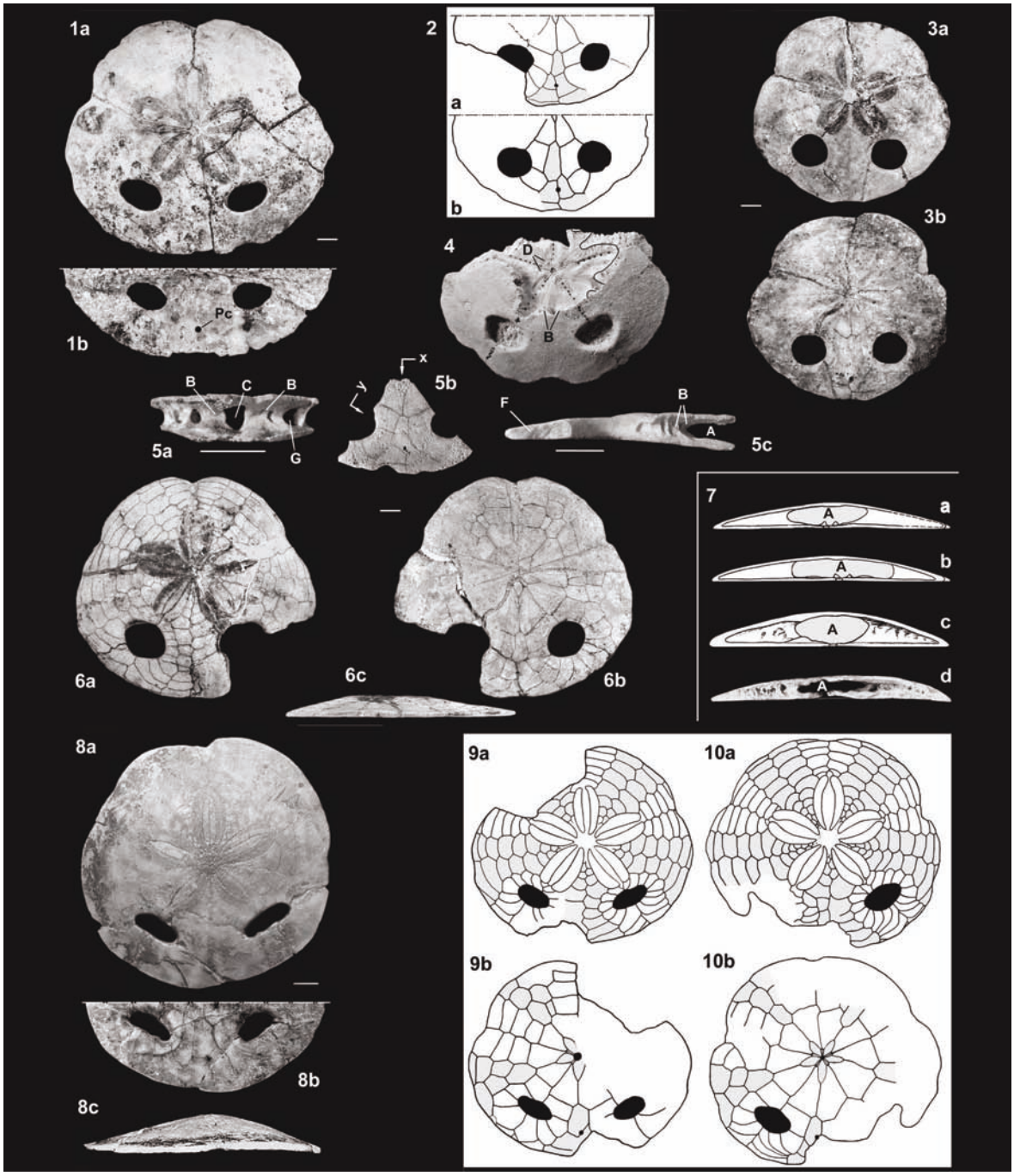

Plate 3. *A. montezemoloi*, San Giorgio and Bonnanaro (Sassari). Figs. 1a-b. Neotype (PL1827): aboral (a) and adoral (b) views , TL=121 mm. San Giorgio. Figs 2a-b. Oral plating structure of PL1675 (a) and PL1676 (b). Bonnanaro. Figs. 3a, b. Specimen PL1676 (TL=90 mm): aboral (a) and oral (b) views. Bonnanaro. Fig. 4. Aboral view of PL1828; margins of the central cavity marked as dotted lines. San Giorgio. Figs. 5a–c. Test fragment (PL1830): adoral (b) and internal views taken from points x (a) and y (c), respectively. Bonnanaro. Figs. 6a–c. Aboral (a), oral (b) and antero (to the left)-posterior (to the right) lateral (c) views of PL1675 (TL=112 mm). Bonnanaro. Figs. 7a–d. Scheme of the internal structure in an antero (to the right)-posterior (to the left) axial section of specimens from: a) *A. montezemoloi*, San Giorgio, b) *A. lovisatoi*, Chiaramonti, c) *A. nuragica*, C.Tuvullao, d) *Amphiope* sp. 2, Bancali. *Amphiope* sp. 1, Nurallao formation, late Chattian-early Aquitanian, of Cuccuru Tuvullao (Cagliari). Figs. 8a–c. PL1834 (TL=95.5 mm); aboral (a), adoral (b) and antero (to the right)-posterior (to the left) lateral (c) views, respectively. Figs. 9a, b. Plating patterns of PL1681 (TL=90 mm); a) aboral side, b) oral side. Figs. 10a, b. Plating patterns of PL1685 (TL=101 mm); a) aboral side, b) oral side. In Figs. 5a–c: A = central cavity, B=first peripheral elements (pillars or straight walls), C=radial cavity of the interambulacrum 5 leading to the periproct, F=massive peripheral support system, G=small cavities. Scale bar equals 1 cm.

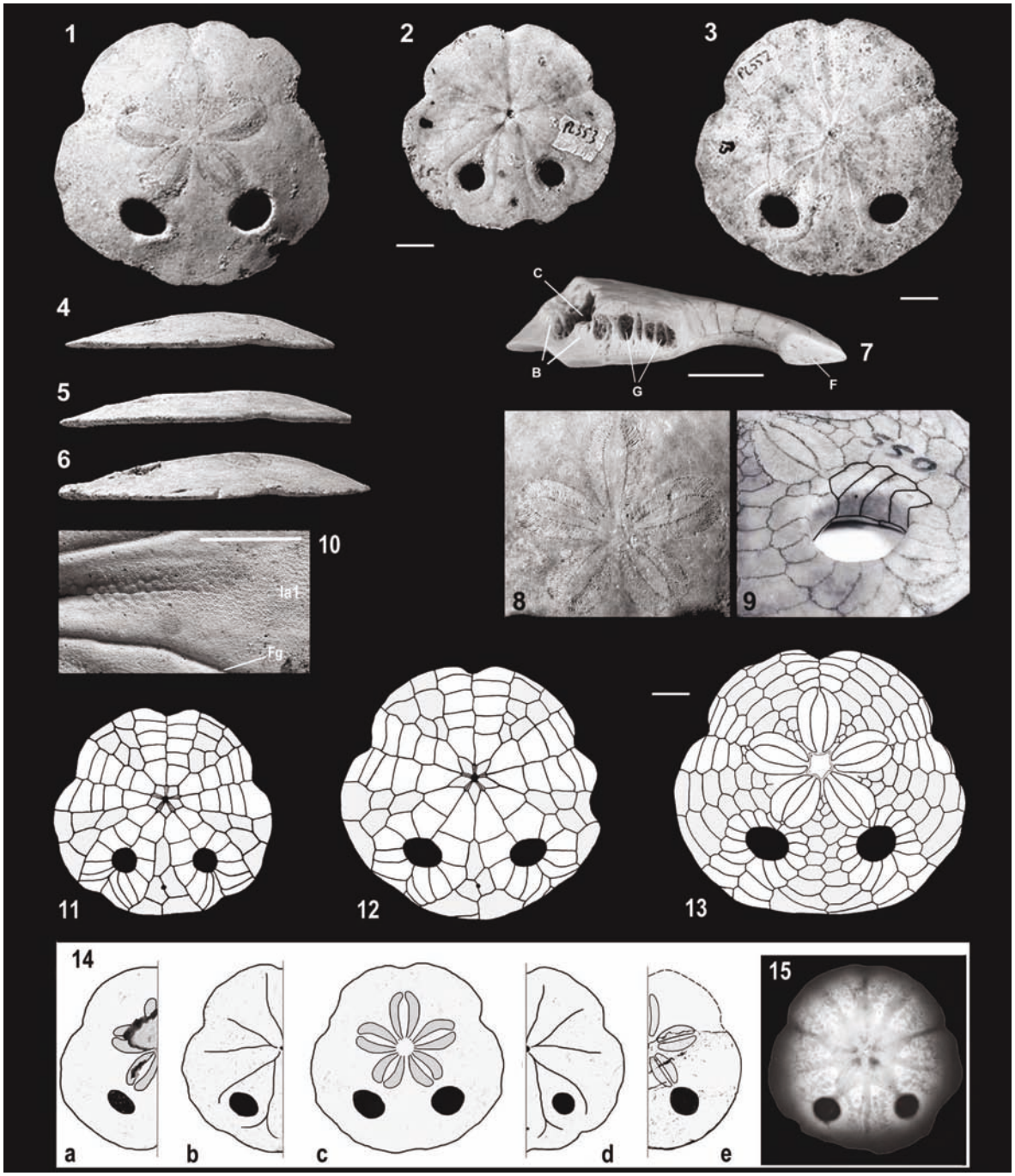

Plate 4. *Amphiope* sp. 2, Calcari di Mores Formation, late Burdigalian-early Langhian, Bancali (Sassari). Figs. 1–3. 1) PL343, TL = 73 mm). 2) PL553, adoral view (TL=55.8 mm). 3) PL552, adoral view (TL=73.4 mm). Figs. 4-6. Antero (to the right)-posterior (to the left) lateral views of PL343 (4), TL=73 mm, PL550 (5), TL=79.5 mm and PL551 (6), TL=88.5 mm. Fig. 7. Close up view of the internal structure: cross-section of a test fragment along the radial axis of ambulacrum I. B = first pillars in the radiating buttresses of interambulacrum 5, C=radial cavity of the interambulacrum 5 leading to the periproct, F=massive peripheral support system, G=small cavities. Figs. 8-9. PL550 (TL=79.5 mm). 8) close up view of the petals; 9) plating scheme of a lunule (oblique view), with cross-linked wall. Fig. 10. Close up view of the tuberculation in the oral interambulacrum 1; fg=food groove. Figs. 11-13. Plate diagrams, with interambulacral plates shaded grey. Oral side: 11) PL551Ba, TL=88.5 mm; 12) PL552, TL=73.4 mm. Aboral side: 13) PL553, TL=55.8 mm. Figs. 14a-e. Variation range of test outline and lunules shape. All specimens in aboral view, if not otherwise specified; a) PL548 (TL=93 mm), b) PL552 (oral view; TL=73.4 mm), c) PL550 (TL=79.5 mm), d) PL553Ba (oral view; TL=55.8 mm), e) PL1281 (TL=81.7 mm). Fig. 15. X-ray photograph (PL549), showing the starring outline of the central cavity. Scale bars equal 1 cm.

time Sardinia begun to separate from Europe and the progressive marine ingression transformed it into an archipelago surrounded by an epicontinental sea (Gattaceca et al., 2007). *A. nuragica* and *Amphiope* sp. 1, from the late Chattian-early Aquitanian Nurallao formation, inhabited shallow water environments of that sea and represent the earliest record of this genus in Sardinia and one of the oldest record of *Amphiope* with transverse lunules (Stara et al., 2012). The resemblance, based on comparison of test and lunules features alone, with the almost coeval population "A" of *A. bioculata* described by Philippe (1998) from the Aquitanian of the Rhône Basin, suggests that at that time closely related, may be the same, species of *Amphiope* inhabited Sardinian and Provencal shallow environments.

In the middle Miocene Sardinia was encircled by a deep sea. During that period *Amphiope* developed into new species (Fig. 6): *A. lovisatoi*, *A. montezemoloi* and *Amphiope* sp. 2 of the Burdigalian-early Langhian of the Calcari di Mores Formation, and *Amphiope* sp. of the Early Serravallian Capo Frasca Sud Formation (Funedda et al., 2000); Spano et al., 2002). Lovisato (1914) cited *Amphiope* also from a "*sottile banco di calcare breccioso compattissimo, sotto al calcare argilloso*" outcropping at Monte S. Michele (Cagliari, n. 24 in Fig. 1). This sediment corresponds to the "Pietra Forte" belonging to the Calcari di Cagliari Formation, dated to the late Tortonian-early Messinian Cherchi et al., 1978), thus representing, so far, the most recent population of the genus *Amphiope*.

A major evolutionary change observed in the studied sample points to the progressive reduction and the increasing complexity of the internal support system. Thus, the dense and strong internal buttress and the thick shell of *A. nuragica*, should be regarded as primitive characters in *Amphiope* with transverse lunules. A decreasing number of plates in the ambulacral and interambulacral columns and the progressive migration of the periproct towards the peristome, from plates 3b/3a in the Aquitanian *A. nuragica*, to the distal part of the suture 2a/3b in the Burdigalian *A. lovisatoi*, to the proximal part of 2a/3b in the early Langhian *A. montezemoloi* and *Amphiope* sp. 2, are also observed (Fig. 6). The only exception to the last two trends is represented by the "ancient" *Amphiope* sp.1 (Fig. 6), with the periproct bounded by the first post-basicoronal plates (2a/2b) and a low number of plates in the oral interambulacrum 5.

Paleoecological data reported for the *Amphiope*-bearing Sardinian localities (Stara et al., 2012) indicate that *Amphiope* was a deposit feeder, living in shallow sandy settings, with middle to high water energy and tropical climate.

CONCLUSIONS

The examined material shows that previously described criteria used to distinguish between the fossil species of *Amphiope* cited in Sardinia are not sufficiently diagnostic, mainly due to the marked intra-specific variation of the external test features.

The well preserved specimens available to study from this region enable to describe the plate patterns and the internal test support system. Based on these features and the results of the morphometric analyses, three different species are recognized in the examined material: *A. nuragica*, late Chattian-early Aquitanian of Cuccuru Tuvullao (Cagliari), *A. lovisatoi*, late Burdigalian of Chiaramonti (Sassari), *A. montezemoloi*, late Burdigalian-early Langhian of San Giorgio and Bonnanaro (Sassari). Two groups of specimens from the late Chattian-early Aquitanian of C. Tuvullao (layer II) and the late Burdigalian-early Langhian of Bancali, though well differentiated, are assigned to *Amphiope* sp. 1 and *Amphiope* sp. 2 respectively, and left in open nomenclature due to the scarcity of the available material.

The stratigraphical distribution of *Amphiope* in Sardinia ranges from the late Chattian-early Aquitanian of Cuccuru Tuvullao, which represents one of the earliest records of *Amphiope* with transverse lunules in the Mediterranean, to the late Tortonian-early Messinian of Monte San Michele (Cagliari), the last being the most recent record of this genus.

The main evolutionary trends observed in the studied sample from Sardinia are the progressive reduction and the increasing complexity of the internal support system of the test. Also a decreasing number of plates in the ambulacral and interambulacral columns and the approaching of the periproct towards the peristome are observed, though they need confirmation based on a larger fossil sample.

The results of this study highlight the validity of the structural characters as taxonomic tools at the

	Species	N	Mean (mm)	Range (mm)	S.E
TL	*A. lovisatoi*	38	76.0	52-100	1.64
	A. montezemoloi	4	109.0	90-121	6.65
	A. nuragica	20	92.7	81-100	1,33
	Amphiope sp. 1	3	95.5	90-101	3.17
	Amphiope sp. 2	9	95.9	55.8-137	8.71
	Species	**N**	**Mean % Dap**	**Range % Dap**	**S.E**
TW	*A. lovisatoi*	38	105.4	94-113	0.69
	A. montezemoloi	4	105.7	100-110	2.10
	A. nuragica	20	106.3	101-116	0.77
	Amphiope sp. 1	3	109.3	102-114	3.71
	Amphiope sp. 2	9	104.7	102-110	0.87
TH	*A. lovisatoi*	36	10.2	6.8-15.1	0.29
	A. montezemoloi	4	9.8	8.3-12.2	0.99
	A. nuragica	20	14.2	10.5 -17.2	0.38
	Amphiope sp. 1	3	20.7	19.8-22.2	0.77
	Amphiope sp. 2	9	12.3	8.8-14.6	0.58
L1	*A. lovisatoi*	38	11.2	8.3-15.1	0.26
	A. montezemoloi	4	14.4	11.6-16.7	1.12
	A. nuragica	20	8.2	6.0-11.2	0.37
	Amphiope sp. 1	3	9.5	8.2-11.9	1.22
	Amphiope sp. 2	9	11.7	10.8-13.9	0.44
L2	*A. lovisatoi*	38	17.1	11-22	0.42
	A. montezemoloi	4	16.9	14.2-18.3	0.93
	A. nuragica	20	18.0	14.1-23.5	0.61
	Amphiope sp. 1	3	18.9	17.8-20.8	0.95
	Amphiope sp. 2	9	15.0	11.1-18.2	0.78
L3	*A. lovisatoi*	37	5.7	2.8-8.5	0.21
	A. montezemoloi	4	5.0	3.9-6.6	0.60
	A. nuragica	20	5.3	2.2-8.0	0.35
	Amphiope sp. 1	3	4.6	3.3-5.4	0.64
	Amphiope sp. 2	9	4.8	3.3-6.8	0.49
L4	*A. lovisatoi*	37	59.4	51.9-65.2	0.51
	A. montezemoloi	4	59.3	55.1-62.2	1.52
	A. nuragica	19	57.4	50.0-63.0	0.68
	Amphiope sp. 1	3	53.3	49.5-57.6	2.35
	Amphiope sp. 2	9	59.7	53-66	1.42
L5	*A. lovisatoi*	37	24.1	20.8-28.5	0.34
	A. montezemoloi	4	24.7	22.8-26.6	0.98
	A. nuragica	19	25.2	23.0-27.2	0.30
	Amphiope sp. 1	3	27.7	26.7-28.7	0.58
	Amphiope sp. 2	9	24.7	21.9-29.0	0.74
L6	*A. lovisatoi*	37	14.8	11.8-17.3	0.20
	A. montezemoloi	4	14.7	13.2-15.6	0.53
	A. nuragica	19	14.1	11.1-16.5	0.27
	Amphiope sp. 1	3	15.3	14.4-16.8	0.75
	Amphiope sp. 2	9	15.1	12.8-16.3	0.43
L9	*A. lovisatoi*	35	22.9	19.3-26.0	0.30
	A. montezemoloi	4	21.4	20.0-22.7	0.59
	A. nuragica	18	22.4	18.4-26.0	0.47
	Amphiope sp. 1	3	21.9	18.8-24.4	1.64
	Amphiope sp. 2	8	21.7	17.9-24.2	0.80
L10	*A. lovisatoi*	35	15.2	12.5-19.0	0.25
	A. montezemoloi	4	13.8	13.4-14.2	0.27
	A. nuragica	18	14.3	11.0-16.2	0.03
	Amphiope sp. 1	3	13.9	11.9-15.6	1.07
	Amphiope sp. 2	8	14.4	11.6-15.8	0.42
L11	*A. lovisatoi*	4	12.0	9.8-14.0	0.91
	A. montezemoloi	3	12.0	12.5-14.9	0.63
	A. nuragica	17	9.1	6.3-12.8	0.38
	Amphiope sp. 1	3	13.8	12.2-15.8	1.06
	Amphiope sp. 2	9	13.0	10.0-15.8	0.69

Table 3. Descriptive statistics of *Amphiope* from Sardinia. N = number of specimens, S.E. = standard error.

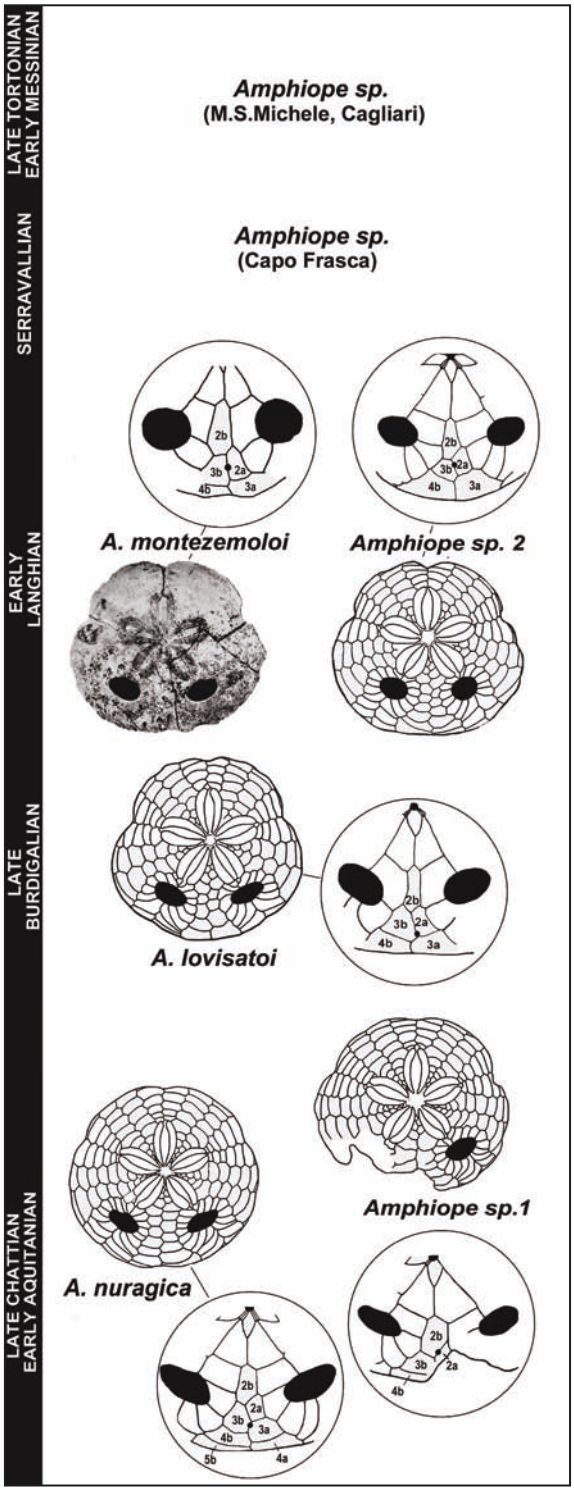

Figure 6. Scheme of the major evolutionary trends observed in the studied sample of *Amphiope* from Sardinia, with the only exception of *Amphiope* sp. 1. Over time the number of plates in the oral interambulacrum 5 decreases and the periproct migrates toward the peristome, in relation to post basicoronal plates number.

Morphological characters	*A. lovisatoi* Cotteau, 1895	*A. montezemoloi* Lovisato, 1911	*A. nuragica* (Comaschi Caria, 1955)	*Amphiope* sp.1	*Amphiope* sp.2
Test size (TL)	small (mean 76 mm)	large (mean 109 mm)	middle sized (mean 92.7 mm)	middle sized (mean 95.5 mm)	very large (> 130 mm)
Test height	low (H=10.2% Dap)	very low (H=9.8% Dap)	middle height (H=14.2% Dap)	very high (H=20.7% Dap)	middle height (H=12.3% Dap)
Test margin	thin	thin	middle thickness	rather thick	middle thickness
Lunules size and shape	small slightly elongate	very large almost subcircular	large narrow elliptical	large narrow elliptical	large subcircular-elliptical
Location of the periproct	distal half of the suture 2a/3b	halfway along the suture 2a/3b	close to the conjunction of plates 2a/3a/3b	bounded by plates 2a/2b	halfway along the suture 2a/3b
Number of plates in interambulacra 2, 3 and ambulacra II-IV	10-13	-	14-16	-	12-14
Number of post-basicoronals in oral interambulacrum 5a	2	2	3	2	2
Number of post-basicoronals in oral interambulacrum 5b	3	3	4	3	3
Central cavity	subpentagonal	starring	subcircular	subcircular	starring
Internal structure	light and complex	rather light, complex	simple and strong	simple and strong	rather strong
Other characteristics	- Shell very thin	- Shell thin - Plate 2b of oral interambulacrum 5 very elongate	- Shell thick - Petal surface convex, including the poriferous areas	- Shell very thick - Lunules very close to posterior petals - Apical disc more centrally located than the others - Frontal petal much longer than the posteriors	

Table 4. Specific characters in the studied species.

specific level in *Amphiope* and indicate that a review, based on these features, of the earlier described species of *Amphiope* is needed to improve the poorly resolved taxonomy of this genus and to bring light into the diffusion of *Amphiope* in the Mediterranean and in the eastern Atlantic.

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