Revision of the genus *Amphiope* L. Agassiz, 1840 (Echinoidea Astriclypeidae) with the description of a new species from the Miocene of France

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ABSTRACT   The taxonomy of *Amphiope* L. Agassiz, 1840 (Echinoidea, Astriclypeidae), an echinoid distributed in the Oligo-Miocene of Central and Southern Europe, is largely unresolved since the description of most species attributed to this genus was based only on the external morphological features, while important characters, such as the oral plating and the internal support system, were poorly illustrated or completely omitted. Additionally, the type material of some species was missing or badly preserved and geographical/stratigraphical information about the type-locality was unclear. This was the case also for *Amphiope bioculata* (Des Moulins, 1837), the type species of the genus. The poor definition of the earlier described species of *Amphiope* prevented comparison with fossils from other localities and ages, subsequently attributed to this genus. A large part of the earlier species of *Amphiope*, key-taxa for the resolution of the complex taxonomy of this genus, are herein revised by modern methods. For this purpose, the type material available in public institutions has been re-examined and, when possible, new topo-typic material has been collected. As a result, the morphological description of *A. bioculata* has been completed based on fossils from the Middle Miocene of Hérault (France), which is here considered as the type area. The redefinition of the type species allowed to extend comparison and taxonomic discussion to other species earlier attributed to *Amphiope*. Seventeen species are herein confirmed as valid and maintained in the genus *Amphiope*. Three additional species so far attributed to *Amphiope* have been transferred to the genus *Paraamphiope* Stara et Sanciu, 2014: *P. agassizi* (Des Moulins in Cotteau, 1865), *P. cherichirensis* (Thomas et Gauthier, 1889) and *P. baquiei* (Lambert, 1907). *Amphiope boulei* Cottreau, 1914, has been assigned to the genus *Sculpsitechinus* Stara et Sanciu, 2014. *Amphiope romani* n. sp. is described on the basis of a sample from the Serravallian-Tortonian of Touraine (France); it is distinguished mainly by the periproct very close to the posterior margin and the lack of sinus in correspondence of the frontal ambulacra.

KEY WORDS   Echinodermata; Astriclypeidae; *Amphiope*; Neogene; western Atlantic and Mediterranean.

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INTRODUCTION

The earliest records of "*Amphiope*" L. Agassiz, 1840 (Echinoidea, Astriclypeidae) date back to the late Oligocene of western France (Des Moulins, 1837; Cotteau, 1858-1880; Tournouer, 1870) and the Proto-Mediterranean area (Agassiz L. & Desor, 1847; Des Gras, 1849; Cotteau, 1877, 1895; Pomel,

1883, 1885, 1887; Lambert, 1907, 1910, 1912, 1915, 1927, 1928; Lovisato, 1911, 1914; Cottreau, 1914; Lecointre, 1952; Comaschi Caria, 1955, 1972; Llompart, 1983; Philippe, 1998b; Stara et al., 2012). This genus diffused above all during the Miocene, towards the Atlantic coast of Africa (de Loriol, 1905; Néraudeau & Masrour, 2008), the Atlantic coast of Europe (de Loriol, 1896; Pereira, 2010) and, through the Parathethys and the Middle East (Laube, 1871; Fuchs, 1882; Ali, 1998; Nebelsick & Kroh, 2002), to north-western India (Smith & Kroh, 2011). It went extinct at the end of the Miocene or during the Pliocene. Indeed, a sole specimen was reported from the Pliocene of Algeria by Aymé & Roman (1954).

The taxonomy of *Amphiope* is largely unresolved since this genus accounts for more than 40 species, most of which are nominal species in need of revision due to high intraspecific variation and poor species definition (Smith & Kroh, 2011). Separation between species has been traditionally based on external morphological features, mainly test outline, size and shape of lunules and petals. Important features for species-level taxonomy in the astriclypeids, such as oral plating and internal test support system, were poorly illustrated or omitted completely. The importance of these characters was emphasised in earlier studies (Dartevelle, 1953; Durham, 1955; Lohavanijaya, 1965; Mooi, 1989, Ziegler et al., 2015) and in Recent researches concerning *Echinodiscus* Leske, 1778 (Jansen & Mooi, 2011, Stara & Sanciu, 2014) and *Amphiope* (Kroh, 2005; Stara & Borghi, 2014).

Most of the earlier described species of *Amphiope* were represented by scanty or badly preserved material, even single specimens, not taking the intraspecific variability into consideration. In some cases, the original illustration was arbitrarily reconstructed, e.g. in *A. hollandei*, as underlined by Cottreau (1914), *A. depressa* Pomel, 1887 and *A. palpebrata*, Pomel 1887. Therefore, they were not completely documented in terms of their morphology, thus preventing a reliable comparison. This condition led to a substantial uncertainty in the species separation within *Amphiope* and to subjective interpretations: e.g. Philippe (1998a) when studying *Amphiope* from the Rhône Basin (France) attributed almost all of the studied specimens to a sole species, *A. bioculata* (Des Moulins, 1837) the type species of the genus, which was interpreted as a taxon with a broad morphological variability. As a consequence, most of the specimens of *Amphiope* subsequently described in the literature have been assigned to *A. bioculata* (e.g. Kroh, 2005; Pereira, 2010).

Recent studies (Stara & Borghi, 2014) revealed that, despite a large morphological variability in *Amphiope*, structural differences enabled to distinguish species and, in some cases, to transfer species to other genera (Stara & Sanciu, 2014). Structural characters are not readily visible in the illustration provided by earlier studies and were rarely reported in the original descriptions. The re-examination of the type material has often been the only mean allowing the reassessment of earlier species. Another problem affecting some species described in the 19th and early 20th centuries, including the type species, was the lack of the type material and/or the uncertainty regarding geographical/stratigraphical information on the type-localities. This condition prevented, so far, a reliable taxonomic discussion also in studies carried on by modern methods (e.g. Stara & Borghi, 2014), since comparison with the key-species of *Amphiope*, inadequately illustrated and diagnosed and whose type material and/or type locality were uncertain/unknown, remained uncertain.

The aim of this study was the re-definition, based on morphological and morphometric analyses, with emphasis on the plate patterns and the internal support system, of the type species, *A. bioculata*, and of the other earlier established species of *Amphiope*. For this purpose, it was necessary to restudy the type-material which was available in public institutions and, when possible, to collect new material from the respective type-localities.

Based on the redefinition of the key-species of *Amphiope*, comparison with other taxa subsequently attributed to the genus *Amphiope* has been carried on.

PREVIOUS STUDIES, AN OVERVIEW

The evolution of the interpretation of *Amphiope* and of the species attributed to this genus is synthetically provided in the following, starting from the institution of *Scutella bioculata* Des Moulins, 1837, which was subsequently designated as the type species of this genus (Lambert, 1907). We intentionally

omitted to cite the endless and inconclusive taxonomic discussions reported in the literature and focused on the development of the studies on this genus, including the chronology of the erection of new taxa. Most of the earlier works on *Amphiope* have been provided by French scholars, who studied fossil material from the Oligocene and Miocene of France and other Mediterranean countries (North Africa, Italy, Spain).

Des Moulins, a zoologist from Bordeaux (France), erected *Scutella bioculata* on the basis of figures 5–6 of *Scutella bifora* Lamarck reported in the Encyclopédie méthodique (Bruguières, 1791; Figs. 13, 14) and distinguished two varieties named Var. A ("*foraminibus subrotundis*") and Var. B ("*foraminibus transversé ovatis*").

These specimens were subsequently consigned to the Muséum Sciences et Nature of Bordeaux.

The specimens labeled MHNBx 2014.6.317 (syntype from Sure, près de Bollène, Vaucluse, France, ex. Requien [N°55]) and MHNBx 2014.6.189 (syntype from Saucats (Gironde, France) [n°4]) were both considered "type for var. A" by Des Moulins (label and 1837 work).

The specimens labeled MHNBx 2014.6.180.1, syntype from carrière Dambert, Gornac, Gironde, France, ex. Laporte ainé [= senior] [n°118] and an incomplete specimen were considered "*type for var. B*". Des Moulins did not provide illustration of those specimens and affirmed that they were too badly preserved to represent a distinct species.

L. Agassiz (1841) established two new genera: *Amphiope* and *Lobophora*. He characterized *Amphiope* by its rounded lunules and provided a doubtful and partial oral plating scheme. He noticed that the arrangement of the plates around the lunules in *Amphiope* was different from that in *Lobophora*, though he did not discuss this particular. He also provided a detailed description and illustration of the species *bioculata*, but based it on a incomplete specimen from the "faluns" of Touraine (L. Agassiz, 1841: pl. 11, figs. 1–3). De Loriol (1901) and Lambert (1907), when examining the mold of that specimen ("Moule 30"), noticed that it was poorly preserved and subjectively restored. The location of the specimen and of its "Moule 30" was never provided; as a matter of fact, they were not recorded in the inventory of the Agassiz collection at Neuchâtel (Jeannet, 1929). This interpretation of the type species was not subsequently accepted (de

Loriol, 1901; Lambert, 1907, 1912a, 1927) since Agassiz's "neotype" was morphologically different from the type of var. A and its finding locality was very far from the two type-localities indicated by Des Moulins (1837). In the same paper L. Agassiz (1841: pl.11, figs. 6–10) instituted *A. perspicillata* based on a single specimen from the "*terrains tertiaire*" of Rennes (north-western France).

L. Agassiz & Desor (1847) interpreted *Amphiope* as a subgenus of *Lobophora*, since they believed that the different plating structure around the lunules was not valuable for a distinction at the generic level. In the same work, Desor instituted a new species, *Amphiope elliptica*, from the Miocene of the Rhône Basin (France), but he did not provide illustration.

A. Agassiz (1872–74), revised some genera with oval, elongated radially, lunules and placed *Lobophora* L. Agassiz (1841) in synonymy of *Echinodiscus* Leske (1778) (see *Lobophora truncata* L. Agassiz, 1841 = *Echinodiscus truncatus* (L. Agassiz, 1841), separating it clearly from *Amphiope*.

Cotteau (1865) described *A. agassizi*, from the "calcaire à Astéries" of Gironde (western France). The specific denomination was inspired by a label attached to a specimen examined by Cotteau in Des Moulins's collection. Cotteau noticed that the plate pattern around the lunules was similar to that in living specimens of *Lobophora truncata* (today *Echinodiscus truncatus*) and *L. bifora* (today *E. bisperforatus*), however he did not provide illustration of that particular feature (Figs. 21, 22) and assigned the new species to the genus *Amphiope*. Also Tournouer (1870) underlined that the lunules of *A. agassizi* were more typical of extant *Echinodiscus* than of *Amphiope*.

Cotteau (1877) erected *Amphiope hollandei* n. sp. from the Burdigalian of Corsica, underlying that the plate pattern around the lunules was characteristic for *Amphiope*. He also suggested that the outline of the lunules, radially or transversely elongated, was important only at the specific level.

Pomel (1887) transferred *A. agassizi* into the genus *Tretodiscus* since "Amphiope *differs from* Tretodiscus *(*Lobophora *Agassiz, non Curtis) by its transversely, instead than radially, elongate lunules*". He suggested that *Tretodiscus* differed from *Amphiope* also by the structure of the lantern. In the same work Pomel assigned four new species to *Amphiope* from the Miocene of Algeria, but he did not

provide the repository of the studied material: *A. palpebrata*, *A. depressa*, *A. villei* and *A. personata*.

Cotteau (1895) instituted *A. lovisatoi* and *A. dessii* on the basis of Miocene fossils from Sardinia. The type material was lost in Cagliari during the Second World War. The type locality of *A. lovisatoi* has been recently rediscovered and new topotypic material collected and studied (Stara & Borghi, 2014).

De Loriol (1902) underlined that the specimen designated by Agassiz as neotype of *Amphiope bioculata* was very poorly preserved and did not correspond to the figures 5–6 of *Scutella bifora* Lamarck reported in the Encyclopédie méthodique (Bruguières, 1791). Consequently he based his description on specimens from the "Helvétien" of St. Christol and Chemin de Tuileries, both of them near Lespignan (Hérault), considered as the closest to that illustration.

Fallot (1903) examined the Des Moulins's collection and noted that all the specimens of Var. A and Var. B were badly preserved (Figs. 15–18). Based on the label attached to two specimens of Var. B, Fallot "wrote: "*one of them was from Dambert quarry near Gornac, the other between Violle and Saint-Croix-du-Mont, whereas a number of test fragments are deprived of the indication of the finding locality*". Another label attached to var. B by Des Moulins reported: "*assigned to a temporary species,* Amphiope ovalifora*, nob. 4 September 1869*". However, Des Moulins did not published any description or illustration of this taxon, likely because the fossils were badly preserved. Although the denomination *A. ovalifora* was utilized by Benoist (1874) and Degrange-Touzin (1882) for some specimens from the Aquitanian of Lariey and Saint-Croix-du-Mont, respectively, the first description and illustration of this taxon was provided by Fallot (1903). However, the photo published by Fallot points to a different species (as suggested by Fallot himself) which, although morphologically close to *A. ovalifora*, has the periproct very close to the posterior margin. Fallot collected a few well preserved specimens from the "middle Aquitanian" of Cabaron, near Castelvieil, in the same area of Gornac, leaving them in open nomenclature since they differed from the syntype of Var. B by narrower lunules.

Labrie (1904) confirmed that the original label in Des Moulins collection indicated Gornac as the type locality: "*La collection de Des Moulins contenait depuis fort longtemps une* Amphiope *provenant de Dambert, près Gornac (Musée de Bordeaux)*".

Lambert (1907, 1912a, 1915a, 1927) gave a significant contribution to the knowledge of the genus *Amphiope*. He designated (1907) *A. bioculata* (Des Moulins, 1837) as the type species of the genus and distinguished it from *A. ovalifora* by its roundish instead than transversely elongate lunules. However, when studying large samples from the Rhône Basin (Lambert, 1912a) and Gornac (Lambert, 1915a), the distinction based only on this feature became uncertain. To test the variability of the lunules, Lambert examined some specimens from the two type-localities indicated by Des Moulins (1837), Sure and Bordeaux, and encountered two main problems:

1) No village or locality named Sure was known near Bollène. Lambert (1907) proposed Suze-la-Rousse as a possible alternative. However, the specimens from Suze (MNHN-F- A22694-L 18.458 and A22695-L18.458-261) resulted to be morphologically different from the syntype of *A. bioculata* and were embedded by a different sediment (Lambert, 1912a) (Figs. 19, 20). In agreement with de Loriol (1901), Lambert (1912a) strongly suggested that the specimens from the "Helvétien" of Hérault (France) were the closest to the syntype of Var. A and based his concept of *A. bioculata* on the fossils from that area.

The specimen from Touraine, proposed by Agassiz (1841) as neotype for *A. bioculata*, was assigned by Lambert (1912a) to the variety *turonensis*.

The type-locality of Var. B was not detailed by Des Moulins (1837), who simply indicated "*Bordeaux*". Lambert (1915b) indicated Gornac as the type-locality of *A. ovalifora*, thus confirming the opinion of Fallot (1903) and Labrie (1904). Lambert (1912b) studied a sample made of 30 specimens from Gornac concluding that the separation between *A. bioculata* and *A. ovalifora* based only on shape and size of the lunules was uncertain.

Lovisato (1911, 1914) erected three new species from the Miocene of Sardinia: *A. montezemoloi*, *A. calvii* and *A. pallavicinoi*. The type material was lost during the Second World War. *Amphiope montezemoloi* has been recently redefined by Stara & Borghi (2014) who found out the type locality and designated a neotype.

Cottreau (1914: plate 5, figs. 1, 8 and plate 6, figs. 1–11) analyzed the morphological variability present in a large sample from Saint-Christol (Les Tuilières), near Nissan (Hérault). He recognized a sole species and affirmed that the differences in the lunules outline alone were not significant for a distinction at the species level.

Lambert & Thiéry (1925) separated the genus *Amphiope* from *Tretodiscus* and indicated the "*Helvétien*" of Hérault (France) as the type area of *A. bioculata*.

Lambert (1927) instituted a new species, *A. labriei*, from the "*Helvétien*" of Aignan (Gers, northwestern France) (Fig. 24).

Mortensen (1948), considered *Amphiope* as a subgenus of *Echinodiscus*.

Although Lovén early in 1874 proposed a method to define the plate position on the test of echinoids and underlined the importance of the plating structure, for almost 180 years the distinction at the species level in *Amphiope* has been based only on external test characters and the taxonomic value of the lunule outline has been debated (see Stara & Fois, 2014 for an overview).

Durham (1955) first utilized the analysis of test scheme, food grooves and growth stages in the ontogenesis in the systematic of clypeasteroids. In particular, he published the oral plating scheme of a specimen (UCMP 33846, Museum of Paleontology of the University of California) attributed to *A. bioculata*. He did not provide the finding locality and the label reported only "Miocene of Europe"; however, the test outline and the oral scheme seem to correspond to some specimens from Nissan (see Fig. 9).

Aymè & Roman (1954) described *A. tipasensis* Aymè et Roman, 1954 from the Pliocene of the Tipasa Province (Algeria), based on a sole specimen. No plating scheme was provided, however the narrow and transversely elongate lunules points to a true *Amphiope*, though the apical disc is not visible.

Philippe (1998a), when studying *Amphiope* from the Rhône Basin (France), attributed almost all the examined specimens from that area and from other Mediterranean localities to *A. bioculata*, subjectively interpreting it as a species with a broad variability range.

Kroh (2005) and Pereira (2010) reported a partial plating scheme of the oral interambulacrum 5 in two specimens of *Amphiope* from the Miocene of Austria and of Portugal, respectively.

Stara & Borghi (2014) introduced the analyses of the plate patterns and of the internal test structure as taxonomic tools useful for species-level taxonomy in *Amphiope*. Five species were identified within the fossil material examined from Sardinia (Italy): *A. lovisatoi* Cotteau, 1895, *A. montezemoloi* Lovisato, 1911, *A. nuragica* (Comaschi Caria, 1955) and two additional species left in open nomenclature. But comparison with key-species of the genus *Amphiope*, whose structural characters were unknown, led to uncertain conclusions. The results of that study indicated that a review, based on those features, of the earlier described species of *Amphiope* was needed to improve the poorly resolved taxonomy of the genus.

Stara & Sanciu (2014) established the new genus *Paraamphiope* Stara et Sanciu, 2014 distinguishing it from *Amphiope* by its axial elongate lunules, separated from the posterior petals by at least 3–4 (rarely 2) couples of plates, by its particular scheme of the oral interambulacrum 5 (see discussion) and by strongly branched food grooves. *Amphiope arcuata* (Fuchs, 1882), from the Miocene of Egypt and Libya, was transferred into the new genus, *A. pedemontana* Airaghi (1901), from the Oligocene of Piedmont and Liguria (northern Italy), was assigned to the genus *Echinodiscus*.

MATERIAL AND METHODS

The material under study, together with that utilized for comparison, consists of 209 specimens from 36 different localities and seven countries (Fig. 1). They have been examined at the Muséum National d'Histoire Naturelle of Paris (MNHN-F), Muséum Sciences et Nature of Bordeaux (MHNBx), Musée Requien of Avignon (MRA), Association Paléontologique of Bordeaux (APBA), Museo di Storia Naturale Aquilegia di Masullas, Sardinia (MAC), Museo di Zoologia ed Ecologia (MZE.UNICA) and Museo di Geologia e Paleontologia "D. Lovisato", at the Università degli Studi di Cagliari, Sardinia (MDLCA). The specimens attributed by Des Moulins (1837) to *Scutella bioculata* Var. A and Var. B are housed at the MHNBx and the specimen attributed by Durham (1955) to *A. bioculata* is housed at the University of California, Paleontological Museum (UCPM).

The species under study were compared with those from Sardinia, described in Stara & Borghi (2014), and from other localities cited in Stara & Sanciu (2014) and Stara et al. (2015), housed at the Museo di Geologia e Paleontologia "Domenico Lovisato" (MDLCA) and the Department of Animal Biology and Ecology, University of Cagliari (MZE.UNICA) and the National History Museum of London (NHMUK).

All the fossil specimens of *Amphiope* studied by Pomel are wanting. After Cleevely (1986), a part of the Pomel collection was purchased by the NHML
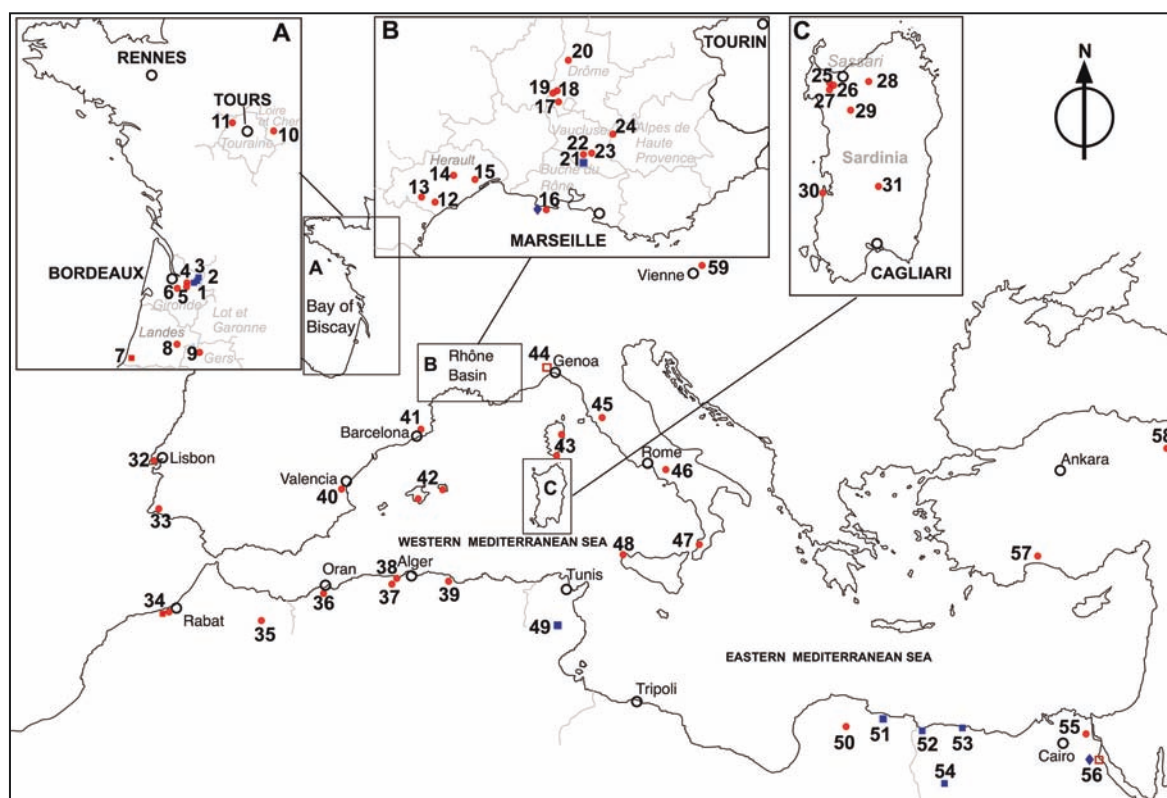
Figure 1. Location map of the findings localities of *Amphiope* and the closely related astriclypeids discussed or cited in this study:box A, western France Atlantic basins; box B, Rhône Basin; box C, Sardinia Basin; D, other localities or basins. ●= *Amphiope*, ■= *Paraamphiope*, ♦= *Sculpsitechinus*, □= *Echinodiscus*. - A, western France, Gironde and other localities: 1=Montségur; 2=La Réole; 3; Pellegrue; 4=Gornac and Saucats; 5= Castellvieil, Cabaron; 6=Léognan (Le Thil); 7=S.t.-Avit; 8=Abesse, S.t-Paul-le-Dax; 9= Montréal; 10=Oisly; 11=Channay sur-Lathan. B, Rhône Basin, France: 12= Nissan-Lespignan; 13= Cruzy; 14=S.t-Felix-de-Lodéne (Lodéve); 15=Aspiran; 16=Carry-Le-Rouet; 17=Souze-La-Rousse; 18 =S.t-Paul-Trois-Chateaux; 19=S. Restitute; 20=Crest; 21= Cadenet, Vaugines; 22= Cucuron and Blanqui; 23=Cabrière d'Aigues; 24=Châteauneuf-Miravail. C, Sardinian Basin, Italy: 25=La Crucca; 26=Bancali; 27=San Giorgio; 28=Chiaramenti; 29=Bessude and Bonnanaro (all in Sassari Province); 30=Capo Frasca, Arbus; 31=Cuccuru Tuvullau, Nuragus (Cagliari Province). D, other Eastern-Atlantic, Peri-mediterranean and Parathetyan localities/basins. Portugal: 32=Lower Tagus Basin (Lisbon); 33= Algarve. Maroc: 34=Miocene Rabat Basin, Zoubia D'Babei (Helvetian) and Talerhza (upper Aquitanian), respectively; 35=Guercif Basin (Late Miocene). Algeria: 36=Mléta, Oran (Langhian ?); 37=Cherchell (Burdigalian?); 38=Tipasa (Pliocene); 39=Sidi Aïch, Bejaja Province. Spain: 40=Valencia; 41 Barcelona; 42=Balearic Basins. Corse (France): 43= Bonifacio and Aleria (Burdigalian). Italy: 44=Ligurian Oligocene Basin; 45=Manciano, Latium (Middle/? Late Miocene); 46=Campania (Lower-Middle? Miocene); 47=Vibo-Valentia Basin, Calabria (Late Miocene); 48= Case Genna (Marsala, Trapani), Sicily (Langhian-Tortonian). Tunisia: 49=Djebel Cherichira and other nearest localities (Burdigalian). Libya: 50= Sebkret El Ghenaien, Cyrenaica (Miocene); 51=Tobruc area (Middle Miocene). Egypt: 52-54: Western Desert localities: El Salum; Marsa Matruh and Siwa, respectively (Early Miocene); 55-56: Western Desert localities; Gebel Gharra (Upper Burdigalian) and Hurghada, Red Sea (Plio-Pleistocene), respectively. Turkey: 57-58= Mut ? Basin (Burdigalian-Serravalian) and Herzincan Province Basin (Burdigalian). Austria: 59= Vienna Basin (Miocene).

in 1851 (Woodward, 1904), but it included only fossil vertebrata. Some type specimens acquired by E.D. Cope, a private collector, were doubtfully (Cleevely, 1986) incorporated in the Poirrier collection at the American Museum of Natural History of New York (AMNH). As a matter of fact, no specimen belonging to Pomel is actually present at the AMNH (personal communication B. Hussaini and I. Bajo Campos, May 2014).

Since 1922, the type material of the species of *Amphiope* instituted by Lovisato was housed at the Museo Sardo di Geologia e Paleontologia, Institute of Geology, University of Cagliari (http://sites.unica.it/geomusei/storia/). On February 28th 1943, the Museum was hit by the bombardment which destroyed almost 80% of the buildings in Cagliari (Pillola & Zoboli, 2014). Only a small part of the fossil material survived that event and was transferred to Ghilarza in 1943. A recent research by one of us (PS) in the unlabelled material stored at the MDLCA confirmed that the type material of *A. desii* Cotteau, 1895, *A. pallavicinoi* Lovisato, 1914 and *A. calvii* Lovisato, 1914 are wanting, but he was able to find the type of *A. montezemoloi* Lovisato, 1911.

Morphology of Amphiope

The scheme of the biometric parameters tradi-tionally used in the taxonomy of *Amphiope* and in this paper is reported in figure 2. Additionally, we tried to transform also the morphological features described in the literature into morphometric data, in particular the shape and size of the lunules, the size of the petalodium and the position of the periproct, taken from as many specimens as possible to avoid subjective interpretations.

The present revision is based also on the study of the internal test structure and the plating arrangement. Measurements and plating pathways have been taken directly from the type-material or newly collected specimens, when possible, and in a few cases from figures presented in the original descriptions.

Morphological abbreviations

See figure 2: ß = angle between the major axis of the two lunules; L1-L2 = lunule length and width, respectively; L3 = distance between the posterior petal-tip and the anterior edge of the corresponding lunule, L4 = distance of the genital pores G2 and G3 from the posterior margin of the test, L5-L6 = length and width of the frontal petal, respectively; L7-L8 = length and width of the anterior paired petals, respectively; L9-L10 = length and width of the posterior petals, respectively; L11 = distance posterior border of the periproct-posterior
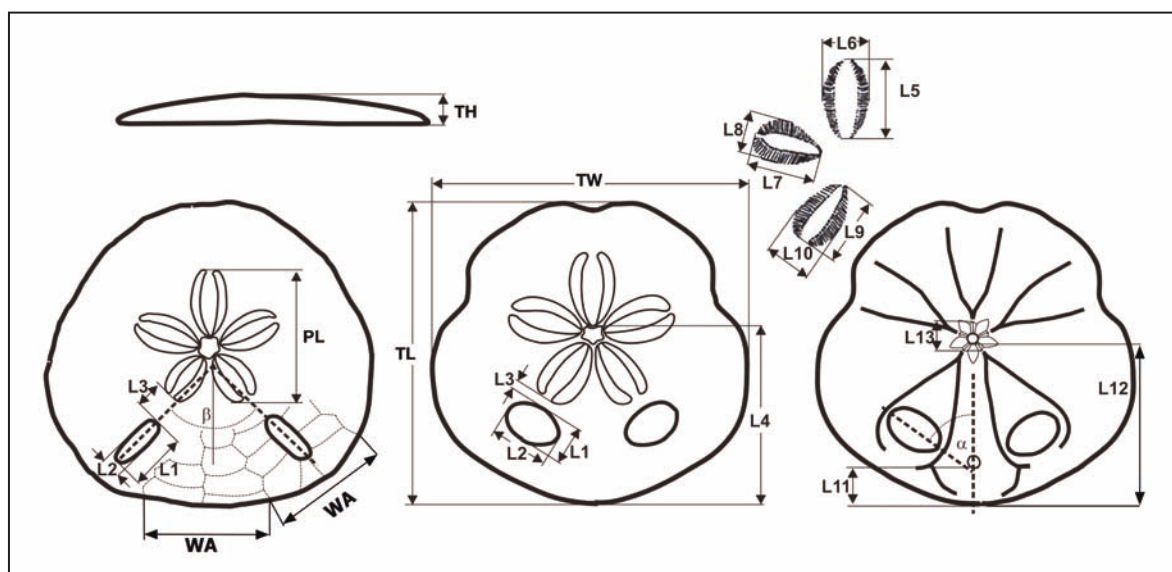

Figure 2. *Amphiope*: scheme of the biometric parameters measured in the studied specimens.

margin of the test; L12 = distance between the posterior border of the peristome and the rear margin, L13 = front-rear diameter of the ambulacral basicoronal circlet. PL = petalodium length; TL-TW-TH = test length, width and height, respectively; WA= width of the interambulacrum 5 at ambitus (measured on the aboral face); ø pc = periproct diameter; ø ps = peristome diameter. TL is expressed in mm, ß angle in degree and all the other measurements in % of TL.

Test morphology

Since the range of TL in the material under study was wide (30-170 mm), species are considered "small sized" if maximum TL is below 60 mm, "middle sized" if maximum TL is between 60 and 100 mm, or "large sized" if maximum TL is over 100 mm.

Similarly, the size of the petalodium (PL) in the studied samples of *Amphiope*, *Paraamphiope*, *Echinodiscus* and *Sculpsitechinus* ranges from about 30 up to 60% TL; a petalodium is here assumed to be "small" if PL is below 47% TL, "medium-sized" if PL is between 47 and 54% TL, or "large" if PL is over 54% TL.

To univocally describe the different shape and size of the lunules, the Shape Index (SI) and the Width Index (WI) are introduced. WI equals the area of the rectangle inscribing the lunule [L1xL2 (both measures expressed as % of TL)]. SI is represented by the ratio L2/L1 in *Amphiope* and L1/ L2 in *Paraamphiope* and *Sculpsitechinus*. Due to the relevant variation in the value of WI (55–420), lunules are considered "small" if maximum WI is lower than 100, "mid-sized" if maximum WI is between 100 and 200, or "large" if maximum WI is larger than 200.

Since the lunules are commonly different in the same specimen, the measures of the lunules (L1, L2) were taken from the left lunule, whenever possible. Lunules show different shape and size when viewed from the aboral or the adoral side; additionally, the entrance of the foramen is more or less flared and the walls are inclined. To tackle these problems, measures were taken as indicated in figure 3 (L1). The position of a lunule is univocally indicated by the number of plates in the ambulacral columns separating it from the tip of the corresponding petal.

Food grooves

Since it was not possible to apply a measurement to the grooves, a terminology is introduced to avoid subjective interpretations. The food grooves system consists of five main "trunks" starting slightly after the basicoronal circlet; each trunk soon bifurcates into two main grooves which extend towards the test margin but not reaching it (Fig. 4). The two bifurcations may "develop by a simple scheme" (Fig. 4B–C), i.e. with only a few and short distal secondary grooves, or they are "well branched" (Fig. 4D–E), i.e. with several and rather long "secondary ramifications" which start along the main grooves (Fig. 4E) and from their distal part. The secondary grooves are finer and may spread into smaller branches. The main grooves may be "well marked", i.e. the depressions are rather large and well visible in the oral face (Fig. 4A), or rather "flush" and/or narrow (Fig. 4B). A short branch of each posterior groove surrounds the corresponding lunule and extends towards the periproct.

Plating pathways

The plating pathways were rarely visible on the test surface and only in a few cases we were allowed to prepare the specimens housed in public institutions, to highlight the sutures between plates. Therefore, topotypic specimens were used when possible to improve data and also partial schemes were taken into consideration, since they turned out to be very useful in the taxonomic discussion.

Durham (1955) and Smith (2005) affirmed that the number of plates present in each ambulacral (the extra-petals part) and interambulacral column does not change significantly during growth. Based on this statement, the total number of the plates present in each interambulacral and ambulacral (extra petals) columns and in the space between the petal tips and the corresponding lunules is here used as a taxonomic tool to compare species.

On the other hand, since Durham (1955) noticed that the number of plates bearing pores pairs in the petals progressively increases during growth, comparison between species is carried out based only on the length and width of the petals and the size of the petalodium (PL).

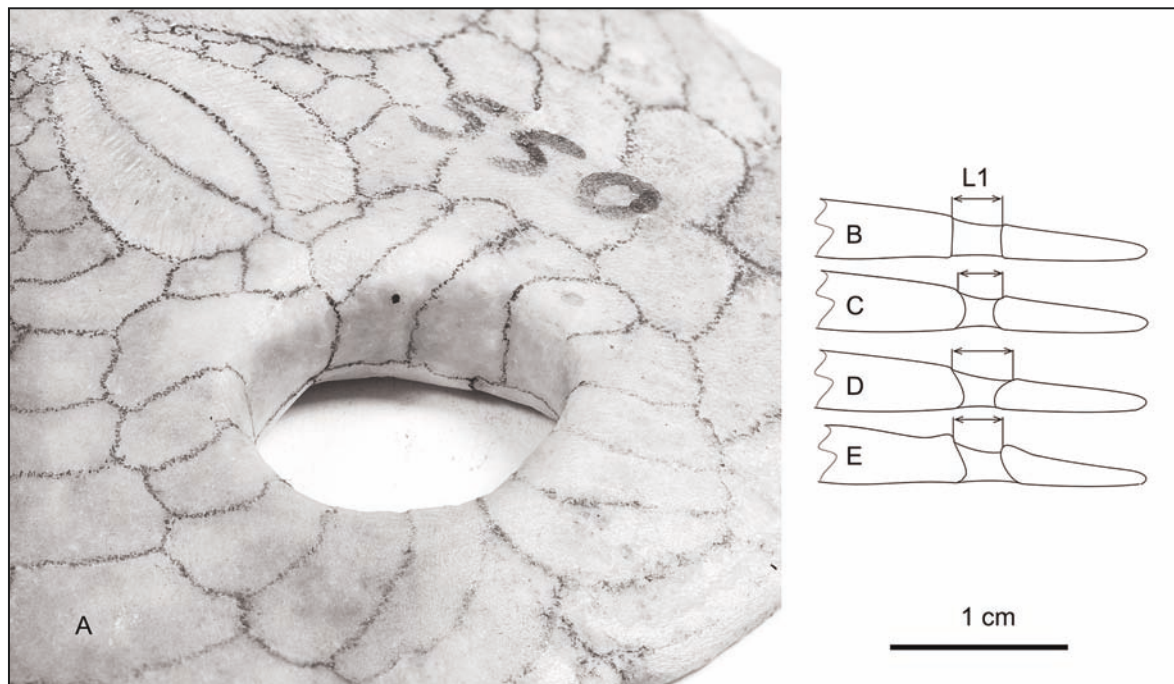The position of the periproct has been univocally indicated by the plates bounding it, numbered

Figure 3. *Amphiope* sp. 2 (MACPL.550), Bancali (Sardinia). A, plating structure of a typical lunule. B-E, schematic sections showing different types of foramen in *Amphiope*: B-C, symmetrical foramen, with perpendicular (B) and convex walls (C), D-E, asymmetrical foramen, with convex walls and much widened (D), with oblique walls (E).
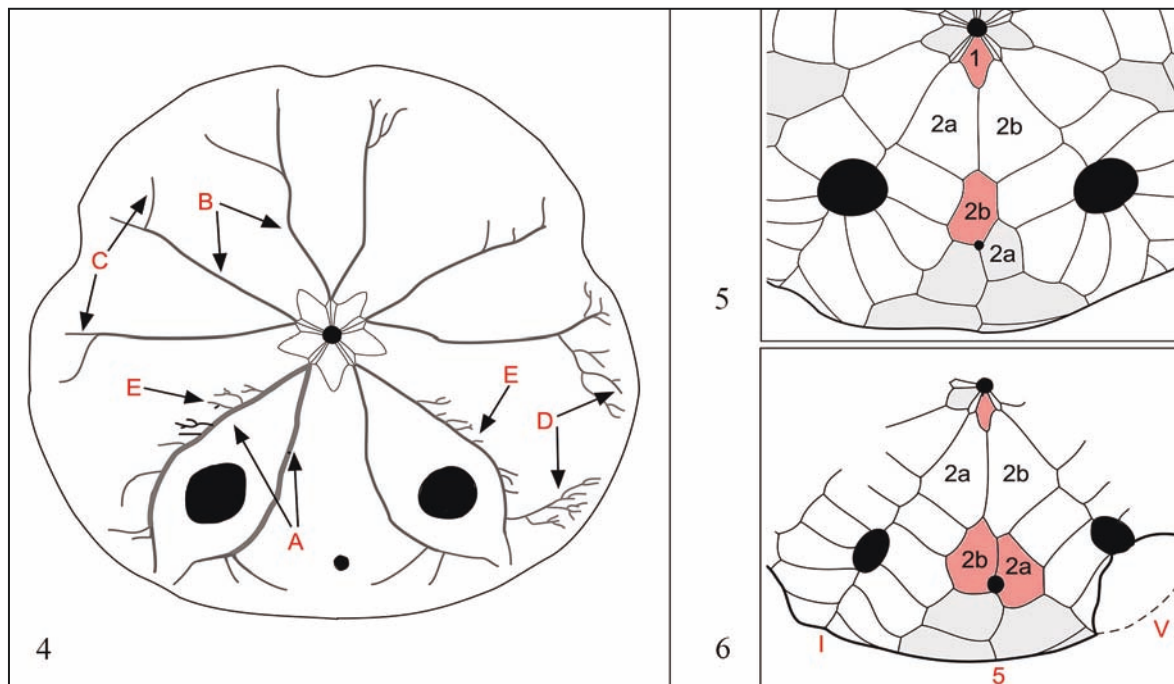

Figure 4. Idealized scheme of the food grooves which can be found in *Amphiope/Paraamphiope*. A, large main trunks; B, thin main trunks; C: simple distal branches; D: complex distal branches; E: additional branches along the main trunks. Figure 5. Adoral scheme of *Amphiope*: in pink plates that characterize the typical arrangement of this genus. Figure 6. Adoral scheme of *Sculpsitechinus*: in pink plates that characterize the typical arrangement of this genus.

after the Lovén's system (Lovén, 1874), in order to avoid the subjective descriptions often reported in the literature, e.g. "far" or "close" from the posterior test margin or the peristome.

In the oral side of almost all of the known species of *Amphiope*, the plates 5.b.2 and 5.a.2 are commonly staggered, with only 5.b.2, which is longer than the others, in contact with both the correspondent ambulacral plates I.a.2 and V.b.2 (Fig. 5). In *Echinodiscus* and in *Sculpsitechinus*, instead, plates 5.b.2 and 5.a.2 are almost paired and both in contact with the correspondent ambulacral plates I.a.2 and V.b.2 (Fig. 6).

Internal test structure

The radiographic analysis has been largely used to study the internal structure of the test, since only in a few cases it was possible to observe sections of the type-material housed in public institutions.

Radiographic photos have always been taken in aboral view, as in all other studies dealing with the scutelliforms (e.g. Ziegler et al., 2015). When possible, specimens of approximately comparable size were chosen for X-Ray imaging. White areas correspond to high-density zones of the test, whereas the darkest areas indicate the presence of internal cavities. The largest dark areas correspond to the central hollow, whose outline may be roundish to sub-pentagonal, and to the radial cavities extending through the interambulacra. The macrocanals running along the interambulacra 2 and 5 contained, respectively, the *caecum* and the *rectum*. The terminology here used to describe the morphological features of the internal support system follows Durham (1955), Mooi (1989) and Mihaljevic et al. (2011). In particular the internal buttressing connecting the lower and upper plated surfaces of the test consists of pillars, which are rounded to oval in cross-section, and bars, connections that are obviously flattened and elongate.

Amphiope bioculata *and* A. nuragica *groups*

The systematics follows Kroh & Smith (2010) in general, and Stara & Sanciu (2014) concerning the genera *Paraamphiope* and *Sculpsitechinus*. However, the species under study were divided into two informal groups, as suggested by Stara et al. (2015): the *A. bioculata* group, including the species with a mean value of SI ≤ 1.6, and the *A. nuragica* group, with SI > 1.6 and more transversely elongate lunules with sub-parallel edges. This grouping likely does not correspond to true phylogenetic lines, however it allowed to limit comparison to the species belonging to the same group, thus making the analysis much easier. Indeed, comparison between all the species studied, indicated other significant differences between the *A. bioculata* and the *A. nuragica* groups.

Type localities

The type localities cited in the literature have been visited, when possible, also to collect new specimens. However, they were often difficult to trace, because old toponyms are often unknown today and some localities, especially when represented by small outcrops, were hidden by natural modifications (e.g. reforestations, landslides) or by changes occurred by the processes starting from the beginning of the '900 (e.g. expansion of towns and villages). Therefore, only a part of the *Amphiope*-bearing localities has been traced and, even in this case, sometimes it was not possible to collect any specimen from them.

The majority of the species attributed to *Amphiope* have been described in the 19th and early 20th centuries and the knowledge about the geology of the *Amphiope*-bearing localities have been greatly improved since then. For example, in earlier studies all the specimens from Saucats were dated to the Aquitanian, while also Burdigalian and Serravallian sediments were recently recognised at that locality (e.g. Londeix, 1991; Nolf & Cahuzac, 2009). A similar situation is known also for Gornac, Nissan and most of the other classic localities of the Aquitaine and Bordeaux basins (Fallot, 1901; Chavanon, 1974; Chauzac et Tourpin, 1999; Chauzac & Janssen, 2010) or of the north-western basins of France (Bouchet et al, 2012).

On the whole, the geographic and the stratigraphic location of the *Amphiope*-bearing outcrops have been updated only when it was possible to trace the localities and geological data were provided by Recent studies. Otherwise, the indication reported in the original labels/descriptions has been used.

Whenever the data concerning the *Amphiope*-bearing deposits were reliable, that was verified on

the field and/or supported by the Recent literature, comparison between species has been carried on based also on the geographical and stratigraphical differences.

DISCUSSION

Redefinition of the type-species, Amphiope bioculata *(Des Moulins, 1837)*

The specimen (type) assigned by Des Moulins (1837) to *Scutella bioculata* Var. *A* (MHNBx 2014.6.317) is poorly preserved. It is represented by a whole test with coarse-grained arenite strongly indenting both faces, thus obliterating the main morphological features and the plate structure (Figs. 15, 16). An attempt by C. Laurent (MHNBx) to remove the sediment was not successful. Since "Sure prés Bollène" (Vaucluse), the finding locality indicated by Des Moulins (1837), was unknown, Lambert (1907) and Philippe (1998) suggested that the type-locality was likely Suze-la-Rousse. Two test fragments from Suze-la-Rousse (Drôme) examined in Lambert's collection (MNHN-F.A22694-L18.458 and MNHN-F.A22694-L18.458-261, Figs. 19, 20) show transversely elongate elliptical lunules (very different from the "foraminibus subrotundae-formis" stated for *A. bioculata*), and are embedded in a brownish fine-grained marly arenite, very different from the pale gray-yellowish arenite indenting the type (Figs. 15, 16). Field research by one of us (PS) confirmed the presence of brownish marly arenite in the surroundings of Suze-la-Rousse (Fig. 1, B17), whereas no pale gray-yellowish arenite was found. Thus, Suze-la-Rousse does not correspond to "Sure prés Bollène", and the type-locality of *A. bioculata* indicated by Des Moulins remains unknown, as well as the stratigraphic position. De Loriol (1902) and Lambert (1912a, 1915a), based on the study on several populations of *Amphiope* from the Oligo-Miocene of France, indicated the specimens from the "Helvétien" of Hérault as those showing the closest similarity with the syntype of *A. bioculata*. Lambert (1927) even affirmed that "*the type from Hérault was replaced by Agassiz (1841) with a specimen from Touraine*". Also Cottreau (1914) based his concept of *A. bioculata* on a sample from the Miocene of Saint Christol (actually Chemin des Tuilières; see Roman, 1974), between Nissan and Lespignan (Hérault).

Following the opinion of de Loriol (1902), Lambert (1912a, 1915a, 1927) and Cottreau (1914), who considered the "Helvétien" of Hérault as the type-area, we based the re-definition of *A. bioculata* on 11 specimens from the Langhian-Serravallian of the surroundings of Nissan and Lespignan. Three of them (MNHN-F.A 57777-9), collected by one of us (PS) from the blue marls of Lespignan ("Marnes blues inférieures" of Roman, 1974), are consistent with those figured by de Loriol (1901: pl. II, figs. 4, 5) and Cottreau (1914: pl. V, figs. 1-8 and pl. VI, figs. 1–11) and close to the morphological features visible in figs. 5, 6 of the Encyclopédie Méthodique (Bruguières, 1791): middle-sized test (TL=55–74 mm) with rather large (using the old terminology) (WI=56–145) and rounded lunules (SI= about 1), food grooves developing by a simple scheme but well-branched distally. After Roman (1974), the blue marls are dated to the Langhian-Serravallian. Other eight specimens (A2270.L18464a-h) labeled as "Nissan les Tuileries" are close to those from Lespignan, although they probably come from a higher level.

Accordingly to the submission of this article, the authors will submit to the Commission of the ICZN, a request for the establishment of a neotype, based on the sample MNHN-F.A 57777 (Figs. 91, 97). The designation of a neotype is needed since several morphological features of this species, based only on the syntype from "Sure" (MHNBx 2014.6.317), are unclear/unknown thus leading to subjective and controversial interpretation of the type species of *Amphiope*, whose definition is necessary to resolve the complex taxonomy of this genus.

The studied sample shows a morphology as close as possible to the original illustration reported in Bruguières (1791: figs. 5–6); additionally, it enables to take the plating scheme, the main morphometric data and to clear the internal structure. In the oral face, plates 5.a.2 and 5.b.2 are very staggered, with only the plate 5.b.2 in contact with the correspondent post-basicoronal plates I.a.2, V.b.2; the scheme of the oral interambulacrum 5 is variable (Figs. 66–69), but maintains the aforesaid characters. In the aboral face, there are 1–2 couples of plates between the petal tips and the corresponding lunules. In the specimen MNHN-F.A 57777, WA is 36% TL, ß is 76°, food grooves develop by a simple scheme, moderately branched distally (Fig. 70, 97).

Distinctive characters of the genus **Amphiope**

Based on the redefinition of the type species, the main diagnostic characters of *Amphiope* described in Smith & Kroh (2011) are here confirmed, with some emendations:

- the lunules in *Amphiope* are commonly rounded or ovoidal and transversely elongate, separated from the petals by only 1–2 (rarely 3) couples of plates;

- food grooves are simple, as well as in the specimen illustrated in figure 5 of the Encyclopédie Méthodique (reported in figure 14), or rather branched distally; only exceptionally (*A. sarasini*, see later) they are strongly branched distally and with some secondary ramifications branching off also from the intermediate part of the main grooves;

- in almost all of the known species of *Amphiope*, in the oral side, plates 5.b.2 and 5.a.2 are commonly staggered, with only 5.b.2, which is longer than the others, in contact with both the correspondent ambulacral plates I.a.2 and V.b.2 (Fig. 5). In *Paraamphiope* the plates of the columns "a" and "b", tend to be parallel to each other along the lunules, while in *Amphiope* the plates of the columns "a" and "b" tend to converge towards the center of the lunules, as we shall see in detail in the following chapters.

Discussion of the earlier species attributed to **Amphiope**

A number of species represented by exhaustive material, that is large samples and/or well preserved specimens, enabled to highlight peculiar distinctive characters for them and to confirm their validity. The description of these well characterised species and the difference between them are reported in detail in the systematics part. In the following, a comparison is carried on between these species and the type-species of the genus, based on the morphological features which are here considered as the most relevant in *Amphiope*.

The visit to Lambert's collection (MNHN-F), where a large number of specimens of *Amphiope* are stored, highlighted the difficulties encountered by earlier echinologists when comparing samples from different localities and ages using only the external test characters, such as shape and size of test,

petals and lunules. Cottreau (1914) admitted that the distinction at the specific level based only on these features led to subjective interpretations and uncertain results in *Amphiope*. Despite the wide intraspecific variability of this genus underlined in several papers (e.g. Lambert, 1915a, 1927; Cottreau, 1914; Philippe, 1998), Recent studies proved that stable structural differences were present in samples from different localities, allowing a separation at the specific level in *Amphiope* (Stara & Borghi, 2014), as well as in other astriclypeid genera (Stara & Sanciu, 2014; Stara & Fois, 2014). Thus, the analysis of the structural characters represents a valuable tool also in the taxonomy of *Amphiope*. Therefore, the present revision, as in our former papers (Stara & Borghi, 2014; Stara & Sanciu, 2014), has been based also on morphological biometric analysis and the study of the internal and external test structure.

Plating pathways. The main differences in the plate arrangement between *Amphiope* and the closely related genera, such as *Paraamphiope*, *Sculpsitechinus* and *Echinodiscus* (Figs. 9–12), are found mainly in the oral ambulacra I, V and in the oral interambulacrum 5 (see Stara & Sanciu, 2014).

The main differences in the test schemes of *Amphiope* are illustrated for the *A. bioculata* group (Figs. 25–34; Figs. 161, 163, 164) and the *A. nuragica* group (Figs. 35–44; Figs. 151–156).

The variability of the oral structure in the specimens of *A. bioculata* from the Langhian-Serravallian of Lespignan and Nissan is illustrated in figures 66–69: in the oral interambulacrum 5 there are always two post-basicoronal plates in column a (seldom three) and three in column b; plates 5.a.2 and 5.b.2 are staggered, 5.b.2 is always very long, its apex being 27–30% TL far from the posterior test margin; the periproct opens between 5.b.2-5.a.2, 5.a.2-5.b.3, or close to the junction point 5.b.2-5.a.2-5.b.3.

In the *A. bioculata* group, there are not many significant differences between *A. bioculata* (Figs. 27, 28) and *A. elliptica* (late Aquitanian-early Burdigalian of Cruzy; Figs. 25, 26). *Amphiope ludovici* (Tortonian of Blanqui; Figs. 33, 34) has a much lower total number of plates in the interambulacrum 5, when compared to *A. bioculata* and *A. elliptica* (11 against 16) and only two plates are present in columns a and b in the oral interambulacrum 5.

Figures 7, 8: Syntype of *Amphiope bioculata drunensis* (MNHN-F. A22379-18.457) from St.-Paul-Trois-Chateaux. Fig. 7: aboral view, Fig. 8: oral view. The lunules are large ovoidal and rather close to the posterior test margin.
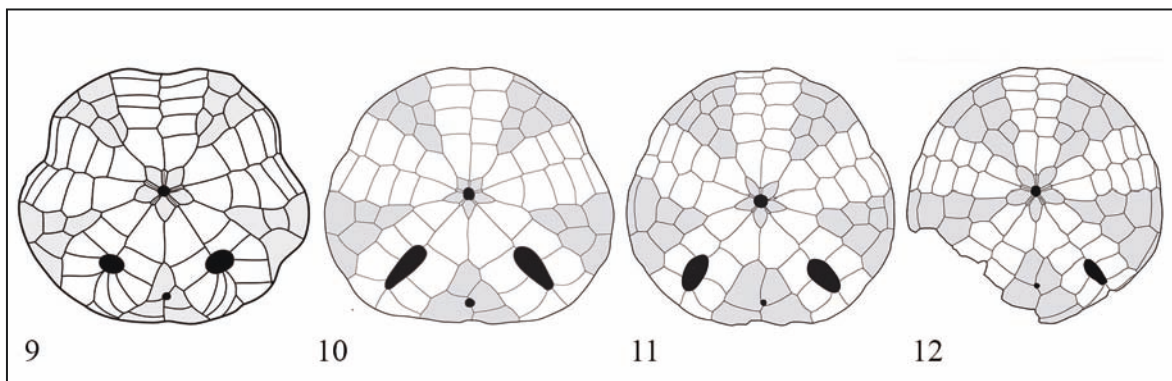

Figures 9–12. Oral plating schemes highlighting the different plate arrangement in the interambulacrum 5 of four genera belonging to the family Astriclypeidae. Fig. 9: *Amphiope bioculata* (UCMP 33846, Miocene, Europe). Fig. 10: *Paraamphiope raimondii* (holotype, MAC.IVM206, Recent, Indonesia). Fig. 11: *Echinodiscus andamanensis* (holotype, PMBC.26346, Recent, Philippines). Fig. 12: *Sculpsitechinus tenuissimus* (neotype, MDL.MAC.IVM207, Recent, Indonesia).

Also *A. lorioli* (Tortonian of St-Félix-de-Lodez; Figs. 31, 32) has a high number of plates (15–16), its petalodium is smaller on the average when compared to the other three species and, as a consequence, the lunules are farther from the posterior test margin.

Within the *A. nuragica* group, in the oral interambulacrum 5 of *A. nuragica* (Chattian-Aquitanian; Figs. 35, 36) there are three and four plates in column a and b, respectively; *Amphiope hollandei* (Burdigalian of Bonifacio, Corse; Figs. 37, 38) has three and three plates; *Amphiope transversifora* (Langhian, Figs. 39, 40) two/three; *Amphiope deydieri* (Serravallian; Figs. 41, 42) two and two, *A. sarasini* (Serravallian-Tortonian; Figs. 43, 44) two and three, though column "a" is only partially visible in the type (but it is well visible in other specimens, e.g. MNHN-F.A.57788-89). As with regard to the whole number of plates in each column of the interambulacrum 5, *A. nuragica* has up to 20 plates;
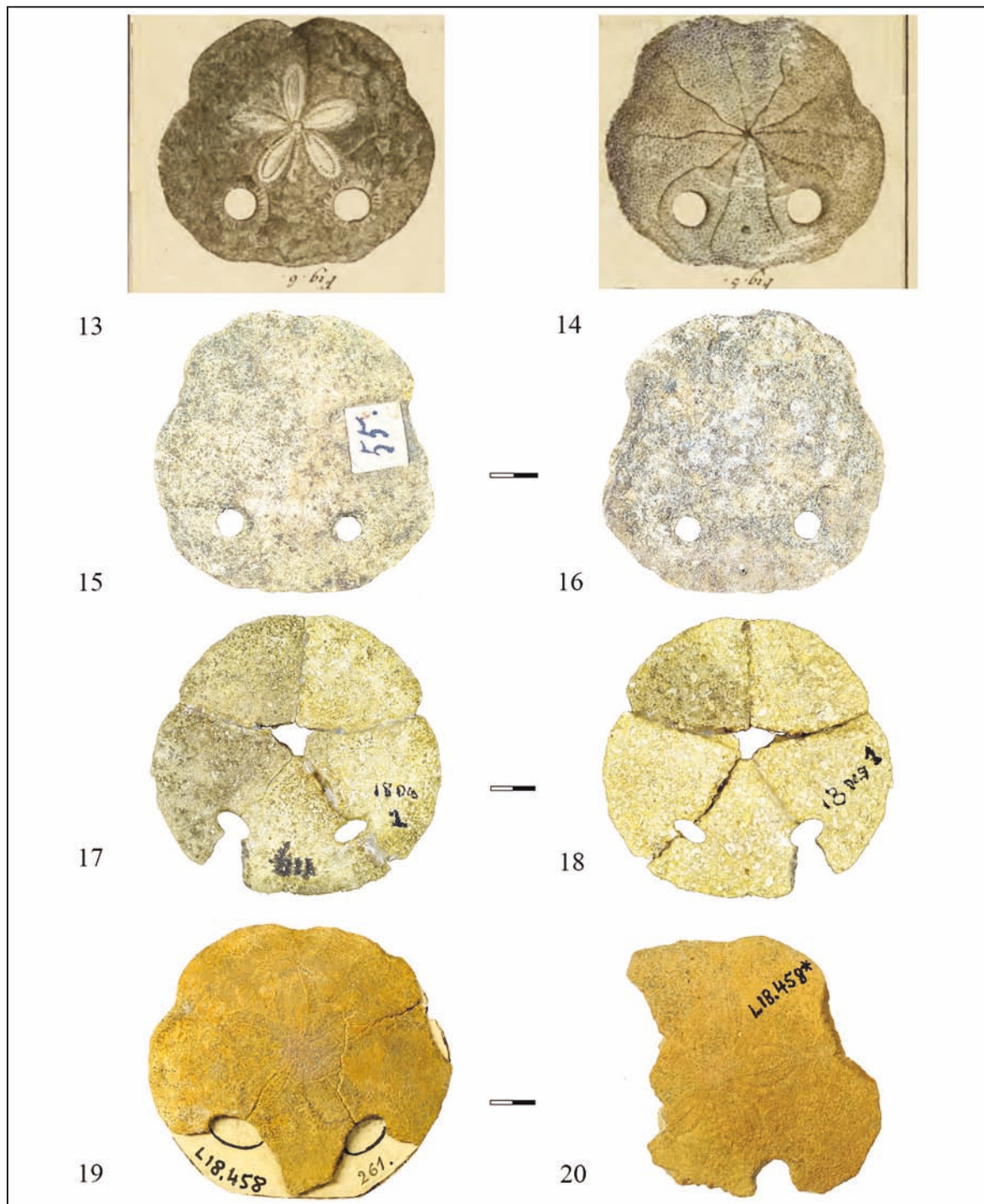
Figures 13–20. *Amphiope bioculata*. Figs. 13, 14: *Scutella bifora* var *c* (foraminibus subrotundis) Lamarck, from an unknown locality; Encyclopédie méthodique (Bruguières, 1791; pl. 147, figs. 5, 6); aboral (Fig. 13) and oral (Fig. 14) views. Figs. 15, 16: type (MHNBx 2014.6.317) of *Scutella bioculata* Var. *A* (foraminibus subrotundis) Des Moulins, 1837, Sure prés Bolléne, Vaucluse (France), aboral (Fig. 15) and oral (Fig. 16) views. Figs. 17, 18: type (MNHBx 2014.6.180.2) of *Scutella bioculata* Var. *B* (foraminibus transversé ovatis) Des Moulins, 1837, Gornac, Gironde (France); aboral (Fig. 17) and oral (Fig. 18) views. Figs. 19, 20: aboral view of the specimens from Suze la Rousse (Drôme) indicated doubtfully as *A.* cfr. *bioculata* by Lambert (1912) (MNHN-F-A L18.458-261; L18.458*); the drawings of missing part of the test and lunule margins (Fig. 19) were originally provided by Lambert.
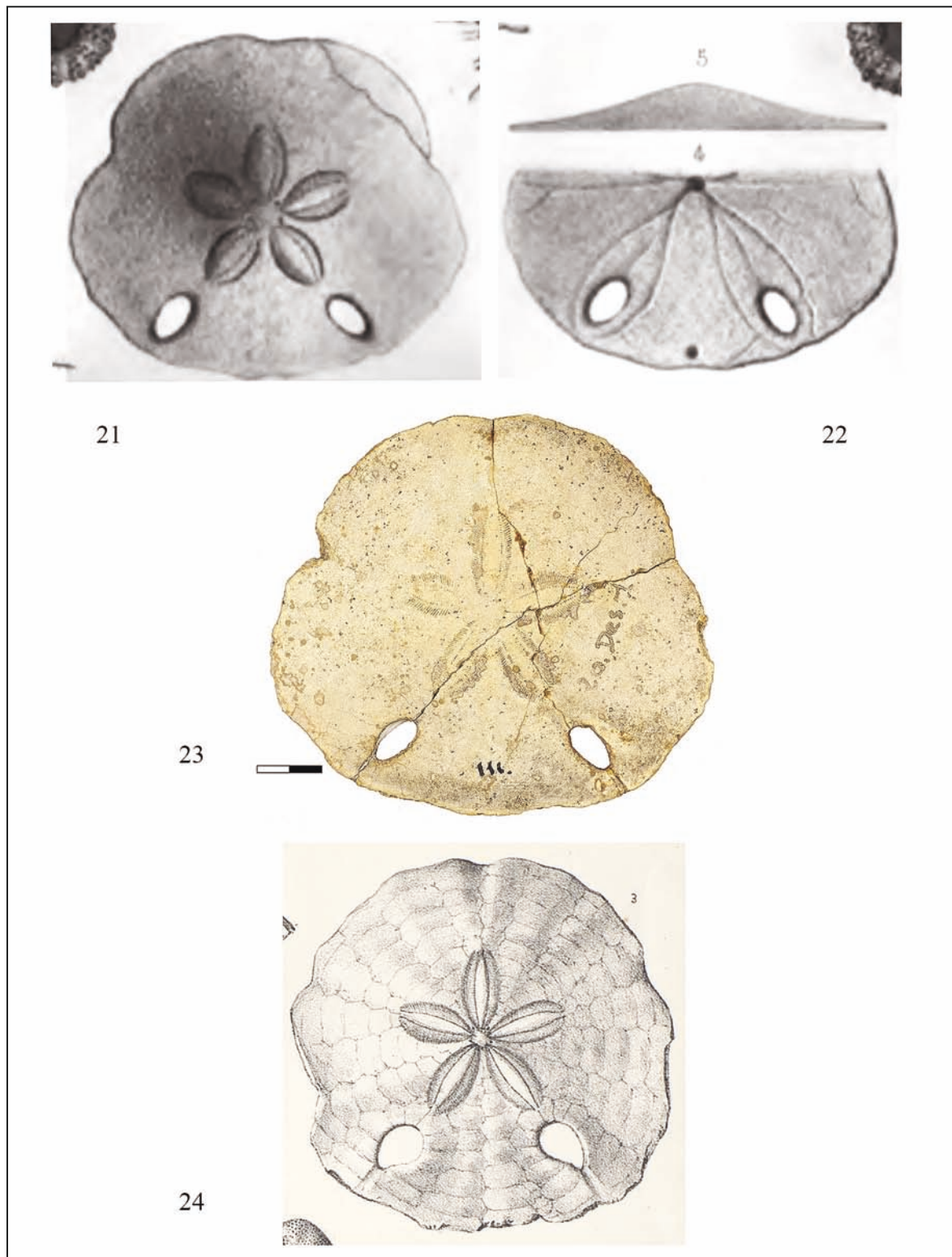
Figures 21–24. *Paraamphiope agassizi*. Figs. 21–22: specimen from unknown locality figured in Cotteau (1864, pl.14, figs. 3–5), aboral (Fig. 21) and lateral (Fig. 22) and oral views; Fig. 23: aboral view of the syntype [MNHNBx (111) 6-194], from S. Albert. Fig. 24: "*Amphiope*" *labriei* Lambert (1928b).
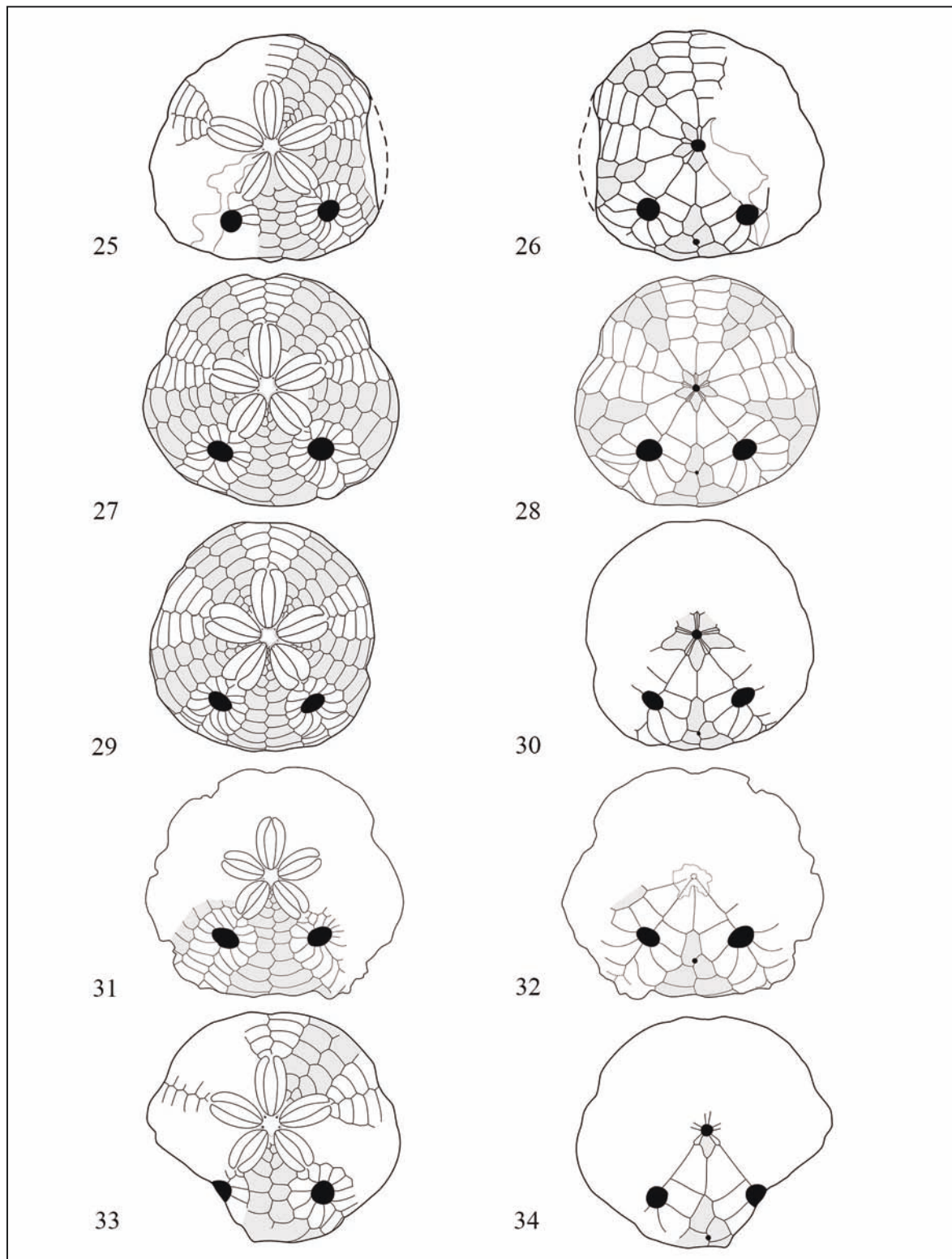
Figures 25–34. Aboral and oral plating schemes of five species belonging to the *A. bioculata* group. Figs. 25, 26: *A. elliptica* from Carry (MNMN-F.A22706-L18.471). Figs. 27, 28: *A. bioculata* from Lespignan (MNHN-F.A 57777). Figs. 29, 30: *A. ovalifora* from Gornac (MNHN-F.A22710-L18.477c). Figs. 31, 32: *A. lorioli* from St-Félix-de-Lodez (MNHN-F.A22707-L 18472Aa). Figs. 33, 34: *A. ludovici* from Blanqui (MNHN-F.J00999-L18473).
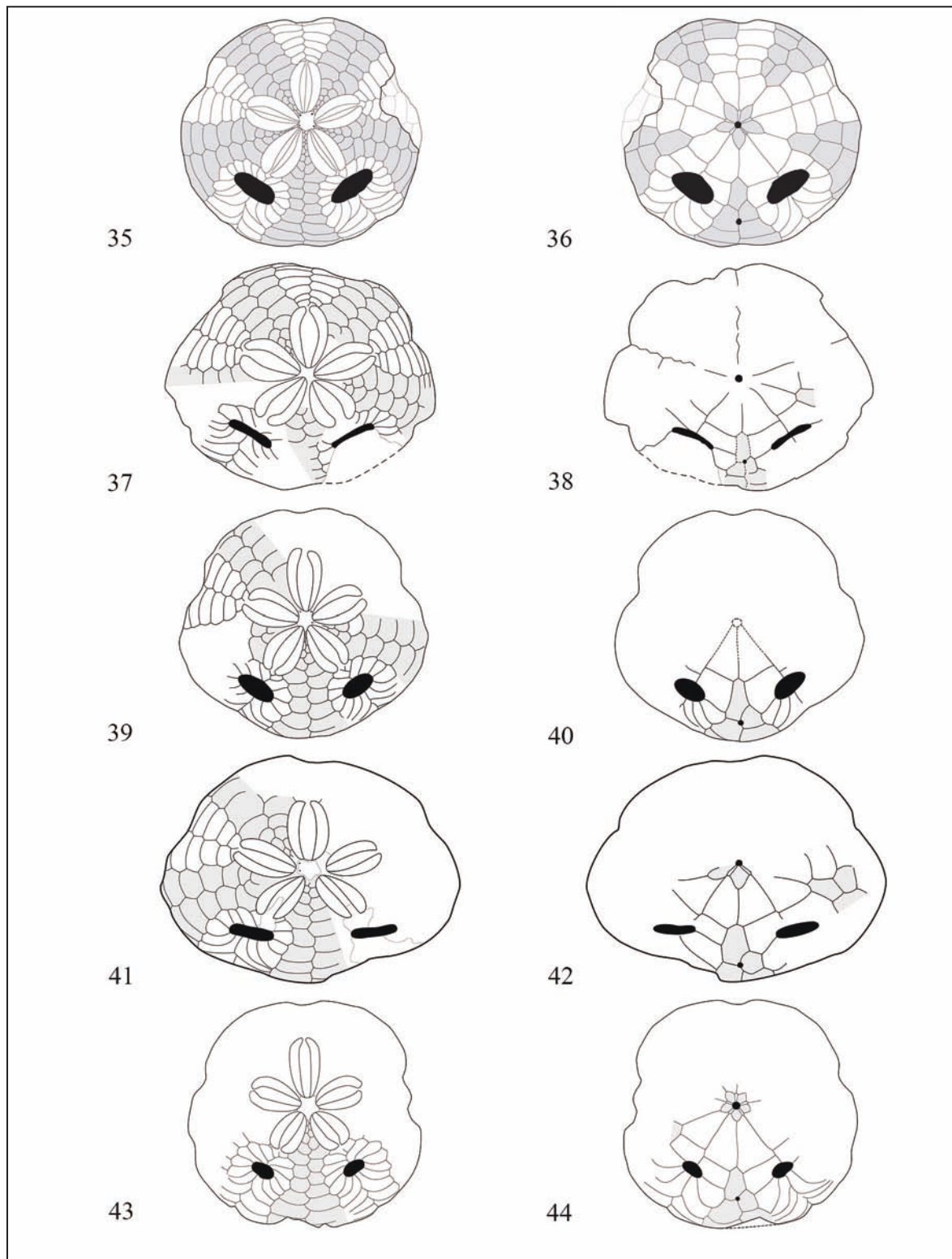
Figures 35–44. Oral and aboral plating schemes of five species belonging to the *A. nuragica* group. Figs. 35, 36: *A. nuragica* from Cuccuru Tuvullau (Sardinia) (MAC.PL1680). Figs. 37, 38: *A. hollandei* from Bonifacio (Corse). Figs. 39, 40: *A. transversifora* from Saint-Paul-Trois-Châteaux (France), syntype. Figs. 41, 42: *A. deydieri* from Cadenet, Vaugine (France) (MNHN-F A22705-L18470a). Figs. 89, 90: *A. sarasini* from Cruzy (France) (MNHN-F J00985.L18480).

A. transversifora and *A. deydieri* 11–12 plates, in *A. sarasini* there are 15 plates on the average, more than expected for a relatively Recent species (Serravallian-Tortonian) (see Stara & Borghi, 2014).

The results of a comparison carried out between the plate structure of *A. bioculata* (Langhian-Serravallian of Lespignan, Figs. 27, 28) and some species from the western basins of France, separated from the type species by large geographical and geological distances, are illustrated in figures 157–164: "*Amphiope*" *agassizi* from the Rupelian of Montségur (Figs. 157, 158) and Pellegrue (Fig. 162, only the oral face is available to study in this specimen), *A. ovalifora* (Aquitanian of Gornac, Figs. 29, 30), *A. romani* n. sp. (Serravallian-Tortonian of Channay-sur-Lathan, Figs. 161, 163) and *A. romani* var. *turonensis* (Serravallian of Oisly; Fig. 164, only the oral face). Although "*Amphiope*" *agassizi* is a more ancient taxon, it clearly differs from *A. bioculata* and *A. ovalifora* by the structure of the ambulacra I and V and the interambulacrum 5, which corresponds to the typical plating scheme of *Paraamphiope* (see Stara & Sanciu, 2014), that is plates 5.a.2 and 5.b.2 more paired than in *Amphiope*, the presence of three to five plates (instead of one or two) separating the petal tips from the correspond-

ing lunules (which are radially elongate) and a lower number of plates in the interambulacrum 5. For this reason this species is here transferred to the genus *Paraamphiope*. *Amphiope romani* n. sp. has the lowest number of plates in this group and shows the typical characters of a relatively recent (Late Miocene) *Amphiope*, that is: plates 5.a.2 and 5.b.2 staggered and the presence of two plates between the petals and the corresponding lunules (at least in the specimen reported in figures 161, 163). It shares with "*A.*" *agassizi* the shape of plate 5.b.2., which is very large and not much elongate, thus similar to *Paraamphiope*. This similarity is even closer when comparing *A. romani turonensis* (Fig. 164) and the specimen of "*A.*" *agassizi* from Pellegrue (Fig. 162). However, the plates surrounding the lunules in "*A.*" *agassizi*, are clearly arranged differently, with respect to those of *A. romani* n. sp. In the former the plates of the column "a" tend to be parallel to each other, as well as those of the column "b". In the later (as in all other *Amphiope*), however, the plates of the columns "a" and "b" around the lunules tend to converge towards the centre of these.

The results of a comparison between "*A.*" *boulei* (Aquitanian of Carry-le-Rouet) and "*A.*" *baquiei* (Tortonian of Cucuron), the sole two species from
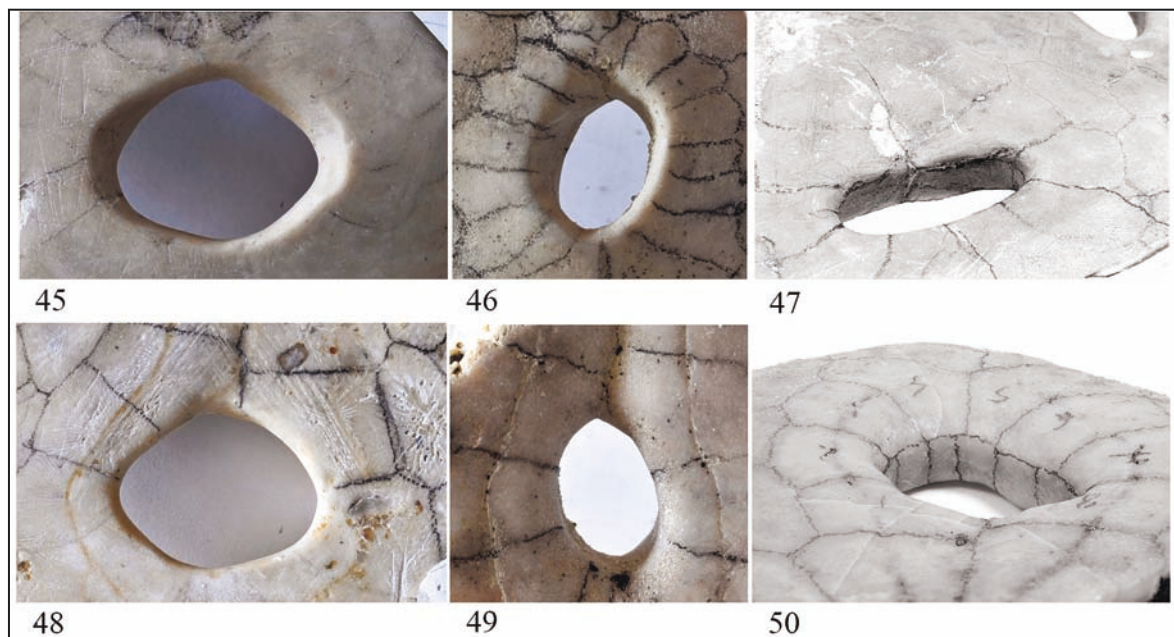
Figures 45–50. Different shapes of lunules in *Amphiope*. Figs. 45, 48: roundish to slightly transversely ovaloid outline, with flared aboral edge. Figs. 46, 49: radially elongate ovaloid lunule, with symmetrical foramen and convex walls. Figs. 47, 50: narrow transversely elongate lunule with symmetrical perpendicular walls.
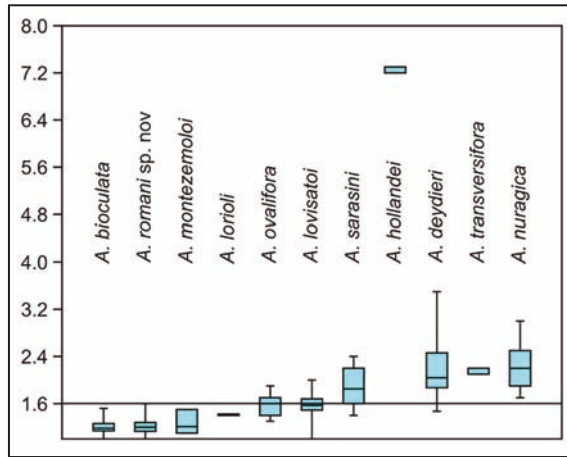
Figure 51. Box-plot showing the mean values and the intra-specific variability range of SI (Shape Index) in different species of *Amphiope*. The horizontal line at SI=1.6 separates two informal groups: The *A. bioculata* group (below the line) and the *A. nuragica* group (above).
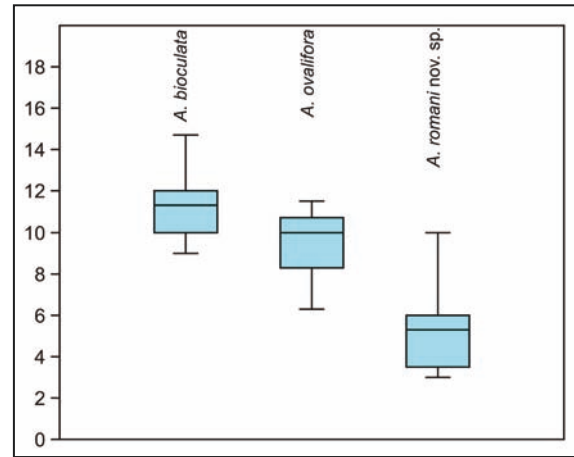

Figure 52. Box-plot comparing the values of L11 (distance of the periproct from the posterior test margin) in three species of *Amphiope*. The number of specimens examined for each species is comparable. Measures are expressed in mm.
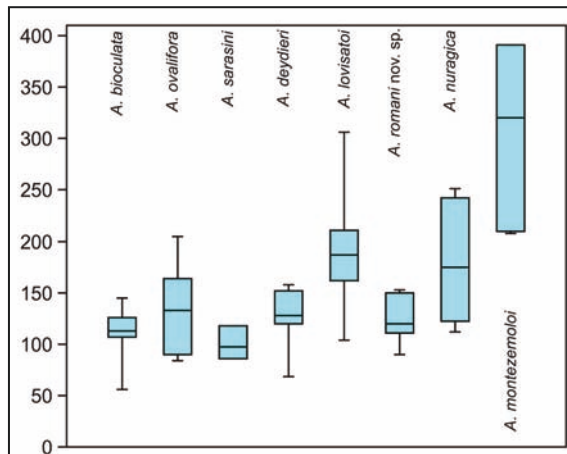
Figure 53. Box-plot showing the intraspecific variability range of WI (Width Index) in different species of *Amphiope*.
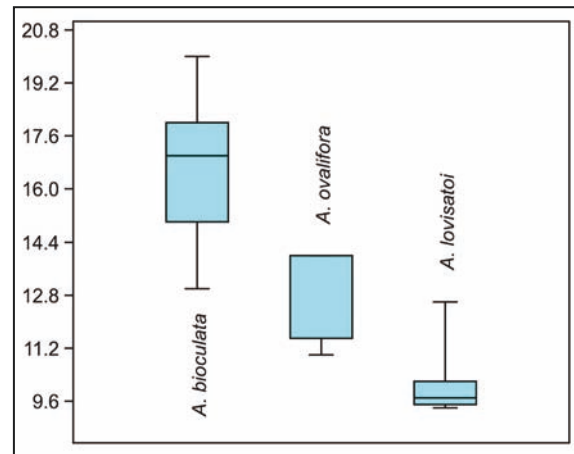
Figure 54. Box-plot comparing the mean value and the variability range of TH (test height), in mm, in some species of *Amphiope* with apparently similar specimens.

the Rhône Basin with radially elongate ovoidal lunules, with *S. tenuissimus* (Recent, Indonesia) and "*A.*" *agassizi* (Rupelian of Pellegrue), are illustrated in figures 55–60. Both "*Amphiope*" *boulei* and "*Amphiope*" *baquiei* have three and four plates, respectively, between the lunules and the tips of the corresponding petals (Figs. 55, 58), and the first post-basicoronal plates in each column of the oral interambulacrum 5 are paired (Figs. 56, 59). But "*A.*" *boulei* matches the typical plating scheme of

Sculpsitechinus with only the plate 5.b.2 in contact with both the correspondent ambulacral plates I.a.2 and V.b.2, as in *S. tenuissimus* (Fig. 57), while "*A.*" *baquiei* matches the plating arrangement of *Para-amphiope* (Fig. 60) just as "*A.*" *agassizi*. In "*A.*" *baquiei* the plates 5.a.2 and 5.b.2 are inversely arranged; however similar cases were observed also in *A. nuragica* (Stara & Borghi, 2014) and do not invalidate the comparison.

Although in the studied specimens the lunules

are roundish or slightly radially elongate, Lambert (1907) based "*A.*" *baquiei* on a specimen from Cucuron with drop-shaped lunules (Fig. 61).

Internal structure. Radiography as a diagnostic tool in *Amphiope* was already used by Dartevelle (1953), who provided an X-ray illustration of *A. neuparthi*. Stara & Borghi (2014) and Stara & Sanciu (2014) described different kinds of internal structures in *Amphiope* and highlighted relevant differences between *Amphiope* and living *Sculpsitechinus*. An example of the correspondence between the test surface and the main internal structures in *Amphiope* is illustrated in Stara & Sanciu (2014: pl. 2, figs. 1–4: *Amphiope* sp. 3 = *A. romani* n. sp.). The main difference is found in the floor of the central hollow, which in *Amphiope* is strengthened internally by radial low ridges, whereas in *Sculpsitechinus* (directly observed only in living specimens) only a net made by thin trabeculae is present on the floor (see Stara & Fois: 2014, pl. 2, figs. 1–8).

The radiographic analysis may highlight relevant differences in species which are otherwise apparently similar on the basis of the external features. This is the case of *A. elliptica*, *A. bioculata* and *A. ovalifora*, whose plating schemes are similar, as seen above. The radiography of *A. elliptica* (Fig. 76) shows a much more complicated buttress system, with several small pillars and small spaces between elements extending towards the periphery of the test; the main central cavity is subcircular; a part of it is filled with coarse sediments since in this case the test is crashed. Also in *A. bioculata* (Fig. 77, MNHN-F A778) the internal buttress system is complicated, but pillars are stronger and more spaced, the internal cavity is much larger, starring to almost pentagonal (which is here considered as a more evolved character). *Amphiope ovalifora* (Fig. 78) differs clearly from the other two species by its central cavity, which is larger and distinctly subpentagonal, the peripheral buttress system, much more developed and densely packed, almost massive, towards the test margin, the macrochannel running along the interambulacrum 4, which is shorter (in this specimen the radial channel leading to the periproct is obliterated by recrystallization processes).

Lunules. Endless discussions occurred between the end of the '800 and the beginning of the '900

about the relevance of lunules in the taxonomy of *Amphiope* and the closely related genera (see L. Agassiz, 1841; Pomel, 1885; Airaghi, 1901; Lambert, 1915a). Recent studies, such as Stara & Borghi (2014) and Stara & Sanciu (2014), demonstrated the validity of this morphological feature as a tool in species distinction when appropriately used.

Amphiope has two ambulacral lunules, rounded or ovoidal transversely elongate, which are surrounded by two groups of plates, one on each face of the test (Fig. 3A). Plates bounding the lunules are more numerous aborally. The suture between the two groups of plates is linear intra-foraminal, that is located on the wall of the foramen connecting the two test faces (Fig. 3A). This feature distinguishes all known astriclypeids from the mellitids, which have a festooned suture (Mooi, 1989, fig. 30). The lunules show a wide intraspecific variability with regard to shape and size and may differ even in the same specimen. The outline may be wide roundish (Fig. 3A), ovaloid and transversely elongate as in *Amphiope* sp. 2 from Bancali, Sardinia (Figs. 45, 48), or sometimes the lunules can vary from roundish to radially elongate, as in *Amphiope* sp. from Capo Frasca, Sardinia (Figs. 46, 49), or narrow as in *A. nuragica* from Cuccuru Tuvullau, Sardinia (Figs. 47, 50). The different kinds of lunules may contribute to separate species within *Amphiope* if the analysis is based on objective tools, that is the Shape Index (SI) and the Width Index (WI). For this purpose, it was necessary to take data from as many specimens as possible, as suggested by Lambert (1912a; 1915a). Also Cottreau (1914) underlined the necessity of examining lunules in large samples and published the illustration of 15 specimens from Saint Christol (actually "Chemin des Tuilières"), to show the variability in the population from that area.

Another peculiar feature, which can help to characterize a species, is the occurrence of a protruding edge on the aboral face, as in *A. palpebrata* (Pomel, 1885: pl. 11, fig. 4).

The values of SI in some species of *Amphiope* are compared graphically in figure 51. Although in some cases the variability range is wide, the modes are well distinct. The dotted line marks the SI=1.6 value, a level proposed by Stara et al. (2015) to separate the two informal groups *A. bioculata* and *A. nuragica*. The data reported in the graphic were taken from 15 specimens of *A. bioculata* from
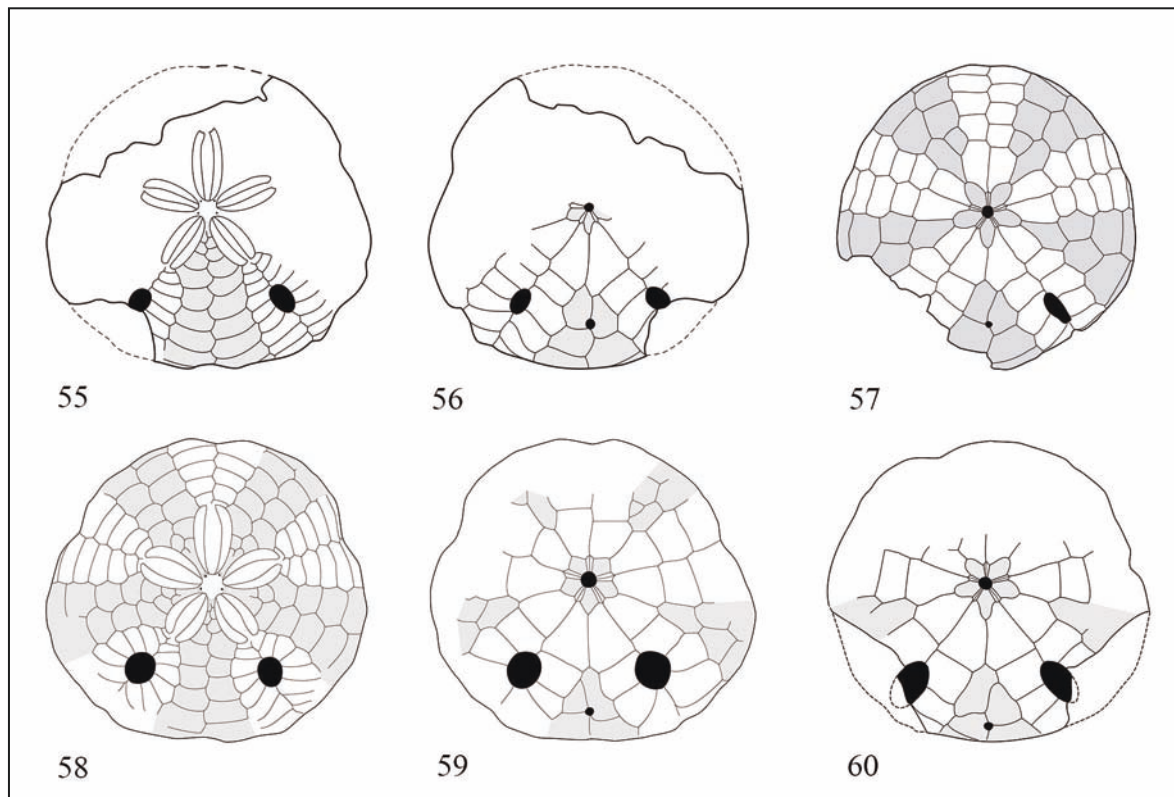
Figures 55–60. Oral and aboral plating schemes of two species belonging to *Paraamphiope* from the Rhône Basin (France) and two belonging to *Sculpsitechinus*. Figs. 55, 56: *Sculpsitechinus boulei* (MNHN-F R62136), Aquitanian of Carry-le-Rouet. Fig. 57: *Sculpsitechinus tenuissimus* (neotype, MAC.IVM207), Recent, Lembeh, North Sulawesi (Indonesia). Figs. 58, 59: *Paraamphiope baquiei* (MNHN-F A22689-L18452), Tortonian of Cucuron. Fig. 60: *Paraamphiope agassizi* (MNHN-F.A22687.L18.450-sn2), Rupelian of Pellegrue.

Figure 61. Original illustration of *Paraamphiope baquiei* from Cucuron,
with drop-shaped and radially elongate lunules.

Nissan les Tuilières and Lespignan, 12 of *A. romani* n. sp. from Channay sur-Lathan; 10 of *A. montezemoloi* from S. Giorgio and Bonnanaro (Sardinia), 13 of *A. ovalifora* from Gornac, 40 of *A. lovisatoi* from Chiaramonti (Sardinia), 10 of *A. deydieri* from the type locality, 20 whole specimens and more than 100 fragments with complete lunules of *A. nuragica*, from Cuccuru Tuvullao (Sardinia). The graphic (Fig. 51) indicates that SI in *A. bioculata* has a low variability range, similar to that in *A. romani* and *A. montezemoloi*.

The box plot of WI, based on the data taken from eight species (Fig. 53), indicates relevant differences. *Amphiope montezemoloi* is distinctly separated from the other species of the *A. bioculata* group, by the wide variability range of WI (200 to almost 400). *Amphiope romani* n. sp. is not well differentiated from *A. bioculata* also based on WI; however, it differs by other characters, e.g. a much lower value of the distance of the periproct to the posterior test margin (L11; Fig. 52).

Amphiope bioculata, *A. ovalifora* and *A. lovisatoi* are closely related species; also the lunules are rather similar on the basis of the mean values of SI and WI.

However, a comparison between these species based on the test height (TH; Fig. 54) indicates that the mean value of TH in *A. bioculata* is higher than that in *A. ovalifora* and, above all, than that in *A. lovisatoi*. This highlights that also the biometric measurements of the test are necessary for a complete and reliable comparison between populations of *Amphiope* from different localities and/or stratigraphical levels.

In the *A. nuragica* group there is a clear difference in the values of WI between *A. sarasini* and *A. nuragica*.

Petalodium. Also the size of the petalodium has a relevant importance in the taxonomy of *Amphiope*. Although in some species it has a large intraspecific variability, such as in *A. romani* n. sp., its range is commonly rather narrow and can be used as a distinctive character at the specific (Fig. 62) or even generic (Fig. 63) level (see also Stara & Sanciu, 2014; Stara et al., 2015), above all when it is associated to other significant characters.

This hypothesis was confirmed by Stara & Fois (2014), on the basis of a sample made of 30 specimens of Recent *S. auritus* from Tulear (Madagascar). A test carried on a sample of *A. ovalifora* from Gornac (Fig. 64) led to the same results, though it was less clear, likely because the sample was smaller (13 specimens) and the range of the test length (58-90 mm) was smaller than that in *S. auritus*. On the other hand, a similar analysis carried on a sample consisting of 30 specimens of *A. lovisatoi* from Sardinia pointed to a different situation (Fig. 65). Notwithstanding that the value of TL almost doubles in the graphic, the size of PL does not significantly increase in proportion to TL: the mean value of PL in proportion to TL remains almost constant during growth.

This indicates the need of carrying similar tests in all species, when significant samples are available to study.

Food grooves. Food grooves are visible only in well preserved specimens. Sometimes it was possible to take only a part of the pathways, consequently some of the schemes reported in figures 70–75 are composite, that is, taken from a group of specimens to provide the typical situation in each species.

In *Amphiope* the main grooves are finer (Figs. 70–73) than those present in *Paraamphiope* and secondary grooves branch off only distally (with the only exception of *A. sarasini* - Fig. 75). In *Paraamphiope* (Fig. 74) and less distinctly also in *A. sarasini*) fine and short secondary grooves branch off also along the median part of the main grooves, and the two main bifurcations are much more strongly branched distally. Intraspecific variability is present in *Amphiope*: the food grooves system develops by an increasing degree of secondary branchings from *A. bioculata*, to *A. ovalifora*, *A. lovisatoi* and finally *A. sarasini*. *Amphiope nuragica* (Fig. 71) shows the simplest scheme so far known in *Amphiope*, since the distal secondary grooves are, on the whole, less numerous and shorter than in *A. bioculata*.

On the whole, the present study highlighted the necessity of analysing all these characters when comparing populations from different localities, since apparently similar forms can be separated at the specific, sometimes even at the generic level, if one or more of these features turn out to differ significantly.
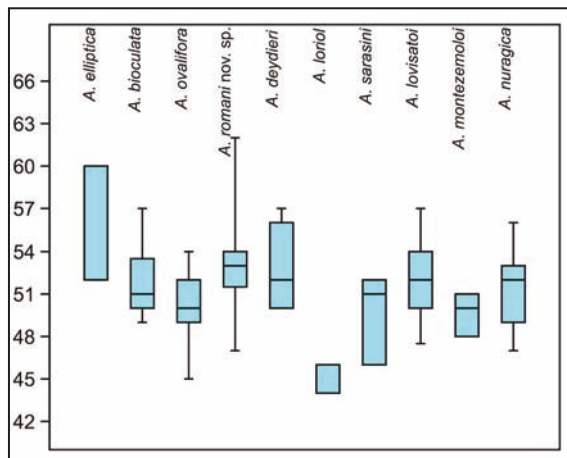
Figure 62. Box-plot showing the mean values and the variability ranges of PL (size of the petalodium) in ten species of *Amphiope*.
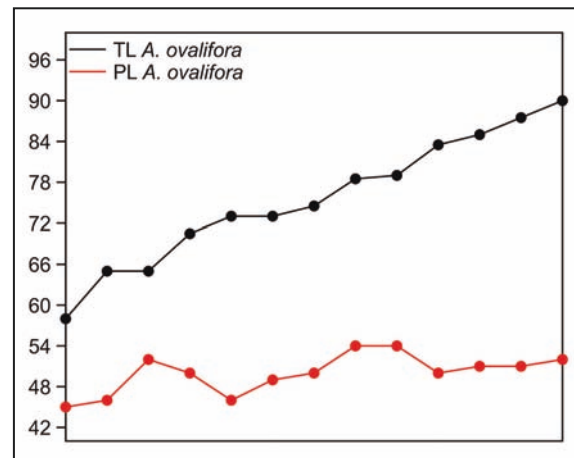

Figure 64. *Amphiope ovalifora*, topotypic sample from Gornac: graphic showing the variation of PL (size of the petalodium) during growth.
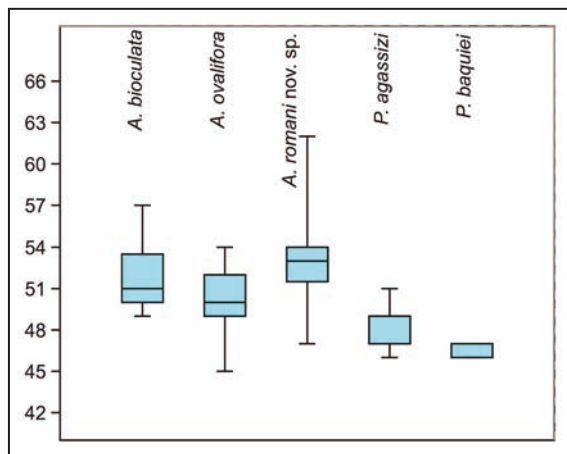

Figure 63. Box-plot comparing the mean values and the variability ranges of PL (size of the petalodium) in three species of *Amphiope* and two of *Paraamphiope*.
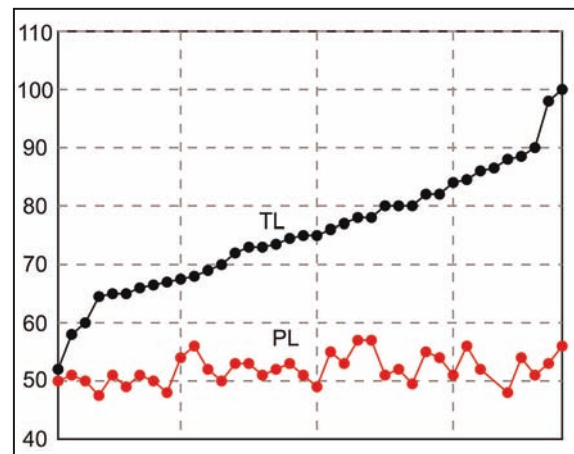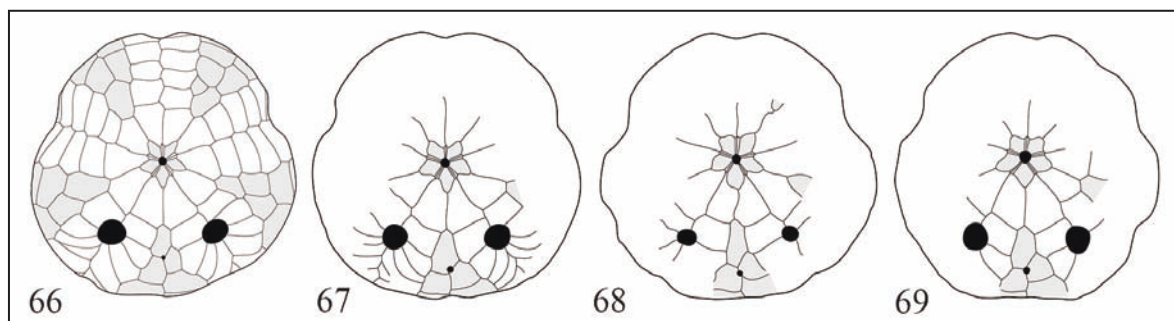

Figure 65. *Amphiope lovisatoi*, topotypic sample from Chiaramonti (Sardinia): graphic showing the variation of PL (size of the petalodium) during growth.

Figures 66–69. *Amphiope bioculata*, topotypic specimens from Lespignan-Nissan (MNHN-F): oral plating schemes showing the variability in the plate shape and arrangement in the interambulacrum 5 and in the position of the periproct. Fig. 66: specimen which will be proposed as neotype (A 57777). Fig. 67: specimen A 57778. Fig. 68: A.22701.L18464f. Fig. 69: A. 22701.L18464h.

Species of Amphiope represented by scanty material

A part of the species examined are represented by scanty or badly preserved material. They are briefly discussed in the following. Only a few of them are here accepted as valid species.

Amphiope perspicillata Agassiz, 1841 was based on a sole badly preserved specimen from "*terrains tertiaire*" of Rennes (northwestern France), without the indication of the exact finding locality. A doubtful plating scheme was reported in the original illustration. The specimen is wanting and also Lambert (1907, 1912a) was not able to trace it. For these reasons *A. perspicillata* is here considered as *species inquirenda*.

Amphiope styriaca Hoernes, 1883, from Seggaubert, Styria (Austria). A plating scheme was provided by Kroh (2005), who synonymised it with *A. bioculata*. However, the sole known specimen is incomplete and lacks a large part of the posterior margin in the interambulacrum 5, thus preventing reliable comparison with the other known species. Therefore, *A. styriaca* is considered as *nomen dubium*.

Amphiope palpebrata Pomel, 1887. Only one out of three specimens from the Cartennian (Burdigalian?) of Djebel Djambeïda (Cherchell, Algeria) was figured by Pomel (1887: pl. 11, figs. 1–4). However, Pomel admitted that the illustration did not correspond to the real preservation of that specimen. No plating scheme can be taken from the original illustration. The lunules are different from those present in the other species which were known at that time. A specimen (MNHN-F. L18.478) collected by Cotteau et al. (1891) from the type-locality, provided us with a partial plating scheme (Figs. 155, 156) and a radiography (Fig. 87), which are different from those in the other species known at that time. For this reason, we temporarily maintain *A. palpebrata* as valid. Studies are in progress to revise the Algerian species of *Amphiope* (personal communication, Mohamed Belkercha, June 2016).

Amphiope depressa Pomel, 1887. The illustration (Pomel, 1887: pl. XII, figs. 1a-c) of the sole specimen known from the "Helvetian" (Langhian? Serravallian) of Aïn-el-Arba (Mléta, Orano, Algeria) was incomplete since a part of the posterior margin was lacking. It is not possible to take a plating scheme from that illustration. The specimen is very close to *A. sarasini* from the Tortonian of the Rhône Basin, however we maintain here *A. depressa* as valid and separated from *A. sarasini*, since the lunules have a peculiar shape and the values SI and WI are almost the lowest in the genus *Amphiope*. Furthermore, according to Pomel (1887), *A. depressa* has 5 genital pores; if this character will be confirmed by new findings, the systematic of this taxon should be revised. Another research group is trying to find out new material to revise this species (personal communication, Mohamed Belkercha, June 2016).

Amphiope villei Pomel, 1887 and *A. personata* Pomel, 1887 were not originally illustrated and the descriptions did not allow a reliable comparison with the other known species of *Amphiope*. Also the repository of the type-material was not indicated. A part of the Pomel collection was bought by a private collector who finally gave it to the Metropolitan Museum of New York (Cleevely, 1986). Another part was obtained by the NHMUK (Woodward, 1904); however, no specimens of *Amphiope* are present among those specimens (personal communication, Bajo Campos, February 2016). Therefore, the type material is wanting. Pomel (1887) indicated the respective type localities in the original descriptions, however Cotteau et al. (1891) were not able to find out any specimen from there, and it was not possible to trace the localities since the old toponyms are actually unknown. For these reasons these two species are here considered as *species inquirenda*.

Amphiope neuparthi de Loriol, 1905, from the Burdigalian of Luanda (Angola). The X-ray photo provided by Dartevelle (1953) of this species shows a peculiar internal structure when compared with the other species of the *A. bioculata* group, in particular with *A. montezemoloi* which shares large roundish lunules. Additionally, a characteristic notch on the posterior margin of the test is present in the original illustration. For these reasons *A. neuparthi* is here maintained as a valid species. A research is in progress based on the type material of this species (personal communication Pedro Pereira, July 2016), which was not available to the present study.

Amphiope dessii Cotteau, 1895 and *A. calvii* Lovisato, 1914. The type localities, represented by ancient toponyms, have been traced on old maps, but
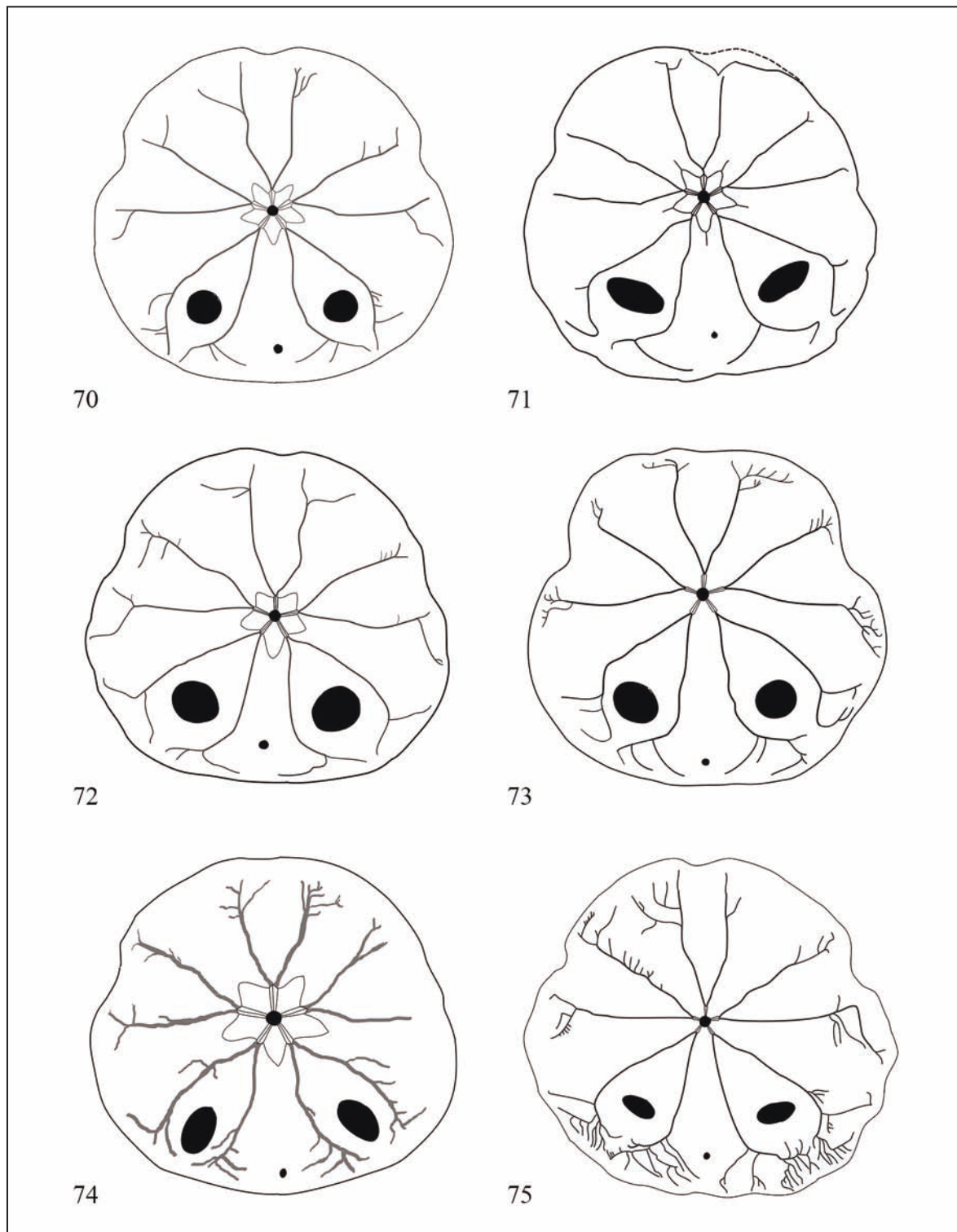
Figures 70–75. Schemes of the food groves in species of *Amphiope* and *Paraamphiope*. Fig. 70: *A. bioculata* (MNHN- F.A 57777), Langhian-Serravallian of Lespignan. Fig. 71: *A. nuragica* (MAC PL1590). Cattian-Aquitanian of Cuccuru Tuvullau, Sardinia. Fig. 72: *A. ovalifora* (MNHN-F A 22710-L 18.447f), Aquitanian (Burdigalian?) of Gornac. Fig. 73: *A. lovisatoi* (MAC.PL2014), late Burdigalian of Chiaramonti (Sardinia). Fig. 74: *P. agassizi*, Rupelian of Pellegrue. Fig. 75: *A. sarasini* MNHN-F.A.57788 , Tortonian of Cruzy.

the original outcrops disappeared due to the enlargement of the village of Nurri (Cagliari Province), in the case of *A. dessii*, and of the village of Ploaghe (Sassari Province), in the case of *A. calvii*. The original description and illustration do not provide characters for a reliable comparison and point to forms close to *A. nuragica* and *A. lovisatoi*, respectively. For these reasons *A. dessii* and *A. calvii* are here considered as *species inquirendae*.

Amphiope bioculata philodonax was proposed by Lambert (1927: p. 112) for the specimen MHNBx 2014.6.189, which was labeled by des Moulins as "*type of* Scutella bioculata *var.* A *from Saucats, Gironde, France*". This specimen is heavily encrusted and does not provide sufficient data for a reliable classification. For these reasons *A. bioculata philodonax* is here considered as *subspecies inquirenda*.

Another variety, *A. bioculata* var. *aequipetala* Lambert, 1927 (Lambert, 1927: 113), was based on a single specimen with rounded lunules from "*Gers*". In this case the repository of the type material was not provided and the stratigraphic position is uncertain. Since the characters described to separate them were unclear, *aequipetala* is here considered as subspecies *inquirenda*.

Amphiope bioculata var. *drunensis* Lambert, 1915. Only two specimens (syntypes: MNHN-F. A22379-L18.468 and 18.457; Figs. 7, 8) from the Langhian of St.-Paul-Trois-Châteaux (Drôme) were available to study and field research at the same locality by one of us (PS) did not provide new material. Those specimens could be easily included within the morphological variability range of the type-series of *A. bioculata* from Hérault, with the exception of the lunules, which are much more ovalised. On the basis of this last feature this variety is here maintained as valid subspecies.

A group of four species earlier attributed to *Amphiope* were described from the Miocene of Libya and Egypt: *A. truncata* Fuchs, 1882, *A. arcuata* Fuchs, 1882, both from Oasis Siouah (Egypt), *A. fuchsi* Fourtau,1901 and *A. miocenica* Ali, 1998, by Fourtau (1899; 1900; 1920); Gregory (1898; 1911); Ali (1998; 2014). No plating schemes and other distinctive characters, necessary for a reliable attribution, were provided in the original descriptions.

Fourtau (1901) renamed *A. truncata* as *A. fucshi*, affirming that the denomination *A. truncata* given by Fuchs in 1882 was pre-occupied by *Lobophora*

truncata L. Agassiz, 1841, and that *Amphiope* and *Lobophora* have been subsequently reunited by Agassiz & Desor (1847). However, *L. truncata* was maintained into the genus *Lobophora* by Agassiz & Desor (1847: 78); additionally, it was represented by a very different specimen, which subsequently turned out (Forteau, 1901) to belong to the genus *Echinodiscus* as claimed by A. Agassiz (1872-74) in his revision of the genus. Consequently *A. fuchsi* is a junior synonym of *A. truncata*. Indeed, Cottreau (1914) considered *A. arcuata* and *A. fuchsi*, from the Middle Miocene of Egypt, as junior synonyms of *A. truncata*.

The type specimen of *Amphiope miocenica* Ali, 1998, from the Langhian-Serravallian of Siwa (Egypt), is very similar to the two specimens of *Paraamphiope arcuata* (NHMUK E76161-2) in Stara & Sanciu (2014, pl. 20). However, it has a larger petalodium (PL= 52% TL, against 42–47% TL in *P. arcuata* and in *A. truncata*), a larger space separates the petal tips from the corresponding lunules and the food grooves were described as strongly branched by Ali (1998). For these reasons that specimen probably does not belong to the genus *Amphiope*. Recently, Ali (2014) compared the species *miocenica*, *fuchsi* and *arcuata* using a consistent morphometric data set; however, he did not provide plating schemes for them.

The taxonomic position of *Amphiope arcuata* has been recently discussed by Stara & Sanciu (2014), who transferred it to the genus *Paraamphiope* based on the plating schemes of five specimens examined at the NHMUK (E76161-2, E76164-6). The illustration provided by Fuchs of the type of this species (1882: pl. 11, figs. 4-6) corresponds to the specimens examined at the NHMUK.

On the basis of the data published so far, the species *truncata* and *miocenica* are here considered as separate species. However, since no plating schemes were provided in the original descriptions, their generic placement remains uncertain, although the attribution to the genus *Paraamphiope* looks probable.

The scheme of the oral plate arrangement is needed for the generic attribution when dealing with species belonging to the genera *Paraamphiope* and *Sculpsitechinus* (see also Stara & Sanciu, 2014), since the sole aboral plate arrangement is not sufficient for a reliable diagnosis.
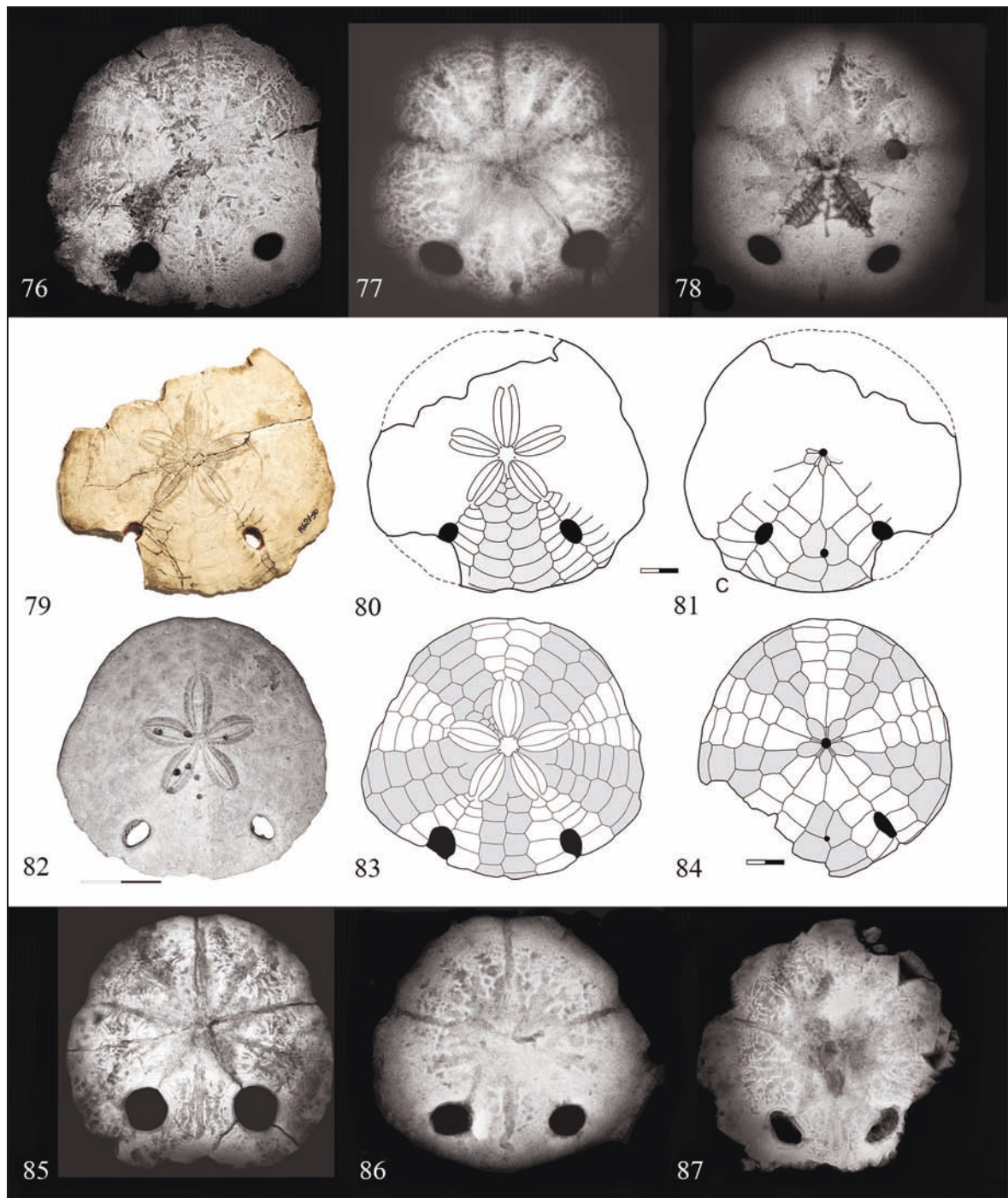
Figures 76–78. X-ray photographs of three species of *Amphiope*. Fig. 76: *A. elliptica* (MNHN-F A22706-L18.471), from Carry. Fig. 77: *A. bioculata* (MNHN-F A 57778), Lespignan. Fig. 78: *A. ovalifora* (MNHN-F A 22710-L 18.447m), Gornac. Figures 79–84. *Sculpsitechinus boulei* (MNHN-F R62136). Fig. 79: aboral view. Figs. 80–81: aboral and adoral plating schemes, respectively. *Paraamphiope arcuata*: Fig. 82: aboral view, Fig. 83: aboral plating scheme of the specimens NHMUK.E76162 and NHMUK.E76164, respectively. The presence of at least three plates or more between the petal tips and the respective lunules excludes the attribution of these specimens to the genus *Amphiope*, however this character alone cannot safely distinguish between *Sculpsitechinus* and *Paraamphiope*. Fig. 84: adoral view of *S. tenuisssimus* (neotype, MAC.IVM207), Recent, Lembeh, North Sulawesi, Indonesia) to compare the adoral view of *S. boulei*. Figures 85–87. X-ray photographs. Fig. 85: *A. montezemoloi* (MACPL1677), Ardara (Sardinia). Fig. 86: *A. lorioli* (MNHN-F A22707-L 18472Aa). Fig. 87: *A. palpebrata* (MNHN-F. L18.478), Djebel Djambeïda (Cherchell, Algeria).

Amphiope laubei Lambert, 1912. Lambert (1912) affirmed that the specimen from Austria attributed by Laube (1871) to *A. elliptica* did not belong to that species and instituted for that specimen a new species, *A. laubei*. After Cottreau (1914) that specimen was deformed and the periproct was not visible, and was likely attributable to *A. bioculata* from Hérault. Kroh (2005), when studying the specimen from Niederkreuzstetten (NHMW 11849/0023/0039) figured in Laube (1871: pl. 16, fig. 5), suggested that the original illustration was likely a composition of a number of different specimens and synonymised it with *A. bioculata*. For these reasons and the bad preservation of the type material, *A. laubei* is here considered as *nomen dubium*.

Amphiope doderleini (Lambert et Thiéry, 1921). After Kroh (2015), it is a junior synonym of *Echinodiscus truncatus* Agassiz (1841), by incorrect original spelling (ICZN 4th ed. Art. 32.5.1., inadvertent error). See also Stara & Sanciu (2014).

Amphiope labriei Lambert, 1927. This species was based on a sole specimen with the posterior edge damaged; the aboral plating scheme (Fig. 24) was subsequently provided by Lambert (1928). The finding locality was not visited by Lambert, who admitted that the stratigraphic position of that specimen was unknown and only tentatively was attributed to the "Helvetian". That specimen was considered by Lambert (1928) as similar to *A. baquiei*, by the lunule shape and the plating arrangement

around them. No specimens attributed to this species have been found in French Institutions. For these reasons *A. labriei* is here considered as *species inquirenda*.

Amphiope dallonii Lambert, 1931. Lambert (1931) received a specimen of *Amphiope* from the Helvetian of Thouanet (Algeria) by M. Dalloni. Given that the specimen was very deformed and with surfaces indented by sandstone clasts, he admitted that it was possible to provide only an incomplete diagnosis (in our opinion, not enough to create a species). Since no repository indication has been reported, we consider this species as *species inquirenda*.

Amphiope bioculata var. *pelatensis* Fabre, 1933, was based on a number of middle-sized specimens with rounded lunules from Pelat, an unknown locality in the Municipality of Condom (Gers). No illustration and repository indication were provided. The sample shows a large morphological variability and the biometric data provided in the original description do not allow a reliable discussion. A nearby locality (Montréal, Gers), was indicated by Lambert (1915) as the type-area for *A. bioculata turonensis*.

Amphiope bioculata var. *bentivegnae* Desio, 1934 was described from the Middle Miocene of Libya. No illustration and indication about the repository of the type material was provided for both these subspecies. These three subspecies are here considered as *subspecies inquirendae*.

Valid species included in the genus **Amphiope**

As a result of this research 17 valid species and a subspecies are here assigned to the genus *Amphiope* (see the list in the systematic chapter), including also those discussed in Stara & Borghi (2014).

A new species, *A. romani* nov. sp., is here instituted on the basis of a group of specimens from the Serravallian-Tortonian of Channay-sur-Lathan, Touraine (France), since the combination of its morphological features distinguishes it from the other known taxa.

Species of Amphiope transferred to other genera

Three species earlier assigned to *Amphiope* have been transferred to the genus *Paraamphiope* Stara
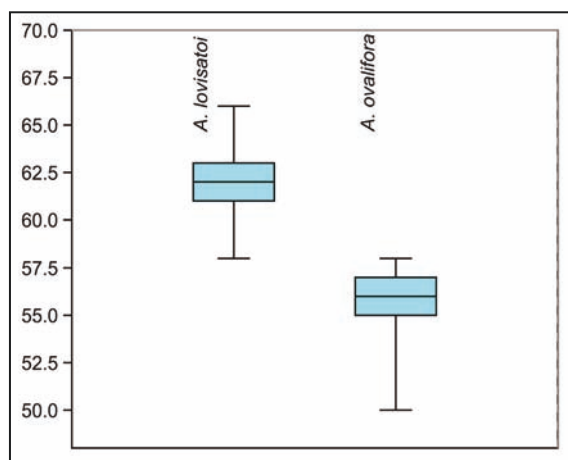

Figure 88. Box-plot comparing the mean values and the variability ranges of L4 (position of the apical disc), expressed as % TL, in *A. lovisatoi* (N30) and *A. ovalifora* (N15).

& Sanciu, 2014, since they have radially elongate lunules separated by at least three-four plates from the posterior petals tips, small or rather small petalodium, plates 5.b.2 and 5.a.2 paired or almost paired and strongly branched oral food grooves:

P. agassizi (Des Moulins in Cotteau, 1864)

P. cherichirensis (Thomas & Gauthier in Gauthier, 1889)

P. baquiei (Lambert, 1907).

Also *A. arcuata* Fuchs, 1882 was placed into the genus *Paraamphiope*, by Stara & Sanciu (2014). Another species earlier attributed to *Amphiope*, with very branched food grooves and axial lunules separated from the posterior petals by four plates and with the plating that matches that of *Sculpsitechinus tenuissimus*, has been assigned to the genus *Sculpsitechinus* Stara et Sanciu, 2014: *S. boulei* (Cottreau, 1914).

Intermediate cases between Amphiope *and the closely related genera*

The distinctive characters separating *Amphiope*, *Paraamphiope*, *Sculpsitechinus* and *Echinodiscus* were stated in Stara & Sanciu (2014). However, some intermediate cases have been encountered in this study and are described in the following.

All the species with radially elongate lunules examined in this study and in Stara & Sanciu (2014) belong to the genera *Paraamphiope*, *Sculpsitech-*

inus or *Echinodiscus*. However this kind of lunule may be rarely present also in *Amphiope* (Figs. 46, 49). They must be considered as border cases within the variability range of a population with mainly roundish or transversely elongate lunules. The occasional occurrence of radial elongate lunules was observed also by Philippe (1998a) when studying the populations of *Amphiope* from the Rhône Basin; unluckily, it was not possible for us to visit the Museum des Confluences of Lyon, where those specimens are stored.

As underlined above, the plate structure of the test is one of the most useful tools for a reliable classification at the generic level. However, also in this case exceptions have been observed. In some specimens of *A. romani* n. sp. from Touraine (Figs. 161, 163) the structure of the interambulacrum 5 and the number of plates separating the petals from the respective lunules are similar to those in *Paraamphiope raimondii* (Fig. 10), and the oral interambulacral plate 5.b.2 is sometimes wide and short, thus resembling the typical shape in *Paraamphiope*, although the structure of the plates around the lunules and the interior floor of the central hollow are typical of all other *Amphiope* species.

Also in a few specimens of *A. sarasini* (e.g. the syntype under study, Fig. 43) there are three plates between the petal tips and the corresponding lunules and the food grooves are strongly branched, thus resembling those in *Paraamphiope*; however they
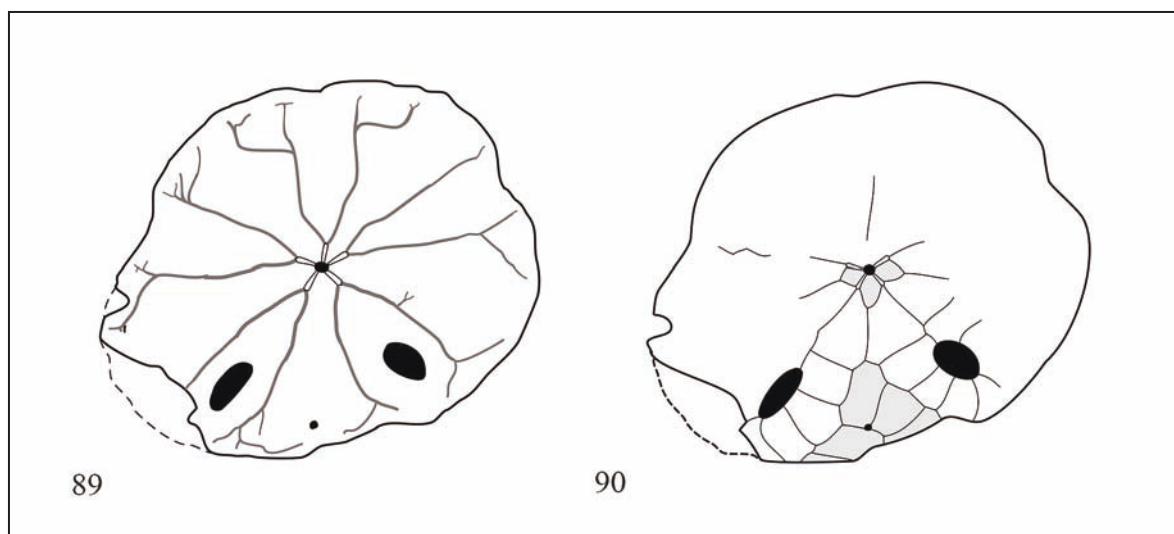
Figure 89, 90. *Paraamphiope cherichirensis*: food grooves and adoral plating in MNHN-F.R67287, Bou Golrine (Libya).

have the interambulacral plate 5.b.2 much staggered with respect to 5.a.2 and clearly transversely elongate lunules, which are typical characters of *Amphiope*.

In the studied specimen of *Sculpsitechinus boulei* (Aquitanian) the plating scheme of the oral interambulacrum 5 (Fig. 56) corresponds to that present in the Recent *S. tenuissimus* from Lembeh (Indonesia; Fig. 57, Fig. 84); this also applies to the number of plates separating the petal tips from lunules (Stara & Sanciu, 2014: fig. 21A and pl. 22, fig. 3). Instead, in some specimens of the Recent *Sculpsitechinus* sp. 1 from the Philippines (Stara & Sanciu, 2014: pl. 11, fig. 3) and from Iran (Fatemi et al., 2016: pl.2 B, D) only the oral interambulacral plate 5.b.2 is in contact with the ambulacral plates I.a.2 and V.b.2, as in *Amphiope* and *Paraamphiope*. On the other hand, this species has always a high number of plates in the oral interambulacrum 5, ranging from three to four plates in column "a" and three to five in column "b", as in the typical *Sculpsitechinus*.

All these intermediate cases underline the need of analysing all the features present in a population, since a sole distinctive character could not provide alone a safe generic attribution if not supported by other significant features.

SYSTEMATICS

Family *Astriclypeidae* Stefanini, 1912

Genera included: *Echinodiscus* Leske, 1778; *Astriclypeus* Verril, 1867; *Amphiope* L. Agassiz, 1840; *Paraamphiope* Stara et Sanciu, 2014; *Sculpsitechinus* Stara et Sanciu, 2014

Genus *Amphiope* L. Agassiz, 1840

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

EMENDED DIAGNOSIS. Partially modified from Smith & Kroh (2011) and Stara & Sanciu (2014). Test low with the highest point corresponding to its centre or slightly anterior of it. Margin thin. Oral side flat to slightly concave. Internal test support well developed, consisting of pillars and walls crossed by cavities; one of them extends along the interambulacrum 5 and terminates into the periproct; towards the ambitus, sometime the peripheral ballast system becomes denser, even massive, and crossed by microcanals. Apical disc monobasal, subcentral or slightly anterior of centre, with four small gonopores. Ambulacra and interambulacra similar in size at ambitus. Petals well developed; short (about half radial length of test), almost closed distally. All five petals similar in length; sometimes the frontal petal slightly longer than the others. Petalodium small to middle sized (40,5–62% TL; see Stara et al., 2015), with ß angle about 88°. Oral interambulacra narrower than the ambulacra, even at their widest point. Oral interambulacra 1, 4 and 5 always with only the first post-basicoronal plate in contact with the first pair of ambulacral plates; the interambulacral zones are separated by a couple of enlarged first post-basicoronal ambulacral plates. Oral interambulacra 2 and 3 may have only the plate 5.2.b, or both plates 5.2.b and 5.2.a, in contact with the two adjacent ambulacral postbasicoronals.

Basicoronal circlet pentastellate with interambulacral plates forming the points. Two to five post- basicoronal plates per column present in the interambulacrum 5 adorally. Two rounded or transversely elongate lunules are present in the posterior ambulacra; they are separated from the tips of the corresponding petals by only one-two (rarely three) couples of plates. 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. Food grooves are rather thin and develop by a simple scheme; the main trunk bifurcates a short after the edge of the basicoronal plate into two main grooves which extend towards the test margin, but not reaching it; distal branches present, whereas almost no secondary grooves branch off the middle part of the main grooves. Posterior pair of the food grooves running around the lunules and behind the periproct. Tuberculation dense, made of very small, perforate and crenulate tubercles. Tubercles are larger on the oral face, with the exception of those located along the food grooves.

DISTRIBUTION. From Oligo-Miocene to Pliocene. Central and Southern Europe, North Africa, Middle East, India, Angola (Smith & Kroh, 2011).

Species and subspecies included:

Amphiope bioculata (Des Moulins, 1837), Langhian-Serravallian, Hérault (France)

A. bioculata var. *drunensis* Lambert, 1915, Langhian, Drôme (France)

A. depressa Pomel, 1887, Miocene, Algeria

A. deydieri Lambert, 1912, Langhian-Serravallian, Vaucluse (France)

A. elliptica Desor, 1847, late Aquitanian, Bouche du Rhône (France)

A. hollandei Cotteau, 1877, Burdigalian, Corsica (France)

A. lorioli Lambert, 1907, Tortonian, Hérault (France)

A. lovisatoi Cotteau, 1895, late Burdigalian, Sardinia (Italy)

A. ludovici Lambert, 1912, Tortonian, Vaucluse (France)

A. montezemoloi Lovisato, 1911, late Burdigalian-early Langhian, Sardinia (Italy)

A. neuparthi de Loriol, 1905, Miocene, Luanda (Angola)

A. nuragica (Comaschi Caria, 1955), late Chattian-early Aquitanian, Sardinia (Italy)

A. ovalifora Des Moulins in Fallot, 1903, late Aquitanian, Gironde (France)

A. pallavicinoi Lovisato, 1914, late Burdigalian, Sardinia (Italy)

A. palpebrata Pomel, 1887, Miocene, Algeria

A. romani n. sp., Serravallian-Tortonian, Touraine (France)

A. romani turonensis (Lambert, 1915), Serravallian-Tortonian,Touraine (France).

A. sarasini Lambert, 1907, Serravallian -Tortonian, Hérault (France)

A. tipasensis (Aymé & Roman, 1954), Pliocene, Algeria

A. transversifora Lambert, 1910, Langhian, Drôme (France)

Amphiope bioculata group (sensu Stara et al., 2015)

This informal group includes species with rounded or transverse elliptical lunules, with a maximum SI <1.6: *A. bioculata*, *A. elliptica*, *A. lovisatoi*, *A. ovalifora*, *A. neuparthi*, *A. lorioli*, *A. montezemoloi*, *A. ludovici* and *A. romani* n. sp. Remarks about *A. neuparthi* are reported in the discussion chapter, for *A. lovisatoi* and *A. montezemoloi*, see Stara & Borghi (2014).

Amphiope bioculata (Des Moulins, 1837) Figs. 27, 28; Figs. 91–99; Figs. 66–69; Figs. 7, 8; Fig. 9; Fig. 70; Fig. 77

1791. *Scutella bifora* Lamarck - Bruguières: pl. 147, figs. 5-6

1816. *Scutella bifora* Var. 3 Lamarck: p. 10

1837. *S.*[*cutella*] *bioculata* Nob. Des Moulins: p. 226

1840. *Amphiope bioculata* (Desmoulins) - Agassiz: p. 6

Non 1841. *Amphiope bioculata* (Desmoulins) - Agassiz: p. 73; pl. 11, figs. 1, 5

1847. *Lobophora bioculata* Agassiz - Agassiz & Desor: p. 78

1902. *A. bioculata* (Desmoulins) - de Loriol: p. 21; pl. 2, figs. 4, 6

1907. *A. bioculata* Desmoulins (*Scutella*) - Lambert: pp. 50-53

1912a. *A. bioculata* Desmoulins (*Scutella*) - Lambert: pp. 75-77

1912a. *A. bioculata* var. *drunensis* Lambert: pp. 77, 85.

1914. *A. bioculata* Desm. (*Scutella*) - Cottreau: pp. 135-139; pl. 5, figs. 1-8; pl. 6, figs. 1-12.

TYPE LOCALITY. Des Moulins indicated "Sure près Bollène", an unknown locality in Vaucluse (France). After de Loriol (1902), Lambert (1912a, 1926) and Cottreau (1914) the Langhian-Serravallian of Nissan-Lespignan (Hérault, France) is the type-area for this species.

TYPE MATERIAL. Two syntypes, the specimen MNHBx 2014.6.317 from "Sure" and A-MHNBx 2014.6.189 (2) from Saucats Gironde) were indicated as types of *Scutella bioculata* var. A by des Moulins (1837 and original label). However the latter was attributed to the "variety" *A. bioculata philodonax* by Lambert (1927).

OTHER EXAMINED MATERIAL. 11 whole specimens from the surroundings of Nissan (Hérault), in the type-area; three of them (MNHN-F.A 57777-9) from Lespignan, and 8 (A2270.L18464a-h) from Nissan les Tuileries (Chemin des Tuilières). All from the Langhian - Serravallian. A well preserved specimen (MNHN-F.A57777) from Lespignan will be proposed to the ICZN as neotype.

DESCRIPTION. Middle sized species (mean in our sample TL=61 mm, range 55–74 mm), with sub-

circular outline (mean TW=107% TL) and restricted anteriorly. Rather deep notches in correspondence of the anterior ambulacra. The test is high (mean TH=16.5% TL). Internal structure: central hollow vaguely pentagonal-starry shaped, with the rear wall located between the two posterior paired ambulacra and at the right side of the interambulacrum 5. From the rear wall to the front, the length of the hollow is about 50% TL. Five long and wide macrocanals, starting from the central hollow, extend along the interambulacra. The internal ballast system is very reduced, with large spaces extending towards the test margin. Apical system anteriorly eccentric (mean L4=57% TL), broad (9.5% TL). Petalodium size variable (PL=49-57% TL, mean PL=52% TL). Frontal petal longer than the posteriors (mean L5=25% TL, mean L9=23% TL). In the frontal petal L6=60% L5, in the posteriors L10=70% L9. Interporiferous zones slightly wider than a poriferous one. In the oral interambulacrum 5 the column "b" is made of three post-coronal plates, column "a" of two with sometimes a part of the third plate. On the whole there is the same quantity of plates (13–15) in each column of the interambulacrum 5 and of the ambulacra I and V. The size of the basicoronal circlet is variable (L13=12–16% TL). The mean length of the oral plate 5.b.1 is 8% TL. Lunules variable in size (range WI=56-145), though commonly middle-sized (mean WI= 114), rounded to slightly transversely ovoidal (mean SI=1.22, range SI=1–1.52). They are separated by two (seldom one) plates from the tip of the correspondent petals (L3= 5.5% TL). Peristome middle-sized (range ø ps=3.4–4% TL) and located centrally (mean L12=50% TL). Periproct small (mean ø pc=2% TL), rather far from the posterior test margin (mean L11=11.6% TL) and located between plates 5.a.2-5.b.3 or 5.a.2-5.b.2, or at the conjunction of plates 5.b.2-5.a.2-5.b.3. Food grooves developing by a simple scheme, though sometimes well branched distally, and not reaching the margin. No secondary ramifications branch off along the main grooves. A short branch of the posterior grooves extends towards the rear of the periproct, but does not reach it.

DISTRIBUTION. Langhian-Serravallian (after Roman, 1974) of Nissan and Lespignan (Hérault-France); Aspiran (Hérault); St.Paul-Trois-Châteaux (Drome; MNHN-F. A22379.18.457, specimen in figures 7, 8).

Amphiope elliptica Desor, 1847 - Figs. 25, 26; Figs. 100–105; Fig. 76

1847. *Lobophora elliptica* Desor in Agassiz & Desor: p. 78
1858. *Amphiope elliptica* - Desor: p. 236
1907. *Amphiope elliptica* Desor - Lambert: p. 54
1914. *Amphiope elliptica* Desor - Cottreau: p. 94; figs. 19-20; pl. 8, fig. 1.

TYPE LOCALITY. Desor (in Agassiz & Desor, 1847) indicated S.te Restitut (Drome - France) and Carry, près de Martigues. However, Cottreau (1914) affirmed that the true type locality was Carry le Rouet (Bouche du Rhône), late Aquitanian-early Burdigalian (after Roman, 1974).

TYPE MATERIAL. The holotype and its cast (T93) are wanting; they were not cited in the catalogue of the Museum of Neuchâtel by Jeannet (1929). The illustration of the cast provided by Cottreau (1914) was utilized in the discussion (see Figs. 103–104).

OTHER EXAMINED MATERIAL. A specimen (MNHN-F A22706-L18.471), collection Lambert; Figs. 25, 26, Figs. 100-102, 105 from the late Aquitanian-early Burdigalian of Carry-Le-Rouet (Bouches-du-Rhône).

DESCRIPTION. Middle-sized species (mean TL=84.5 mm), with subcircular to elliptical outline (mean TW=104% TL). Only shallow sinuosities, no deep notches, are present on the margin in correspondence of the anterior ambulacra. Test high in the holotype (TH=17% TL). Margin rather thick. Internal structure: in the radiograph (Fig. 76) the shape of the central cavity is not clearly visible, however it seems roundish. The internal support system is well developed and highly complicated especially in the anterior half of the test, it is denser around the lunules and towards the posterior test margin. The spaces between the pillars are wide, as in *A. montezemoloi* (Fig. 85). Apical system slightly eccentric anteriorly (mean L4=56% TL), large (about 9% TL). Petalodium size variable (PL=52–60% TL). Frontal petal long (L5=25-30% TL), L6=12.5–16% TL. Width of poriferal and interporiferal areas=3.5–4.8% TL and 5.1-6.4% TL, respectively. Anterior paired petals are 24%TL long and 13% TL wide. In the posterior petals, L9=22–27 %TL and L10=13–16% TL. Lunules almost subcircular (mean SI=1.3) and rather small (mean WI=82.2). The distance between the tip of the pos-

terior petals and the corresponding lunules is rather short (range L3=4–7 % TL); the space is occupied by only one or two plates per column. In the oral interambulacrum 5, column "a" includes two post-basicoronal plates, three plates are present in column "b", and there are on the whole 15–16 plates, as well as in the ambulacra I and IV. The length of the oral interambulacral plate 5.b.2 is about 8% TL. Peristome large (ø ps= 4,8% TL), roundish and slightly anterior to the centre (L12=47–54% TL). Basicoronal circlet rather large (L13=13–14% TL). Periproct small (ø pc=2.2% TL), not far from the posterior test margin (L11=7% TL) and positioned halfway along the suture between plates 5.a.2-5.b.3. Food grooves not well visible, however it seems that they develop by a simple scheme and do not reach the margin; a short branch of the posterior grooves surrounds the lunules.

REMARKS. *Amphiope elliptica* differs from *A. bioculata* by the lack of notches along the margin in correspondence of the anterior paired ambulacra, by the higher number of plates in the posterior ambulacra and a different internal structure, with its roundish central cavity instead of sub-pentagonal. It differs from *A. lorioli* by the internal structure, which is more reduced almost in the whole test (compare Fig. 76 with Fig. 86), by its smaller lunules, which are roundish instead of ovaloid, its higher test and above all a much larger petalodium (PL=52–60% TL, against 44–46% TL). *A. ovalifora* has ovaloid lunules, as well as *A. lovisatoi*, which has also a higher value of L4 (mean L4=62% TL, against 57% TL). *A. elliptica* differs from *A. ludovici* in having a larger and higher test, higher whole number of plates in the ambulacrum I (15–16 against 11–12). *A. montezemoloi* has much larger lunules (WI ranges from 200 to 400, mean 330, instead of 82). *Amphiope romani* n. sp. lacks the sinuosities on the margin in correspondence of the anterior paired and odd ambulacra, has less numerous plates in the interambulacrum 5 and a different internal structure.

Based on its stratigraphical and geographical position, *A. elliptica* likely represents a link between *Amphiope* from the Burdigalian of southeastern France and the species subsequently diffused in Corsica, Sardinia and Italy mainland, e.g. *A.* "*bioculata*" of Aleria (Corse), described in Cottreau (1914) and that we'll redescribe in a subsequent work.

DISTRIBUTION. Carry-le-Rouet (Bouche du Rhône), late Aquitanian-early Burdigalian. After Lambert, 1907) also S. Restitute, Drôme (Langhian-Serravallian), but this citation needs verification.

Amphiope ovalifora Des Moulins in Fallot, 1903 (Figs. 29, 30; Figs. 106–111; Fig. 72; Fig. 78)

1837. *Scutella bioculata* Var. B. foraminibus transversé ovatis Nob. Des Moulins: p. 226
1847. *Lobophora bioculata* Var. B - Agassiz in Agassiz & Desor: p. 78
1874. *Amphiope ovalifora* Desmoulins - Benoist: p. 449
1903. *Amphiope ovalifora* des M. - Fallot: p. 82 (pars)
1907. *Amphiope ovalifora* Desmoulins (in Fallot, 1903) – Lambert: pp. 55-56
1927. *Amphiope ovalifora* Desmoulins (in Benoist) - Lambert: pp. 39-44.

TYPE LOCALITY. Gornac, near Bordeaux (Gironde-France). Aquitanian (Burdigalian?).

TYPE MATERIAL. One syntype (as indicated in the original label), consisting of a complete specimen (MNHBx 2014.6.180.1) from Gornac.

OTHER EXAMINED MATERIAL. Thirteen whole specimens (MNHN-F A 22710-L 18.447a-o) and a large fragment from the type-locality. A fragment (labeled as syntype MNHBx 2014.6.180.2) from Cazeneuve (Bazadais) but doutfully assigned to this species. Four specimens and a large fragment (APBA 20151015_204113) from the Aquitanian of St. Avit (Carrière de Préhac, Landes).

DESCRIPTION. Middle-sized species (mean TL= 75 mm, range 58–90 mm), with subcircular outline (mean TW=106% TL) and the anterior part restricted starting from the anterior paired ambulacra. Test of medium height (mean TH=14%TL) (Figs. 110, 111). Margin rather thick, with only shallow sinuosities, no deep notches, in correspondence of the anterior ambulacra. On the oral face, middle ambulacral areas with a shallow and broad depression. Internal structure: central hollow sub-pentagonal (Fig. 78; Fig. 109), its length, from the rear wall to the front, equals about 40% TL. Four main cavities branch from the central hollow: the first, containing the *caecum*, runs along the interambulacrum 2, other two correspond to the interambulacra

3 and 4, the last one being shorter than the other. The fourth cavity extends along the interambulacrum 5, leading to the periproct. The internal ballast system is dense and becomes almost massive, and crossed only by micro-canals, towards the margin. The geometric shapes within the central cavity (Fig. 78) are due to calcite re-crystallization occurred during fossilization and have no diagnostic value. Apical system slightly anteriorly eccentric (mean L4=54% TL), large (9% TL). The petalodium (mean PL= 50% TL) increases in size during growth: PL=45 and 54% TL in specimens with TL=58 and 79 mm, respectively (Fig. 64). Paired anterior petals shorter than the frontal one (L7=84% L5); mean L5=24.5% TL against L9=21 %TL. On the average, in the frontal petal L6=60% L5, in the posteriors L10=70% L9. Interporiferous zones slightly wider than a poriferous one. In the frontal petal L6=60% L5, in the posteriors L10=70% L9. Interporiferous zones slightly wider than a poriferous one. In the oral interambulacrum 5, column "a" is made of two plates (sometime also a part of the third plate), column "b" is made of three plates, with 2b very elongate (up to 15% TL). On the whole, there are 14–16 plates in each column of the interambulacrum 5. Basicoronal circlet well developed (L13 up to 20% TL); the size of the basicoronal interambulacral plates is up to 27% TL. The length of the plate 1 in the interambulacrum 5 is up to 14% TL. Lunules transverse elliptical to sub-circular (mean SI=1.6, range SI=1.3–1.9), they are never narrow and their edges are never parallel. Lunules may be irregularly shaped and different even in the same specimen. Size much variable (range WI=93–205, mean WI=125). The space between the tip of posterior petals and the corresponding lunules (L3= 6.5% TL) is occupied by only one or two plates per column. Peristome middle-sized (ø ps=3–5.2% TL, mean 4) and subcentral (L12=51% TL). Periproct small (mean ø pc= about 2% TL), opening rather close to the posterior margin (mean L11=9.6% TL, range 7–11.5 %TL) near the conjunction of plates 5.a.2-5.b.2-5.a.3. Aristotle's lantern: the radius of a single wing (Mooi, 1989) is about 12% TL. Food grooves well marked and developed by a simple scheme (Fig. 72), though sometimes they are well branched distally. Secondary ramification almost missing along the middle part of the main grooves. A short branch of the posterior grooves surrounds the lunules and extends towards the rear of the periproct.

DISTRIBUTION. This species seems common in south-western France, above all in the Departments of Gironde and Landes. Faluns de Gonin near Gornac (Lambert, 1926). It was reported also from Cabaron, near Castelvieil, but this citation needs verification. Cited by Fallot (1903) at Sainte Croix-du-Mont, Château du Cros near Louplac, Garries near Cabanac and Cazeneuve, in the Bazadais. Also S.t Avit (Carrière de Préhac), Landes (personal communication, F. Meunier, APBA Bordeaux). All these records were dated to the Aquitanian.

REMARKS. *Amphiope ovalifora* differs from *A. bioculata* by its lower test (Fig. 54), and from *A. lovisatoi* and *A. bioculata* by higher values of L13, lower values of SI and WI, and a denser internal ballast system, above all towards the margin (Figs. 77, 78 and Fig. 109). Differs from *A. lovisatoi* also by a higher value of L11, a lower mean value of L4 (Fig. 88) and a denser internal structure. *Amphiope elliptica* has roundish lunules and the internal structure is much more reduced and more complicated, also towards the periphery (Figs. 76, 78). Also *A. lorioli* has a much lighter internal structure (Figs. 109, 113). *Amphiope ludovici* has less numerous plates in the interambulacrum 5 and in the ambulacra I and V. *Amphiope montezemoloi* has much larger lunules with roundish shape (WI ranges from 200 to 400, mean 330) (Fig. 53). *Amphiope romani* n. sp. lacks notches in correspondence of the paired anterior ambulacra and the value of L11 is very low (Fig. 52). The specimen attributed to *A. ovalifora* figured by Fallot (1903) from Cazeneuve (Bazadais) (not Des Moulins collection), some of those from Prehac and those with narrow lunules from Le Thil examined in Lambert collection (MNHN-F), likely do not belong to this species. Also the specimens from the Aquitanian of Castelvieil (Cabaron) differ from the type series of *A. ovalifora* from Gornac, by the lower height (mean H=8% TL, against 14%TL).

Amphiope lorioli Lambert, 1907 - Figs. 31, 32; Figs. 112–115

1902. *Amphiope perspicillata* (non Agassiz) - de Loriol: p. 23; pl. 3, figs. 2, 3
1907. *Amphiope lorioli* Lambert: p. 56.

TYPE LOCALITY. St-Félix-de-Lodez (Lodéne or Lodéve *auctorum*) (Hérault - France). Tortonian (Roman, 1974).

TYPE MATERIAL. A complete specimen (MNHN-F A22707-L 18472Aa) from the type locality.

OTHER EXAMINED MATERIAL. A specimen (MNHN-F.A22707-L 18472Ab) from the type locality).

DESCRIPTION. Middle-sized species (mean TL=84 mm), with elliptical to sub-circular outline (TW=111% TL). Test rather low (mean TH=11.7% TL). Margin with slightly deep notches in correspondence of the anterior ambulacra. Internal structure: the central hollow is vaguely pentagonal-starry shaped, with the rear wall lying between the two posterior paired ambulacra and located at the right side of the interambulacrum 5. From the rear wall to the front, the length of the size of the hollow equals 44–48% TL. Five long and wide extensions, starting from the central hollow, extend along the interambulacra. The internal buttress system is reduced, it becomes denser only towards the test margin. Apical system medium-sized (7.5–8.5% TL) and eccentric anteriorly (mean L4=55% TL). Petalodium small to medium-sized (mean PL=45% TL, range 44–46% TL). Frontal petal longer (L5=24.5% TL; L9=18.5 %TL) and proportionally narrower than the posteriors (L6=12.5% TL, L10=12% TL). The mean width of poriferal and interporiferal areas is 4% TL and 5% TL, respectively. Lunules mid-sized (mean WI=130% TL), slightly transversely ovoidal (mean SI=1.4). The space between the tip of posterior petals and the corresponding lunules (L3=7% TL) is occupied by two or three plates per column. In the oral interambulacrum 5, column "a" is made of two (sometimes also a part of the third) plates, column "b" of three. The basicoronal interambulacral plate 1 seems short (about 6% TL). On the whole there are 15-16 plates in each column of the ambulacra I and V and in the interambulacrum 5. Peristome small (mean ø ps=3.6–4% TL) and centrally located (mean L12=52%TL). Periproct small (ø pc=2%TL), far from the posterior margin (mean L11=12.5%TL, range 10–15% TL), opened between plates 5.b.2-5.a.2 in the studied sample. Food grooves not well visible, however they develop by a simple scheme and do not reach the margin; a short branch of the posterior grooves surrounds the lunules and extends towards the periproct.

DISTRIBUTION. Serravallian-Tortonian of S. Felix de Lodez (Hérault, France). Probably also the Langhian-Serravallian of La Crucca and Porto Torres (Sardinia, Italy) (see Stara et al., 2012).

REMARKS. *Amphiope lorioli* differs from *A. bioculata* by a different internal structure, with smaller central hollow, and internal ballast system that becomes denser towards the test margin. It differs from *A. ovalifora* by smaller petalodium (PL=45% TL, against 50% TL), less elliptical lunules and different internal structure. It differs from *Amphiope lovisatoi* by the lower value of L4 (mean L4=55% TL, against 62) and PL (45% TL, against 53%TL). *Amphiope ludovici* has smaller and lower test, lower number of plates in each column of the interambulacrum 5 (11–12 against 15–16). *Amphiope lorioli* is distinguished from *A. montezemoloi* by smaller test and lunules (WI=130 against 330) and denser internal structure. *Amphiope romani* n. sp. lacks notches along the margin in correspondence of the anterior ambulacra, has a different internal structure and lower distance of the periproct from the margin, greater petalodium (PL=53%TL, against 45% TL) and a lower number of plates in the oral interambulacrum 5.

Amphiope ludovici Lambert, 1915 - Figs. 33, 34; Figs. 116–120

1912a. *Amphiope elliptica* Desor - Lambert: p. 77; pl. 6, figs. 1-3
1915a. *Amphiope ludovici* Lambert: p. 220; pl. 6, fig. 1a; pl. 16, figs. 14, 15.

TYPE LOCALITY. Blanqui, near Cucuron (Vaucluse - France). Tortonian (Roman, 1974).

TYPE MATERIAL. Two syntypes (MNHN-F J00999 L18473, L18474), from the type locality.

DESCRIPTION. Very small-sized species (mean TL=29 mm). The specimens under study are adults since they have four open gonopores (Fig. 119). Test sub-circular, wider than long (mean TW=108% TL) (Figs. 116, 117). The test is domed and low (mean TH=9% TL) with the highest point anterior to the apical disc (Fig. 118). Margin sharp, with only shallow sinuosities, no deep notches, in correspondence of the anterior paired ambulacra. Oral face flat. Internal structure: central hollow subpentagonal (Fig. 120). From the rear wall to the front, the length of the hollow is about 49% TL. Three short macrocanals extend from the central

hollow, along the interambulacra 2, 3 and 4; another long channel runs along the interambulacrum 5 and leads to the periproct. Internal ballast system well developed in the whole test. Apical system eccentric anteriorly (L4=59% TL) and broad (10% TL). Petalodium medium-sized (PL=50% TL). Anterior petal longer than the posteriors (L5=25% TL against L9=22.4; L7=24 % TL); the width of the anterior and the posterior petals is comparable (L6=14 % TL, L10=13.5 %TL; L8=14 % TL). Width of interporiferous and poriferous zones=6.4% and 4.2% TL, respectively. In the oral interambulacrum 5, the length of the basicoronal plate 1 is 9% TL, that of plate 5.b.2 is 16% TL. There are two post basicoronal plates in column "a" and two, seemingly three, in column "b". In the interambulacrum 5 there are, on the whole, only 10–11 plates per column. In the ambulacrum I there are 11–12 plates per column (Figs. 33, 34). Lunules rounded (mean SI=1.1) and small-middle-sized (mean WI=100). The space between the tip of posterior petals and the corresponding lunules (L3= 7% TL) is occupied by only 1-2 plates per column. Peristome eccentric anteriorly (L4=59% TL); ø ps=4.5% TL. Periproct small (ø pc=1.6%TL), very close to the posterior margin (L11=4.6% TL) and positioned between plates 5.a.2–5.b.3. Food grooves partially visible, likely developing by a simple scheme and not reaching the margin.

DISTRIBUTION. Blanqui near Cucuron (Vaucluse - France), Tortonian.

REMARKS. *Amphiope ludovici* differs from *A. bioculata*, *A. elliptica* and *A. lorioli* by the lower number of plates in each column of the posterior ambulacra and in the interambulacrum 5. *Amphiope ovalifora* has a different internal structure, more transversely elongate and larger lunules and much higher test. *Amphiope ludovici* differs: from *A. lovisatoi* by its rounded lunules and a lower value of L4 (mean L4=55% TL against 62), from *A. montezemoloi* by much smaller lunules (WI=88 against 330), from *A. romani* n. sp. by the presence of notches on the test margin, the different internal structure and the lower number of plates in the interambulacrum 5 and the posterior ambulacra. It is probable that the specimens from Cucuron (les Castellas) assigned to *A. baquiei*, examined at the MRA, belong to *A. ludovici*. Unluckily it was not possible to detect the plating structure.

Amphiope romani n. sp. - Figs. 121–124; Figs. 161, 163

1915. *Amphiope bioculata* (var. *turonensis*) Desmoulins - Lambert: p. 77
2014. *Amphiope* sp. 3 Stara & Sanciu: pp. 318, 320; pl. 1, figs. 1–7; pl. 2, figs. 1–6.

TYPE LOCALITY. Faluns of Channay-sur-Lathan, Touraine (France), late Serravallian-early Tortonian (after André et al., 2003).

TYPE MATERIAL. Holotype (MNHN-F.A57780. PL1669), represented by a complete specimen, and a paratype (MNHN-F.A57781.PL1821).

OTHER EXAMINED MATERIAL. 16 specimens, 12 of them (MNHN-F.A57781.PL1821-6; MNHN-F.A57781a-f; MACPL 1668) from the late Serravallian-early Tortonian of Channay-sur-Lathan (Touraine - France) and four (MNHN-F.A.22713-L18482a, b; MNHN-F.R7277a, b, f) from Oisly (Loir-et-Cher - France). The outcrops of Oisly were attributed to the Langhian-Serravallian by André et al. (2003).

DIAGNOSIS. A species of *Amphiope* characterized by a middle-sized test with sub-circular outline, margin thin and almost deprived of notches, lunules rounded, separated by only one or two (rarely three) plates from the tips of the posterior petals and rather close to the rear margin; internal ballast system very light and becoming very dense near the margin.

DESCRIPTION OF HOLOTYPE. Test middle sized (TL=68 mm), with subcircular outline (TW=108% TL). Margin rather thin, lacking notches in correspondence of the anterior ambulacra. Test of middle height (TH=13.2%TL) (Fig. 122). Oral face with interambulacral areas slightly inflated and ambulacral areas with a shallow and broad depression deepening towards the peristome. Internal structure: central hollow sub-pentagonal to star-shaped (Fig. 121). From the rear wall to the front, the length of the hollow is about 49% TL. A long and wide macrocanal extends from the central cavity along the interambulacrum 2; another long and narrow channel runs along the interambulacrum 5 and leads to the periproct. The internal buttress system is very reduced, becoming densely packed near the test margin. Apical system an-

teriorly eccentric (L4=59% TL), large (about 10% TL). Petalodium large (PL=53%). Paired posterior petals shorter than the frontal one (L5=26,5% TL, L9=24,3% TL). The width of the petals is comparable (L6 and L10=15 %TL. Width of an interporiferous zones 1.2–1.5 times than that of a poriferous one. In the oral interambulacrum 5, column "a" is made of two plates, column "b" is made of two plates. The length of plate 5.b.2 is 16,4% TL. On the whole, there are 14 plates per column in the interambulacrum 5 and 13-14 in the ambulacra I and V. Basicoronal circlet large (L13=14% TL); the length of interambulacral plate 1 is about 9.5% TL. Lunules mid-sized (WI=121,5), transverse elliptical (SI=1.5). The distance between the tip of posterior petals and the corresponding lunules is long (L3= 7% TL) and is occupied by two plates per column. Peristome middle-sized (ø ps=4% TL) and opening centrally (L12=50% TL). Periproct small (ø pc=1.7% TL), very close to the posterior margin (L11=6,7% TL) and located between plates 5.a.2-5.b.3. Food grooves well marked, developing by a simple scheme but well branched distally; they almost reach the margin; a short branch of the posterior grooves surrounds the lunules and proceeds towards the periproct, not reaching it.

VARIABILITY. Middle sized species: the test length ranges from 46.5 to 73 mm, the test height ranges from 13 to 16.5%TL (mean TH=14.5%TL) in the studied sample. Margin lacking notches or with only shallow sinuosities in correspondence of the anterior ambulacra. The internal buttress system is always very reduced, becoming densely packed near the test margin. Apical system anteriorly eccentric (mean L4=58% TL). Petalodium size variable, ranging from 51 to 62% TL (mean 54% TL,). Also petals variable in size; paired posterior shorter than the frontal one (mean L5=26% TL, L9=24% TL). The width of the petals is almost comparable (mean L6 and L10=15 %TL. In the oral interambulacrum 5, column "a" is always made of two plates, column "b" is made of two plates, sometimes with also a part of the third plate. The whole number of plates is constant: 13–14 plates per column in the interambulacrum 5 and 12–13 in the ambulacra I and V. Basicoronal circlet large (mean L13=12.5% TL). Lunules small to mid-sized (mean WI=123, range 90–157), commonly rounded to transverse elliptical (mean

SI=1.2, range 1-1.6). The distance between the tip of posterior petals and the corresponding lunules is occupied by one or two (rarely three) plates per column. Periproct close to the posterior margin (mean L11=5.2% TL, range 3–10% TL) and located between plates 5.a.2-5.b.3 or at the conjunction of plates 5.a.2-5.b.2-5.b.3.

DERIVATIO NOMINIS. This new species is dedicated to the French geologist, paleontologist and echinologist Jean Roman.

DISTRIBUTION. The species is common in the late Serravallian-early Tortonian Faluns of Channay-sur-Lathan (Touraine, France); a variety is present in the Langhian-Serravallian of Oisly (Loir-et-Cher, France).

REMARKS. The specimens from Oisly differ from those from Channay-sur-Lathan by higher test, larger lunules, smaller petalodium and by the presence of shallow notches along the test margin in correspondence of the paired anterior ambulacra. Given the small sample available for the study and the different stratigraphic position of the *Amphiope*-bearing sediments at Channay and Oisly, the subspecies *A. romani turonensis* (Lambert, 1915), established for the specimens from Oisly, is maintained. *Amphiope romani* n. sp. is distinguished mainly by the periproct very close to the posterior test margin (with the exception of *A. elliptica* and *A. ludovici*) and by the lack of notches on the margin in correspondence of the anterior ambulacra. *A. elliptica* has a greater whole number of plates in the interambulacrum 5 (15–16) than *A. romani* n. sp. (12–14) and *A. ludovici* (only 10–12). *Amphiope romani* n. sp. has a different internal structure when compared with *A. elliptica* and *A. ludovici*. *Amphiope montezemoloi* has much larger test and lunules.

The *Amphiope nuragica* group
    (sensu Stara et al., 2015)

This informal group includes the species with transversely elongate lunules and values of SI > 1,6: *A. hollandei*, *A. depressa*, *A. palpebrata*, *A. sarasini*, *A. transversifora*, *A. deydieri*, *A. pallavicinoi*, *A. tipasensis*, *A. dessii* and *A. nuragica*. Remarks about *A. depressa* and *A. palpebrata* are reported in

the discussion chapter, for *A. nuragica* see Stara & Borghi (2014).

Amphiope hollandei Cotteau 1877 - Figs. 37, 38; Figs. 125–128

1877. *Amphiope hollandei* Cotteau: p. 241; pl. 9, figs. 6, 7; pl. 20, fig. 1
1907. *Amphiope hollandei* Cotteau - Lambert: p. 57
1925. *Amphiope hollandei* Cotteau - Lambert & Thiéry: p. 122
1998a. *A. bioculata* (Desmoulins) - Philippe: p. 152.

TYPE LOCALITY. Bonifacio (Corse - France), Burdigalian.

TYPE MATERIAL. Holotype (MNHN-F.A22378. L18472).

DESCRIPTION. Large-sized species (TL=106 mm). Test ovoid, much wider than long (TW=120% TL). The test is domed and very low (TH=6.5% TL). Margin thick, with rather deep notches in correspondence of the anterior paired ambulacra. Oral face flat. Apical system sub-central (L4 about 57% TL). Petalodium rather wide (PL=54% TL). Frontal petal longer (L5=30% TL, L9=24% TL) and wider than the posteriors (L6=17.5% TL, L10=16 %TL). The width of the interporiferous and poriferous zones is 8.3% TL and 4.7% TL, respectively. The plating pattern in the interambulacrum 5 is partially visible. There are three plates in column "a" and, at least, three in column "b". In the aboral ambulacrum V there are eight or nine plates per column around the lunules, pointing to the presence as a whole of 14–15 plates per column. Lunules transverse, long and narrow L1=3.2% TL (SI=7.3, WI=72). Peristome slightly anterior to the centre (L12 about 60% TL). Periproct rather far from the posterior margin (L11 about 12% TL), opening at the conjunction of plates 5.a.2-5.b.2-5.b.3.

DISTRIBUTION. Bonifacio (Corse - France), Burdigalian.

REMARKS. *Amphiope hollandei* is distinguished mainly by its very low test and the particular shape of the lunules, which are very long and narrow (SI up to 7, against a maximum SI= 3 in *A. nuragica*).

Amphiope sarasini Lambert, 1907 - Figs. 43, 44; Figs. 129–133

1902. *Amphiope perspicillata* (non Agassiz) - de Loriol: p. 23; pl. 3, figs. 2, 3
1915. *Amphiope sarasini* Lambert: p. 222; pl. 4, figs. 8, 10; pl. 3, fig. 24.

TYPE LOCALITY. Cruzy (Hérault - France). Serravallian-Tortonian, after Roman (1974).

TYPE MATERIAL. A syntype (MNHN-F J00985.L18480), consisting of a complete specimen from the type locality.

OTHER EXAMINED MATERIAL. Three specimens (MNHN-F.A22379 L18.469; MNHN-F.A.57788-89) from the type locality.

DESCRIPTION. Middle-sized species (TL=60-93 mm in the studied sample), with elliptical outline (TW=108.5% TL). Test with middle-height (mean TH=14% TL). Margin with shallow notches in correspondence of the anterior paired ambulacra. In the oral face the anterior ambulacral areas and the first half of the interambulacra are distinctly sunken (Fig. 133). Internal structure: the central hollow is sub-pentagonal to starry shaped. From the rear wall to the front, the length of the hollow ranges from 44 to 48% TL. Ten long and wide extensions, starting from the central hollow, extend in correspondence of the interambulacra. The peripheral ballast system is of middle density and becomes stronger only towards the test margin. Apical system medium-sized (8-10% TL) and eccentric anteriorly (mean L4=57% TL). Petalodium increases in size with growth (range PL=46-52% TL; mean PL=49% TL). The mean width of the frontal and the posterior petals is comparable: L6=13% TL, L10=14% TL. The mean width of poriferal and interporiferal areas is 4% TL and 5.2% TL, respectively. Lunules small (mean WI= 97% TL), transversely ovoidal (mean SI=1.8). The distance between the tip of posterior petals and the corresponding lunules (L3= 7% TL) is occupied by two plates per column. In the oral interambulacrum 5, column "a" is made of two or three post-basicoronal plates, column "b" of three. The basicoronal interambulacral plate 1 is short (about 6% TL). On the whole, there are 13–15 plates per column in the interambulacrum 5 and 16–17 in the ambulacra I and V. Peristome small (mean ø ps=3.4–4% TL) and centrally located (mean

L12=51% TL). Periproct small (ø pc=1.8%TL), far from the posterior margin (mean L11= 12, range 10–13% TL) and opened between plates 5.a.2–5.b.3 or 5.a.2–5.b.2–5.b.3. Food grooves well marked and strongly branched distally; numerous short secondary ramifications branch off also long the main grooves.

DISTRIBUTION. Serravallian-Tortonian of Cruzy.

REMARKS. *Amphiope sarasini* is distinguished from the other species belonging to the *A. nuragica* group by its very small lunules, the smallest so far observed in *Amphiope*, the distinctly sunken oral anterior ambulacral areas and the food grooves, which are the most strongly branched in the genus *Amphiope*. This species is apparently close to *A. depressa*, however the plating patterns and the internal structure of the last species are unknown, thus preventing a reliable comparison.

Amphiope transversifora Lambert, 1912
    Figs. 39, 40; Figs. 134–137

1912a. *Amphiope transversifora* Lambert: pp. 84–85; pl. 7, figs. 3-5
1925. *Amphiope transversifora* Lambert - Lambert & Thiéry: p. 122.

TYPE LOCALITY. Saint-Paul-Trois-Châteaux (Drôme - France), Langhian.

TYPE MATERIAL. A syntype (MNHN-F.J01682), represented by a slightly damaged specimen, from the type locality. The other syntypes cited by Lambert (1912a) are wanting.

DESCRIPTION. Small-sized species (TL=46 mm). Test sub-circular, wider than long (TW=108% TL). The test is domed and rather low (TH=13% TL). Margin thick, with rather deep notches in correspondence of the anterior paired ambulacra. Oral face flat. Internal structure: central hollow roundish, its size is not measurable because the perioral area is damaged. The internal buttress system is reduced, with sparse supports and large spaces. Also the peripheral ballast system is reduced and becomes densely packed only close to the test margin. Apical system slightly eccentric anteriorly (L4=58% TL), broad (9% TL). The only specimen available to study has three small gonopores. Petalodium large (PL=55% TL).

The frontal petal is longer than the posteriors (L5=27% TL, L9=24% TL); the width of the petals is almost proportionally comparable (L6 and L10= 15% TL). Width of the interporiferous and poriferous zones 5.8–7.2% TL and 4.1–4.8% TL, respectively. In the oral interambulacrum 5 there are on the whole about 12-13 plates per column; adorally there are only two post-basicoronal plates in column "a" and two, plus a small part of the third, in column "b". The length of plate 5.b.2 is 18% TL. Lunules transversely elongate, rather narrow (mean SI=2) and medium sized (WI=149). The distance between the tip of posterior petals and the corresponding lunules (L3= 6.5% TL) is occupied by two plates per column. Peristome slightly anterior to the centre. Periproct small (ø pc=2.4%TL), rather close to the posterior margin (L11=7.4% TL) and positioned near the conjunction of plates 5.a.2–5.b.2–5.b.3. Posterior food grooves partially visible, it seems that they develop by a simple scheme.

DISTRIBUTION. Saint-Paul-Trois-Châteaux (Drôme - France), Langhian.

REMARKS. *Amphiope transversifora* is distinguished mainly by the presence of only two post-basicoronal plates in each column of the oral interambulacrum 5, the lowest in the *A. nuragica* group. It differs from the apparently similar *A. nuragica* by its delicate internal structure, from *A. sarasini* by its lunules, which are larger and much closer to the posterior test margin.

Amphiope deydieri Lambert, 1912
    Figs. 41, 42; Figs. 138–142

1912a. *Amphiope deydieri* Lambert: pp. 85–86; pl. 6, figs. 5, 7.

TYPE LOCALITY. Cadenet, near Vaugines (Vaucluse - France). Serravallian.

TYPE MATERIAL. Holotype (MRA 3.000.157). The type series studied by Lambert (1912) consists also of 10 whole specimens (MRA3000.159–162, MRA 3000-164; MNHN-F A22705–L18470a-d), from the type locality.

OTHER EXAMINED MATERIAL. Six additional specimens (MRA) from the type locality, not belonging to the series studied by Lambert.

DESCRIPTION. Small-sized species (TL=49-53 mm). Test wider than long (mean TW=122% TL), with the anterior part restricted. Test domed (mean TH=12%; range 10-16% TL). Margin sharp, with shallow notches in correspondence of the anterior ambulacra. Oral face slightly concave, with inter-ambulacral areas slightly inflated and the median ambulacral areas with a shallow and broad depression. Internal structure: though the X-ray photograph is not very clear (Fig. 140), due to the high density of the material, the central hollow is broad and vaguely roundish in shape. A large cavity extends from the central hollow trough the interambulacrum 2, another one leads to the periproct. Internal buttress system reduced, with large spaces towards the test margin. Apical system medium sized (8.3 % TL), slightly eccentric anteriorly (L4=56% TL), with small gonopores. Petalodium large (mean PL= 53% TL). Posterior petals shorter than the others (mean L5=27% TL against L9=23 %TL. The petals width is similar: L6=15% TL, L10= 15.5% TL. Interporiferous zones slightly wider than a poriferous one. Basicoronal circlet large. In each column of the interambulacrum 5 there are on the whole 10-11 plates, only two post-basicoronal plates are present adorally in each column. Lunules narrow transverse, ovate or slit-like (mean SI=2.3), always mid-sized (mean WI=113.5). They are separated from the posterior petal tips by two plates per column (L3= 5.3% TL). Peristome sub-central (mean L12=56%TL) and mid-sized (ø ps= about 4.4% TL). Periproct small (ø pc=2.8% TL), located at the conjunction of plates 5.a.2–5.b.2–5.b.3. Distance from the posterior margin much variable (range L11=6–13% TL). Food grooves well marked, developing by a simple scheme, not reaching the margin.

DISTRIBUTION. Cited only from the Langhian-Serravallian of Cadenet, near Vaugines (Vaucluse - France).

REMARKS. *Amphiope deydieri* is distinguished mainly by its transversely elongate test: it has the highest value of TW in this group (TW=122% TL). Only *Amphiope hollandei* has a similar test shape (TW=120% TL), however the shape of the lunules in this species is much different (SI=2.3 against 7). *Amphiope deydieri* differs from *A. sarasini, A. transversifora* and *A. nuragica* by the lower whole number of plates in the interambulacrum 5 and am-

bulacra I e V. *A. sarasini* is distinguished from *A. deydieri* also by its much smaller lunules, *A. transversifora* by its much more reduced internal structure.

Amphiope pallavicinoi Lovisato, 1914
Figs. 143–147; Figs. 151, 152

1914. *Amphiope pallavicinoi* Lovisato: p. 115; pl. 2, fig. 5a–b.

TYPE LOCALITY. Lovisato (1914) indicated Torralba (Sassari Province, Sardinia) as type-locality. The type-stratum crops out also at Bessude, near Torralba, 40°33'18.94"N , 8°43'11.33"E. late Burdigalian.

TYPE MATERIAL. The type material of *A. pallavicinoi* is wanting and no other specimens from Torralba, the type locality indicated by Lovisato (1914), are known. We were able to collect new specimens from the type stratum which crops out also at Bessude, some 6 km far from Torralba. A neotype is here proposed (MDLCA 23583); it is represented by an almost complete specimen (TL=100 mm), from Bessude.

OTHER EXAMINED MATERIAL. A fragment from Bessude (MAC.PL1474), a specimen photographed in situ and a figure published by Lovisato (1914: pl. 2, fig. 5a).

DESCRIPTION. Large-sized species (TL=100–105 mm in the studied sample). Test rounded, as long as wide (TW=111 % TL). Test low (range TH=9–13% TL). Margin relatively thick, with notches in correspondence of the anterior ambulacra. Internal structure: the visceral hollow is sub-pentagonal to starry shaped. From the rear wall to the front, the length of the hollow measures 46% TL. Two long extensions, starting from the central hollow, extend into the interambulacra 1 and 5. The peripheral buttress system is reduced and becomes denser only rear to the lunules, towards the test margin. Apical system large (range 10–11.5% TL), located far from the posterior margin, range L4= 58–66% TL). Petalodium large (PL=56–62% TL). Petals almost equal in size: L5=28% TL, L7=27–28% TL, L9=26–30 %TL. Petal width variable: L6, L8 and L10 range from 16 to 18% TL. Interporiferous zones similar or slightly wider than a poriferous one, not rising over the test surface. Ba-

sicoronal circlet not detectable. In the oral interambulacrum 5 there are likely two plates in column a and three in column b. In the ambulacra I and V there are on the whole 15-16 plates. Lunules narrow (mean SI= 2.45) and middle sized (mean WI=151). They are separated from the posterior petal tips by one or two plates per column (L3=4% TL) and their distance from the rear margin equals 14% TL. Peristome anterior to centre (L12=65%TL) and large (ø ps=5.6% TL). Periproct small (ø pc=1.9% TL), located at the conjunction of plates 5.a.2–5.b.3. Its distance from the posterior margin is short (mean L11= 9% TL). Food grooves not well visible; they seem to develop by a simple scheme and do not reach the margin.

DISTRIBUTION. Late Burdigalian of Torralba (Lovisato, 1914) and Bessude, Sassari Province (Sardinia, Italy).

REMARKS. *Amphiope pallavicinoi* is distinguished mainly by its large but low test and large petalodium; *Amphiope tipasensis* has roundish test outline and higher whole number of plates in the ambulacra (17 against 14) and smaller lunules. *Amphiope nuragica* has the highest number of plates in this group. At equal size, *A. sarasini* has smaller lunules, *Amphiope hollandei* has a much wider test (TW=120% TL) and much narrower lunules (WI=7, against 2.4). *Amphiope transversifora* differs by the lower whole number of plates in the interambulacrum 5 and the ambulacra I e V.

Amphiope tipasensis Roman in Aymé et Roman, 1954 - Figs. 148–150; Figs. 153, 154

1954. *Amphiope tipasensis* Roman: p. 168; pl. 1, fig. 1–2.

TYPE LOCALITY. Tipasa Province, Algeria. Pliocene ("Astian" after Aymé & Roman, 1954).

TYPE MATERIAL. Holotype (MNHN-F.R06930).

DESCRIPTION. Medium-sized species (TL=92 mm). Test rounded, as long as wide (TW= 118% TL). Test domed but rather low (TH=13% TL). Margin sharp, with shallow notches in correspondence of the anterior ambulacra. In the oral face, interambulacral areas slightly inflated and the median ambulacral areas with a shallow and broad

depression. Internal structure: not detected. Apical disc not visible. Petalodium small (PL= 46% TL). Petals almost equal in length: L5≅23% TL, L7≅22 % TL, L9≅20 % TL. Also their width is similar: L6, L8, L10= 12% TL. Interporiferous zones similar in size or slightly wider than a poriferous one; they are slightly raised over the test surface. Basicoronal circlet small. In the interambulacrum 5 the length of the basicoronal plate 1 is 6.5% TL. In the oral interambulacrum 5 there are three post-basicoronal plates in column a and four in column b. In the ambulacra I and V there are on the whole 15–17 plates. Lunules narrow transverse, slit-like (mean SI= 2.1) and always small (mean WI=99.3). Foramen with oblique walls. The lunules are separated from the posterior petal tips by only 2 plates per column (L3= 4,8% TL). Peristome central (L12=50%TL) and small. Periproct small (ø pc=1.9% TL), located at the conjunction of plates 5.a.2–5.b.2–5.b.3; it is far from the posterior test margin (L11= 12.5% TL). Food grooves well marked, developing by a simple scheme and do not reaching the margin.

DISTRIBUTION. Pliocene of Tipasa Province (Algeria).

REMARKS. *Amphiope tipasensis* is distinguished mainly by its roundish test and the high number of oral interambulacral plates. Only *A. nuragica* has a similar number of plates, but it has larger lunules. At equal size, *A. sarasini* has a larger petaloid and much more complex ramifications in the food grooves. *Amphiope hollandei* has a wider test (TW= 120% TL) and much narrower lunules (WI=7 against 2.1). *Amphiope transversifora* differs by the lower whole number of plates in the interambulacrum 5 and ambulacra I e V. *Amphiope palpebrata* differs in having larger petalodium and lunules and a higher number of plates in the oral ambulacra I and V (compare Figs. 153, 154 and 155, 156).

Genus *Paraamphiope* Stara et Sanciu, 2014

TYPE SPECIES. *Paraamphiope raimondii* Stara et Sanciu, 2014

TYPE MATERIAL. The holotype (MZE.UNICA-

MAC.IVM206) is represented by a well preserved whole specimen (Recent, Indonesia).

DIAGNOSIS. Emended from Stara & Sanciu (2014):

- Test low with thin margin; highest point corresponding to the centre or slightly anterior to it. Oral side flat to slightly concave.

- Ambulacra a little wider than interambulacra at ambitus. Petals short (about half radial length of test). All five petals similar in length. Petalodium small (42–51% TL) with petals almost closed distally; ß angle about 88°.

- Width of the sub-pentagonal visceral central hollow equals almost that of the petalodium. Five cavities branch from the central hollow along the interambulacra; the longest one extends along the interambulacrum 5 and leads to the periproct.

- Apical disc monobasal, subcentral or slightly anterior to centre, with four small gonopores.

- Interambulacra narrower than the ambulacra adorally, even at their widest point. The first two plates in the interambulacrum 5 are slightly staggered with only the plate 5.b.2 in contact with the two first ambulacral post-basicoronal plates.

- Width of the interambulacrum 5 at the margin is almost 36% TL.

- Basicoronal circlet pentastellate with interambulacral plates forming the points.

- Two radially elongate ellipsoidal lunules or narrow slits present in the posterior ambulacra; three or four pairs of plates separate the lunules from the tip of the corresponding petals.

- Peristome small, sub-central or slightly anteriorly located.

- Periproct circular, small, with distance periproct-posterior margin <13% TL.

- Main food grooves well marked, large and strongly branched distally. They do not reach the margin; the posterior grooves extend towards the periproct. Fine and short secondary grooves branch off also along the middle part of the main grooves. Tube-feet extend also into the interambulacral zones.

- Tuberculation dense, made of very small, perforate and crenulate tubercles which are larger on the oral face.

DISTRIBUTION. France, North Africa and Indonesia, Oligocene to Recent.

REMARKS. *Paraamphiope* differs from *Echinodiscus* in having the first two post-basicoronal plates of the interambulacrum 5 staggered, whereas they are always large and paired in *Echinodiscus*. Additionally, in *Paraamphiope* the contact with the post-basicoronal ambulacral plates in the interambulacrum 5 is the same as that in *Amphiope*, while in *Echinodiscus* and usually in *Sculpsitechinus* both plates 5.a.2 and 5.b.2 are in contact with the adjacent ambulacral postbasicoronals. However, some populations of Recent *Sculpsitechinus* show a certain variability. *Paraamphiope* differs from *Amphiope* by axial lunules, separated by three or four (rarely two) couples of plates from the posterior petals, in the latter they are rounded or transverse and separated from petals tip by only one or two (rarely three) couples of plates. *Paraamphiope* has strongly branched food grooves; that are developed on the entire adoral surface in *Sculpsitechinus*. The petalodium size commonly ranges from 42 to 50% TL in *Paraamphiope*, while it frequently gets up to 60%TL in *Amphiope* and 30–60% TL in *Sculpsitechinus*. *Paraamphiope* differs from *Sculpsitechinus* also by the position of the periproct, which is closer to the rear margin (2.5–13% TL against 11–26% TL).

Species included:

- *P. agassizi* (Des Moulins in Cotteau, 1864), Rupelian, Gironde (France).
- *P. arcuata* (Fuchs, 1882), Miocene of Libya and probably Egypt.
- *P. cherichirensis* (Thomas & Gauthier in Gauthier, 1889), Burdigalian of Tunisia.
- *P. baquiei* (Lambert, 1907), Langhian-Serravallian, south-eastern France.
- *P. raimondii* Stara & Sanciu, 2014, Indonesia (Borneo), Recent.

Species previously assigned to the genus *Amphiope* herein transferred to *Paraamphiope*:

Paraamphiope agassizi (Des Moulins in Cotteau, 1864) - Figs. 157, 158, 162; Figs. 165–170; Fig. 74

1864. *Amphiope agassizi* Desmoulins - Cotteau: p. 103; pl. 14, figs. 3, 5

1870. *Amphiope agassizi* Des Moulins - Tournouer:
  p. 21

1903. *Amphiope agassizi* des Moul. - Fallot: p. 82

1907. *Amphiope agassizi* (Desmoulins in Cotteau)
  - Lambert: p. 55

1914. *Amphiope agassizi* Des Moul. - Cottreau: pp.
  92, 97

1926. *Amphiope agassizi* Desmoulins (in Cotteau)
  - Lambert: p. 36.

TYPE AREA. Includes the localities of S. Albert near La Réole and S. Gemme near Montségur (Gironde, France). "*Couches supérieures du Calcaire ad Astéries*", Rupelian (Oligocene).

TYPE MATERIAL. Two syntypes, one of them (MHNBx 111. 6-194) from S. Albert, the other (MNHN-F.B23973) from S. Gemme.

OTHER EXAMINED MATERIAL. A topo-typic specimen from S. Gemme (MNHN-F.A22688) and five specimens from Pellegrue (MNHN-F.A22687a-e); Rupelian (Oligocene).

DESCRIPTION. Small sized species (mean TL=46 mm, range TL=37-54.5 mm). Test wider than long (mean TW=110% TL), with the anterior part restricted. Shallow to rather deep notches present on the margin in correspondence of the anterior ambulacra. Test low (mean TH=12.5% TL). Oral face flat, with interambulacral areas slightly inflated and ambulacral areas with a shallow and broad depression deepening towards the peristome. Margin rather thin with rather shallow notches in correspondence of the anterior paired ambulacra. Internal structure: central hollow pentastellate (Fig. 167). From the rear wall to the front, the length of the hollow corresponds to PL. Five cavities branch from the central hollow along the interambulacra; the longest one extends along the interambulacrum 5 and leads to the periproct. The internal buttress system is reduced anteriorly and becomes denser towards the posterior test margin. Apical system slightly anteriorly eccentric (mean L4=55% TL), large (8.6% TL); the anterior left pore is closed in three specimens of five in which it was visible. Petalodium size increasing during growth (mean PL=46% TL, range PL=42–48% TL). Posterior petals shorter than the frontal petal (mean L9=85% L5). Width of frontal petal (L6=50% L5) comparable to that in the posteriors (L10=60% L9). Poriferous zones about half the width of an interporiferous one. Petals may be open distally. In the oral interambulacrum 5, columns "a" and "b" are made of two or three post-basicoronal plates; plate 5.b.2 has a very broad base and is partially paired to 5.a.2, however it remains in touch with the two post-basicoronal plates of the ambulacra I and V (Fig. 158). Basicoronal circlet large (L13=19%TL, taken from MNHN-F A22688); the length of the interambulacral plate 1 is about 11% TL. Lunules radially elongate, ovoidal (mean SI=1.6), never narrow. The lunules outline may be different even in the same specimen. Size is variable (range WI=32–142, mean WI=106). They are rather far from the tip of the corresponding posterior petal (range L3=7–15% TL), the space is occupied by three to five plates. Peristome middle-sized (ø ps=4.5% TL), opening sub-centrally. Periproct middle-sized (ø pc=2.3% TL) and close to margin (mean L11=5.6% TL, range L11=2.8–8.2% TL), it opens close to the conjunction of plates 5.a.2–5.a.3-5.b.3. Food grooves: as in the diagnosis of the genus (Fig. 74).

DISTRIBUTION. Rupelian of S. Gemme, Ariège, and Saint Albert (Gironde, France). Cited by Labrie (1904) at Pellegrue and by Tournouer (1870) at Meilhan. Cited by Chauzac & Roman (1994) also in the Chattian of Abesse (southern Aquitaine, France).

REMARKS. *Paraamphiope agassizi* differs from *P. raimondii* by much larger basicoronal circlet, much smaller and less radially elongate lunules. *Paraamphiope agassizi* has tubercles along the perradial sutures as in *P. arcuata*, but differs from it by the higher whole number of plates in the interambulacrum 5 and in ambulacra I and V and the lunules closer to the tips of the posterior petals.

Paraamphiope cherichirensis (Thomas et Gauthier in Gauthier, 1889) - Figs. 175–179; Figs. 89, 90

1889. *Amphiope cherichirensis* Thomas & Gauthier: p. 104; pl. II, figs. 9–11

1914. *Amphiope cherichirensis* Gauthier - Cottreau: p. 138

1925. *Amphiope cherichirensis* Gauthier - Lambert & Thiéry: p. 122.

TYPE LOCALITY. Djebel Cherichira, near El Houfia, Kairouan (Tunisia). Burdigalian.

TYPE MATERIAL. Holotype (MNHN-F R62290).

OTHER EXAMINED MATERIAL. A large fragment from the type-locality (MNHN-F-R62288) and an almost complete specimen (MNHN-F R67287) from the Burdigalian of Bou Golrine (Tunisia).

DESCRIPTION. Middle-sized species (max TL=75 mm), wider than long (mean TW=123% TL), with the anterior part restricted. Margin thin, with shallow to rather deep notches in correspondence of the anterior paired ambulacra. Test low (mean TH=10% TL). Internal structure: although the X-ray photograph is not clear, due to the poor preservation of the studied specimen, the central hollow is small, likely equaling the size of the petalodium. Internal ballast system very dense. Apical disc slightly anteriorly eccentric (L4=56% TL) and large (10% TL); structure not visible. Petalodium wide (PL=50% TL). Posterior petals shorter than the frontal petal (mean L9=84% L5). L6=50% L5, L10=46% L9. Poriferous zones about the same width of an interporiferous one. The space between the posterior petal tip and the corresponding lunule (range L3=6-8% TL) is occupied by three or four plates in each column. In the oral interambulacrum 5 (MNHN-F R67287) column "b" is made of three post-basicoronal plates, column "a" at least of two (possibly, also a part of the third). Lunules middle-sized (mean WI=140), radially elongate, ovoidal (mean SI=1.4). The plate arrangement around the lunules is characteristic, with three or four plates in each column separating the tip of each petal from the corresponding lunule (range L3=7.6–9). Peristome small and subcentral (L12≈60% TL). Periproct small, close to the posterior margin, it opens near the conjunction of plates 5.a.2–5.b.2–5.b.3 (taken from MNHN-F R67287). Food grooves well branched and not reaching the margin.

DISTRIBUTION. Burdigalian of Djebel Cherichira valley and Bou Golrine (Tunisia).

REMARKS. *Paraamphiope cherichirensis* differs from *P. agassizi* by its wider test (TW=123% TL against 110) and much wider ß angle (mean 100°, against 78°). It is distinguished from *P. arcuata* by

the presence of 5 couples of plates around the lunules on the oral face, instead of 4, and larger petalodium (PL=47–49% TL against 42–47). *Paraamphiope raimondii* has smaller petalodium (PL=42%TL) and more radially elongate lunules. *Paraamphiope baquiei* has much smaller test with different outline, more rounded lunules, larger stoma, lower total number of plates in the posterior ambulacra (13–14 against 14–15) and much smaller petalodium.

Paraamphiope baquiei (Lambert, 1907)
Figs. 159, 160; Figs. 171–174; Figs. 58, 59, 61

1907. *Amphiope Baquiei* Lambert: pp. 56-57; pl. 2
1912. *Amphiope Baquiei* Lambert - Lambert: pp. 83-84; pl. 5, figs. 6, 8; pl. 6, fig. 4.

TYPE LOCALITY. The species was originally described by Lambert (1907) from the "Helvétien" of St-Chrystol, near Nissan (Hérault). The neotype subsequently designated by Lambert (1912) was from Blanqui near Cucuron (Vaucluse - France), Tortonian, after Roman (1974).

TYPE MATERIAL. The "type" described by Lambert (1907) was lost just a short time after the institution of the species. The neotype was available to study at the MRA (3.000.154).

OTHER EXAMINED MATERIAL. Three whole specimens, one of them (MNHN-F A22689-L18452) from Cucuron, another (MNHN-F A22691 L18454) from S. Restitute (Drôme), the third (MNHN-F A22690-L18453) from S. Paul Trois Châteaux.

DESCRIPTION. Very small-sized species (TL=20–38 mm). Test a little wider than long (mean TW=110% TL), with the anterior part restricted and rounded posteriorly. Test low (mean TH=10% TL). Margin rather thin with shallow sinuosities in correspondence of the anterior ambulacra. Internal structure: central hollow sub- pentagonal. From the rear wall to the front, the length of the hollow roughly corresponds to PL. Radial cavity: as in the diagnosis of the genus. Internal buttress system very reduced around the central hollow, the peripheral ballast system is densely packed above all close to the test margin. Apical system slightly anteriorly eccentric (L4=56% TL) and middle-sized (8.4% TL). Petalodium rather

small (mean PL= 46.5% TL). Posterior petals shorter than the frontal one (mean L5=24%TL, L9=20% TL); the width of the petals is comparable: L6=12% TL, L10=12% TL. Interporiferous zone 1.5 times larger than a poriferous one. Petals likely open distally. Tips of the posterior petals rather far from the corresponding lunules (mean L3= 9% TL), the space is occupied by two or three plates in each column. Basicoronal circlet large (L13=15.9% TL). The length of plate 1 in the oral interambulacral 5 is about 10% TL. In the oral interambulacrum 5, columns "a" and "b" are made of only two post-basicoronal plates; plate 5.a.2 has a very broad base and is paired to 5.b.2 but remains in touch with the two post-basicoronal plates of the ambulacra I and V. As a whole, there are only 10 plates per column in the interambulacrum 5. Lunules middle-sized (mean WI=140), subcircular to radially elongate ovoidal (range SI=1.09–1.34); they may be different in the same specimen. They are separated from the respective petal tips by three plates per column. Peristome large (ø ps=5.2% TL), opening subcentrally. Periproct middle-sized (ø pc=2.3% TL), not too far from the posterior margin (L11=8.2% TL); it opens close to the conjunction of plates 5.a.2–5.a.3–5.b.2–5.b.3.

DISTRIBUTION. Langhian-Serravallian of Blanqui, near Cucuron (Vaucluse - France). Saint-Paul-Trois-Châteaux and S. Restitute, may be also Cadenet, near Vaugines (Drome - France). After Lambert (1907) also "Helvétien" of St-Chrystol, near Nissan (Hérault).

REMARKS. *Paraamphiope baquiei* is distinguished mainly by its very small size (mean TL=30 mm), almost rounded lunules and in having only 10 plates on the whole in the interambulacrum 5, the lowest number so far known for an astryclipeid. *Paraamphiope agassizi* differs also by the presence of three to five plates in each column between the tips of the posterior petals and the respective lunules.

Genus *Sculpsitechinus* Stara et Sanciu (2014)

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

TYPE MATERIAL. The neotype (Stara & Sanciu, 2014), represented by a well preserved Recent specimen (MZE.CA.MAC.IVM109) from Tulear, Madagascar.

DIAGNOSIS. Partially emended from Stara & Sanciu (2014):
- Test flat with thin margin. Oral face flat to slightly concave.
- Internal visceral hollow almost as wide as the petalodium, sub-circular to polygonal in shape, with walls reinforced by a network of thin trabeculae.
- Apical disc monobasal, subcentral or slightly anterior to centre, with four small gonopores.
- Interambulacra a little wider than ambulacra at the ambitus.
- All five petals similar in length; the anterior one sometimes longer. Petalodium generally small, ranging from PL=30 to 48% TL. In a Recent Iranian population, it reaches 60% TL (Fatemi et al., 2016). Petals well developed and often open distally; angle ß= 48–70°.
- Three to four post-basicoronal plates per column in interambulacrum 5, with the first two normally partially paired (or slightly staggered) and normally with only the plate 5.b.2 in contact with the adjacent ambulacral plates.
- Width of the interambulacrum 5 at the margin about 30–38% TL.
- Basicoronal circlet pentastellate with interambulacral plates sometime elongated distally and commonly separated from the post-basicoronal ones.
- Two radially elongate ellipsoidal lunules or slit-like notches present in the posterior ambulacra; two to five couples of plates separate the tip of the petals from the corresponding lunules.
- Peristome small, subcentral or slightly anteriorly located.
- Periproct circular, small, rather far from the posterior margin (L11>12% TL; mostly 13÷26% TL).
- Main food grooves strongly branched; several short and fine secondary ramifications branch off distally and also along their middle part. Tube-feet extending into the interambulacral zones.
- Tuberculation dense, made of very small, perforate and crenulate tubercles, which are larger on the oral side.

DISTRIBUTION. Early Miocene of France, Middle

Miocene of Papua New Guinea and Pliocene of Red Sea (Egypt) and Khark Island, Persian Gulf (Iran). Recent: Red Sea, Persian Gulf, Indian Ocean, Australia, Indonesian Archipelago and West-Pacific.

Species included:

- *Sculpsitechinus auritus* (L. Agassiz, 1838), Recent; Madagascar, Red Sea, Indian Ocean and West Pacific.
- *Sculpsitechinus tenuissimus* (L. Agassiz, 1847), Recent; Indonesia, New Caledonia, Papua New Guinea and Palau, Micronesia.
- *Sculpsitechinus boulei* (Cottreau, 1914), Early Miocene, France.
- *Sculpsitechinus* sp. 1 Stara & Sanciu (2014), Recent, Philippines.
- *Sculpsitechinus* sp. 2 Stara & Sanciu (2014), Middle Miocene, Papua New Guinea.
- *Sculpsitechinus iraniensis* Fatemi, Attaran-Fariman et Stara, 2016, Recent; Chabahar Bay, Persian Gulf.

Species previously assigned to *Amphiope* herein transferred to the genus *Sculpsitechinus*:

Sculpsitechinus boulei (Cottreau, 1914)
Figs. 180–184; Figs. 79–81

1914. *Amphiope boulei* nov. sp. Cottreau: pp. 92–94; figs. 17–18; pl. 5, fig. 9
1915. *Amphiope boulei* Cottreau - Lambert: p. 219
1988. *Amphiope boulei* Cottreau - Philippe: pp. 167–169; pl. 16, fig. 9.

TYPE LOCALITY. Carry-le-Rouet (Bouche du Rhône - France). Aquitanian.

TYPE MATERIAL. Holotype (MNHN-F R62136).

DESCRIPTION. Medium sized test (TL ≈ 95 mm), slightly longer than large (TW=97% TL). Outline likely roundish, with the anterior part slightly restricted. The test is very low (TH=8% TL), with highest point anterior to the apical disc. Oral face flat, with interambulacral areas slightly inflated and ambulacral areas with a shallow and broad depression deepening towards the peristome. Margin rather thin with shallow notches in correspondence of the anterior paired ambulacra. Internal structure: central hollow sub-circular and

very small (Fig. 180). Ten cavities branch from the central hollow along the ambulacra and the interambulacra; the longest one extends along the interambulacrum 5 and leads to the periproct. The internal structure is reduced anteriorly and becomes denser only towards the posterior test margin. Apical system slightly anteriorly eccentric (L4 about 56% TL) and medium-sized. Petalodium small (PL=47% TL). Posterior petals shorter than the frontal one (L5=23% TL, L9= 20% TL), their width is proportionally almost comparable (L6 and L10=10% TL). In the posterior petals the width of the interporiferous and poriferous zones is 2.9% and 3.9% TL, respectively. In the frontal ambulacrum, the width of an interporiferous zone is 1.3 times that of the poriferous one. Petals likely open distally. In the oral interambulacrum 5, column "b" is made of three post-basicoronal plates column "a" of two and a small part of the third (Fig. 81). Plate 5.a.2 is almost paired to 5.b.2 but remains in touch with the two post-basicoronal plates of the ambulacra I and V. As a whole, there are 12–13 plates in each column of the interambulacrum 5. Lunules small (WI=71), radially elongate, ovoidal (SI=1,6). The tips of the posterior petals are rather far from the corresponding lunules (L3=11% TL) and separated by four plates per column. Peristome middle-sized (ø ps=4% TL), opening centrally. Periproct wide (ø pc=4% TL), rather far from the posterior margin (L11= about 12% TL) and opening at the conjunction of plates 5.a.2–5.b.2-5.b.3. Food grooves very branched distally; however, only a part of the secondary branches are visible due to the bad preservation of the oral surface.

DISTRIBUTION. Aquitanian of Carry-le-Rouet (Bouche du Rhône - France).

REMARKS. *Sculpsitechinus boulei* is distinguished from *S. auritus*, *S. iraniensis* and *Sculpsitechinus* sp.1 in having elliptical lunules, instead of open notches. It differs from *S. tenuissimus* by its smaller lunules, which are not elongate and closer to the posterior margin, by much large petalodium (mean PL=47% TL against 30%). *Sculpsitechinus boulei* is apparently close to *Sculpsitechinus* sp. 2, however they are here maintained separate, since the plate-patterns are unknown and they likely lived in different climatic and paleoecological conditions.
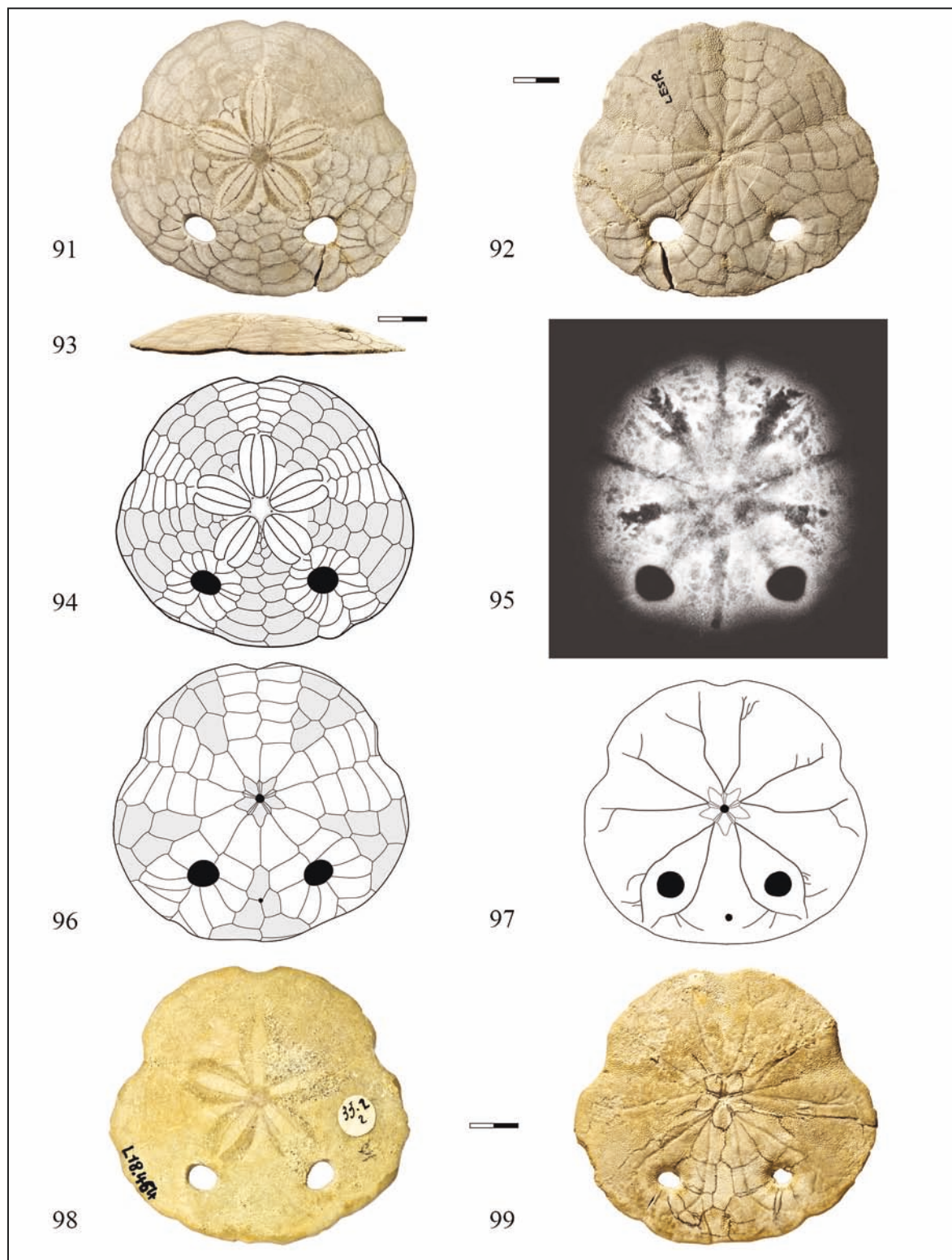
Figures 91–99. *Amphiope bioculata.* Aboral (Fig. 91), oral (Fig. 92) and lateral (Fig. 93) views of the specimen that will be proposed as neotype (MNHN-F.A 57777), from Lespignan. Fig. 94, 96: scheme of aboral and oral faces. Fig. 95, 97: radiograph and food grooves scheme, respectively of the proposed neotype (MNHN-F.A 57777). Figs. 98, 99: aboral and oral view of a spe- cimen (MNHN-F.A22701.L18464e) from Nissan les Tuilières.
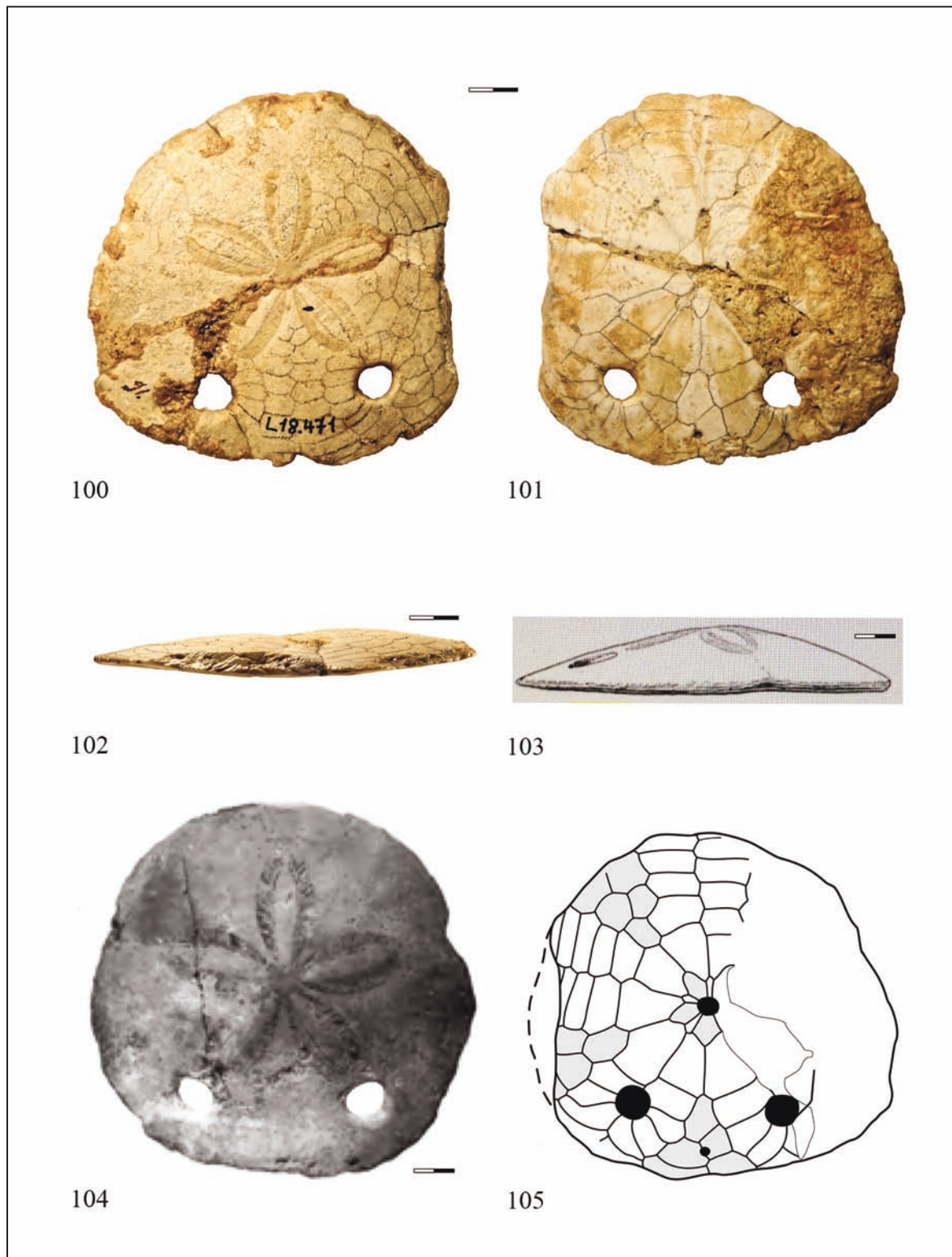
Figures 100–105. *Amphiope elliptica*. Aboral (Fig. 100), oral (Fig. 101), lateral (Fig. 102) views and (Fig. 105) adoral scheme of specimen (MNHN-F.A22706-L18.471) from Carry-le-Rouet (Bouche du Rhône, France); Mold T9 of the type: lateral drawing (Fig. 103) and aboral view (Fig. 104), from Cottreau (1914).
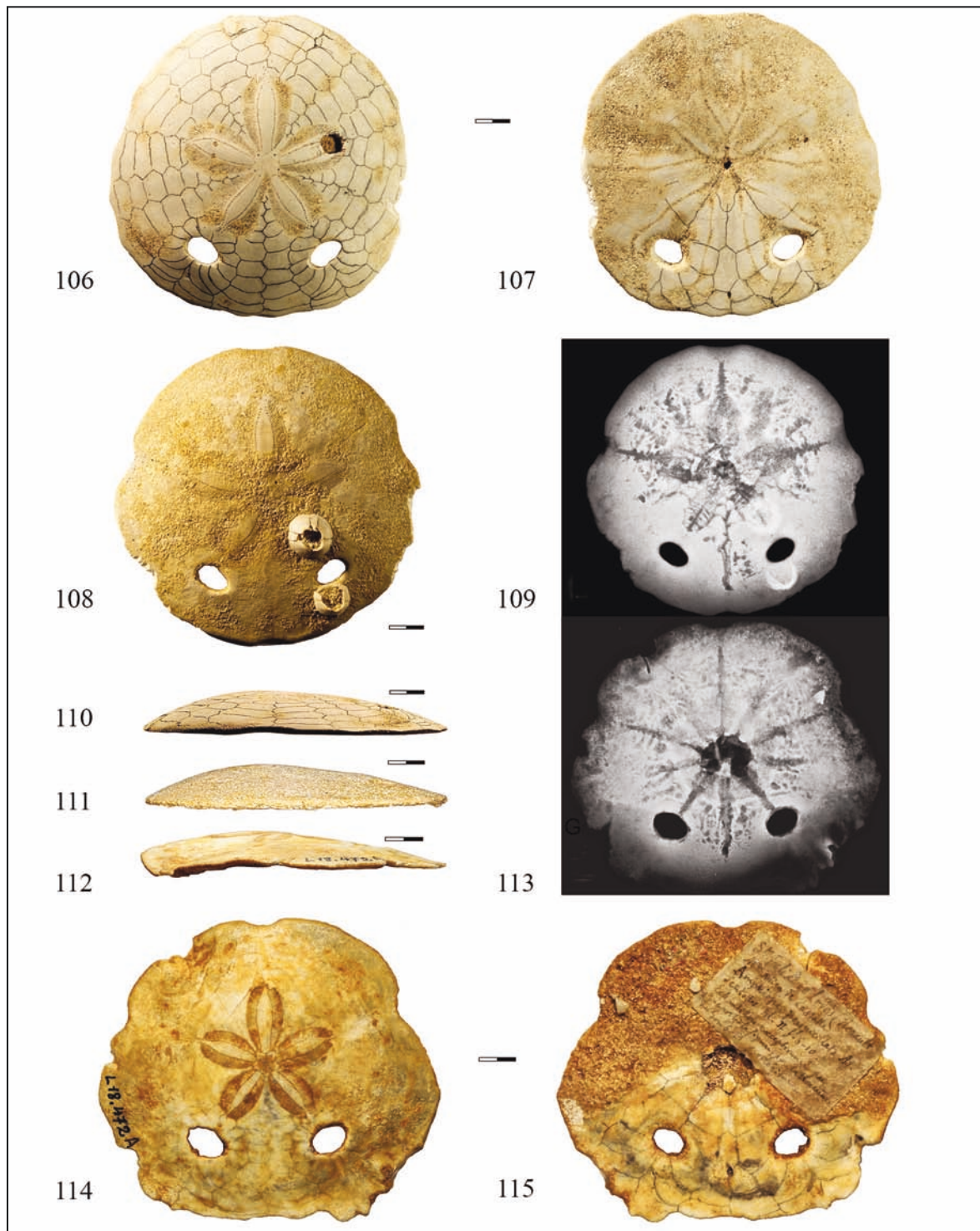
Figures 106–115. *Amphiope ovalifora* (Figs. 106–111) and *A. lorioli* (Figs. 112–115). Figs. 106, 107, 110: *A. ovalifora,* aboral, oral and lateral views (MNHN-F. A22710 L18.477c), topo-typic specimen from Gornac (France): the test surface has been artificially abraded to highlight the plating structure. Figs. 108, 109: specimen MNHN-F. A22710 L18.477l, from Gornac, Fig. 108: aboral view, Fig. 109: radiography showing the high density of the internal support system towards the margin in this species; Fig. 111: lateral view. Figs. 112–115: *A. lorioli,* topotypic specimen from St-Félix-de-Lodez (Hérault - France). Specimen (MNHN-F A22707-L 18472Aa): lateral (Fig. 112), aboral (Fig. 113) and oral (Fig. 114) views; radiography (Fig. 115) showing the high density of the internal support system only towards the margin in this species.
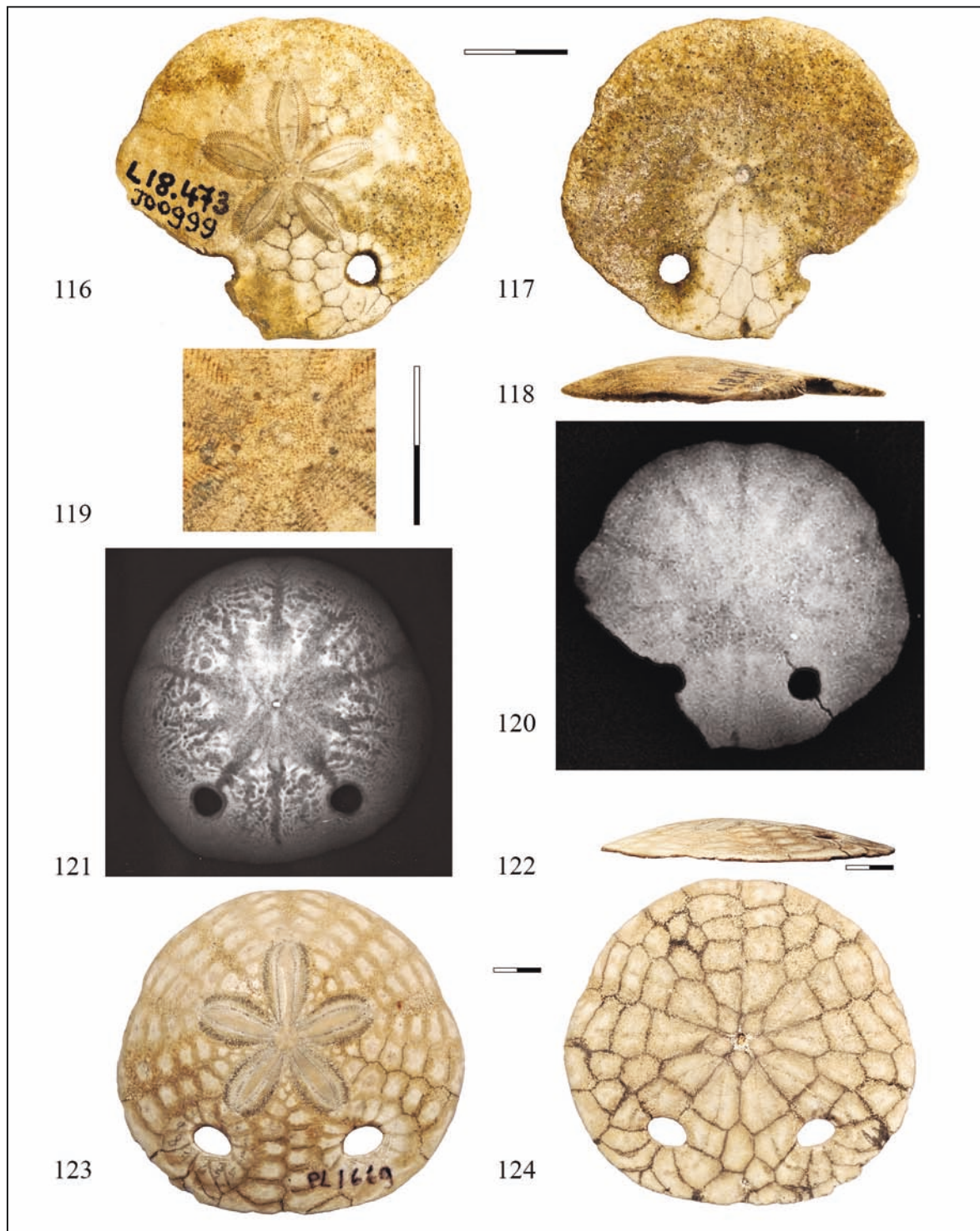
Figures 116–124. *Amphiope ludovici* (Figs. 116–120) and *A. romani* n. sp. (Figs. 121–124). *Amphiope ludovici*: syntype (MNHN-F.J00999 L18473) from Blanqui (Vaucluse - France). Aboral (Fig. 116), oral (Fig. 117) and lateral (Fig. 118) views; magnification of the apical system (Fig. 119) highlighting the presence of 4 gonopores in adult individuals, radiography (Fig. 120). *Amphiope romani* n. sp., holotype (MNHN-F.A57780.PL1669) from Channay-sur-Lathan, Touraine (France): radiography (Fig. 121) and lateral (Fig. 122), aboral (Fig. 123) and oral (Fig. 124) views; the test surface has been partially abraded to highlight the sutures between the plates.
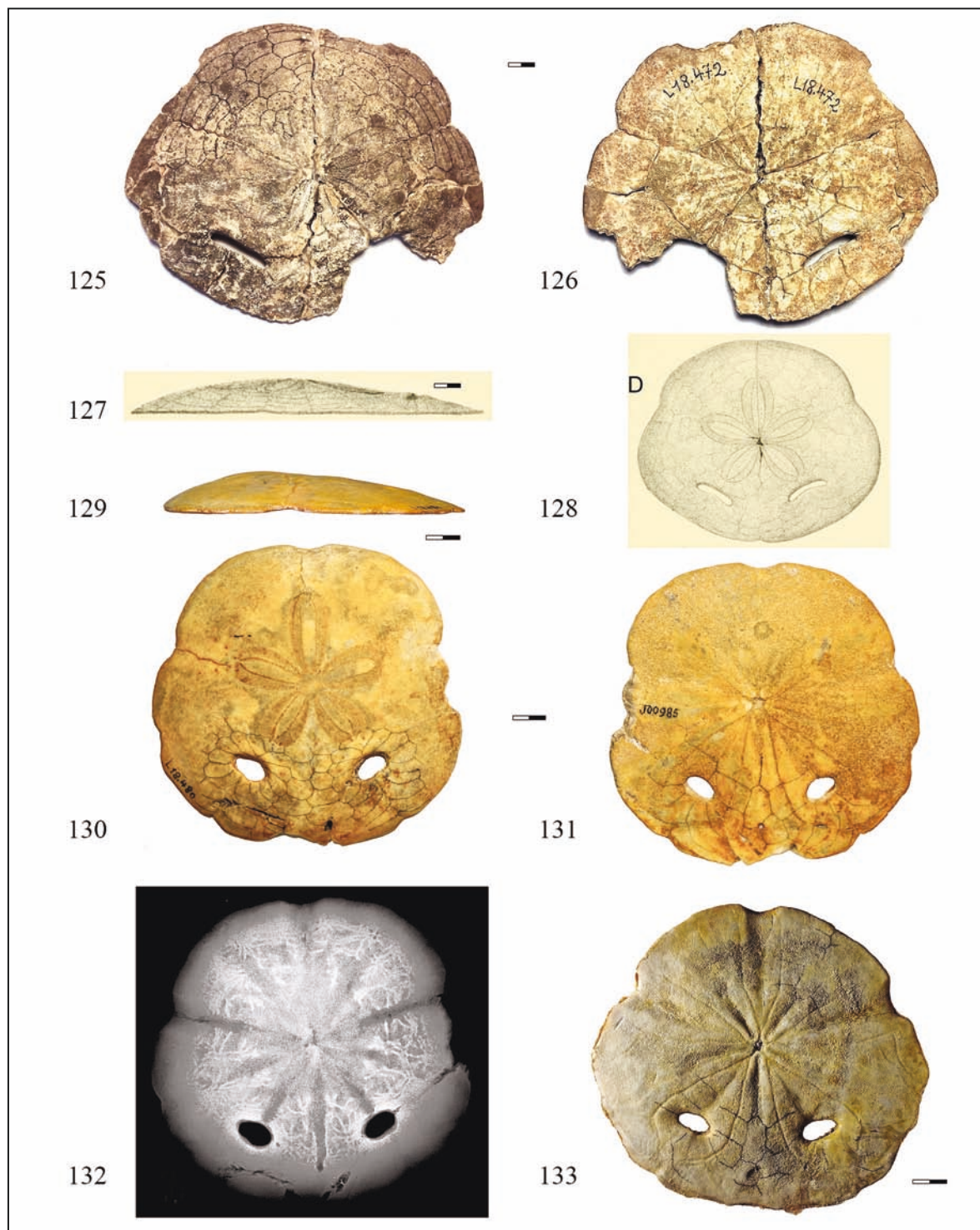
Figures 125–133. *Amphiope hollandei* (Figs. 125–128) and *A. sarasini* (Figs. 129–133). *Amphiope hollandei*, holotype from Bonifacio (Corsica, France): aboral (Fig. 125) and oral (Fig. 126) views; subjective reconstruction (Figs. 127, 128) reported in Cotteau (1877: pl. 9, figs. 6, 7). *Amphiope sarasini*, syntype (MNHN-F J00985.L18480) from Cruzy: lateral (Fig. 129), aboral (Fig. 130) and oral (Fig. 131) views and radiography (Fig. 132); oral face view (Fig. 133), taken with grazing light to highlight depressions and food grooves in specimen MNHN-F.A.57789 from Cruzy.
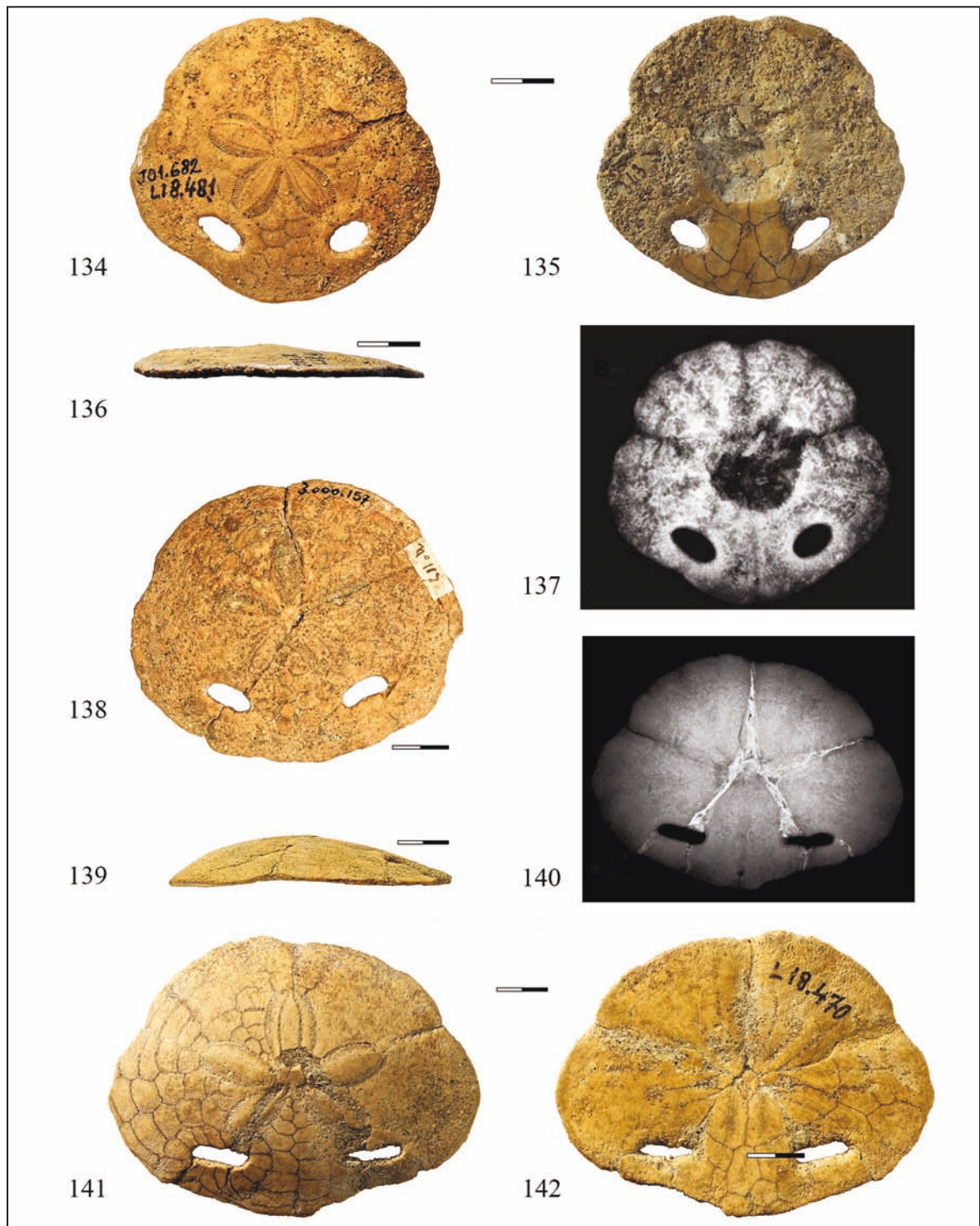
Figures 134–142. *Amphiope transversifora* (Figs. 134–137) and *A. deydieri* (Figs. 138–142). *Amphiope transversifora*, syntype (MNHN-F J01682): aboral (Fig. 134), oral (Fig. 135) and lateral (Fig. 136) views; radiography (Fig. 137). *Amphiope deydieri* holotype (MRA3.000.157 (117), from Vaugines, aboral view (Fig. 138); specimen MNHN-F.A22705.L18.470b from Cadenet, Vaugines (Vaucluse - France): lateral (Fig. 139), aboral (Fig. 141), oral (Fig. 142) and radiography (Fig. 140).
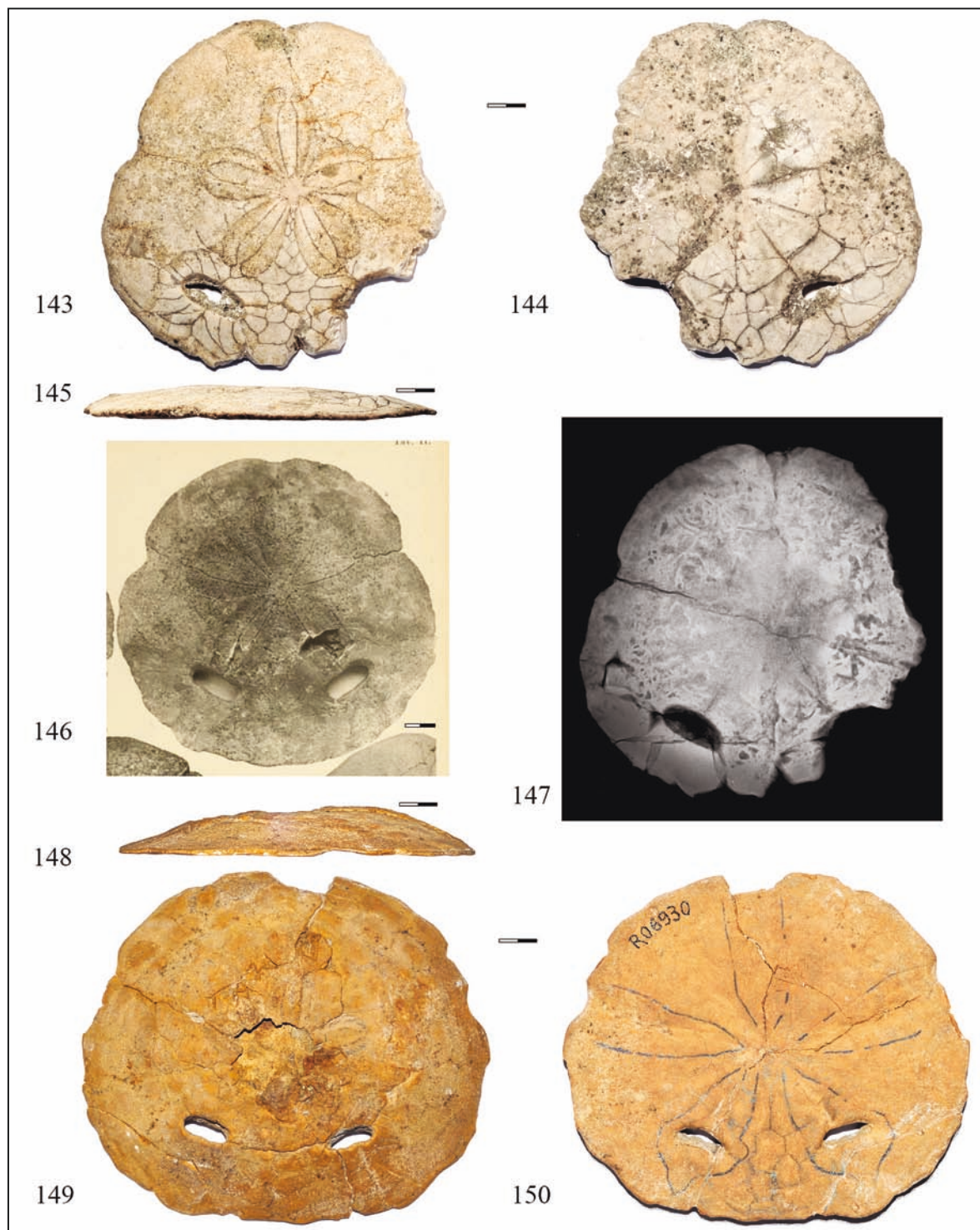
Figures 143–150. *Amphiope pallavicinoi* (Figs. 143–147) and *A. tipasensis* (Figs. 148–150). *Amphiope pallavicinoi*, neo-type MDLCA 23583 from Bessude (Italy): aboral (Fig. 143), adoral (Fig. 144) and lateral (Fig. 145) views, original il-lustration (Lovisato, 1914) of a specimen from Torralba (Fig. 146) and radiography (Fig. 147). *Amphiope tipasensis*, holotype (MNHN-F.R06930), from Tipasa province (Algeria): lateral (Fig. 148), aboral (Fig. 149) and adoral (Fig. 150) views.
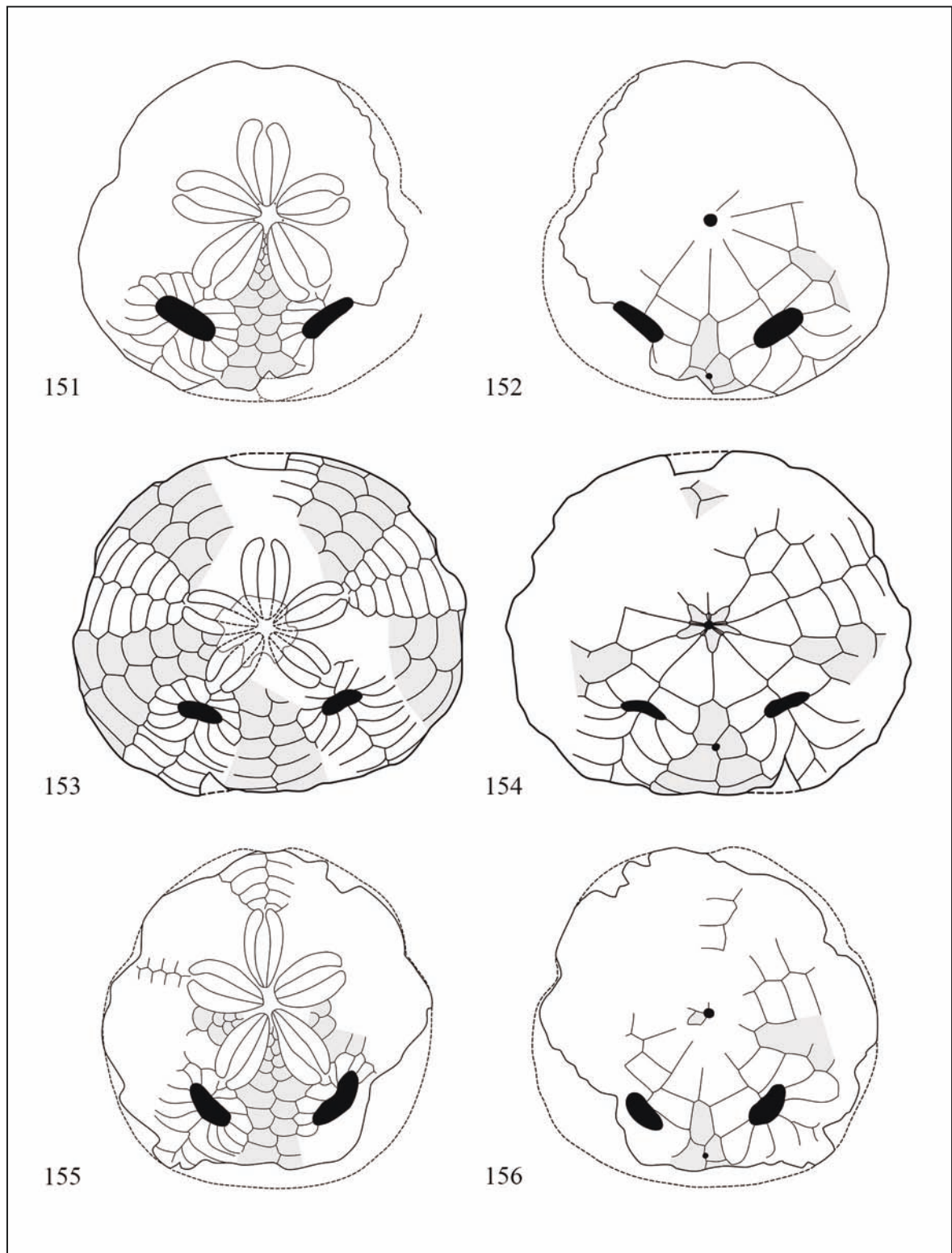
Figures 151–156. Aboral and oral plating schemes of *Amphiope pallavicinoi* (MDLCA 23583) (Figs. 151, 152), *A. tipasensis* (MNHN-F.R06930) (Figs. 153, 154) and *A. palpebrata* (MNHN-F. L18.478) (Figs. 155, 156).
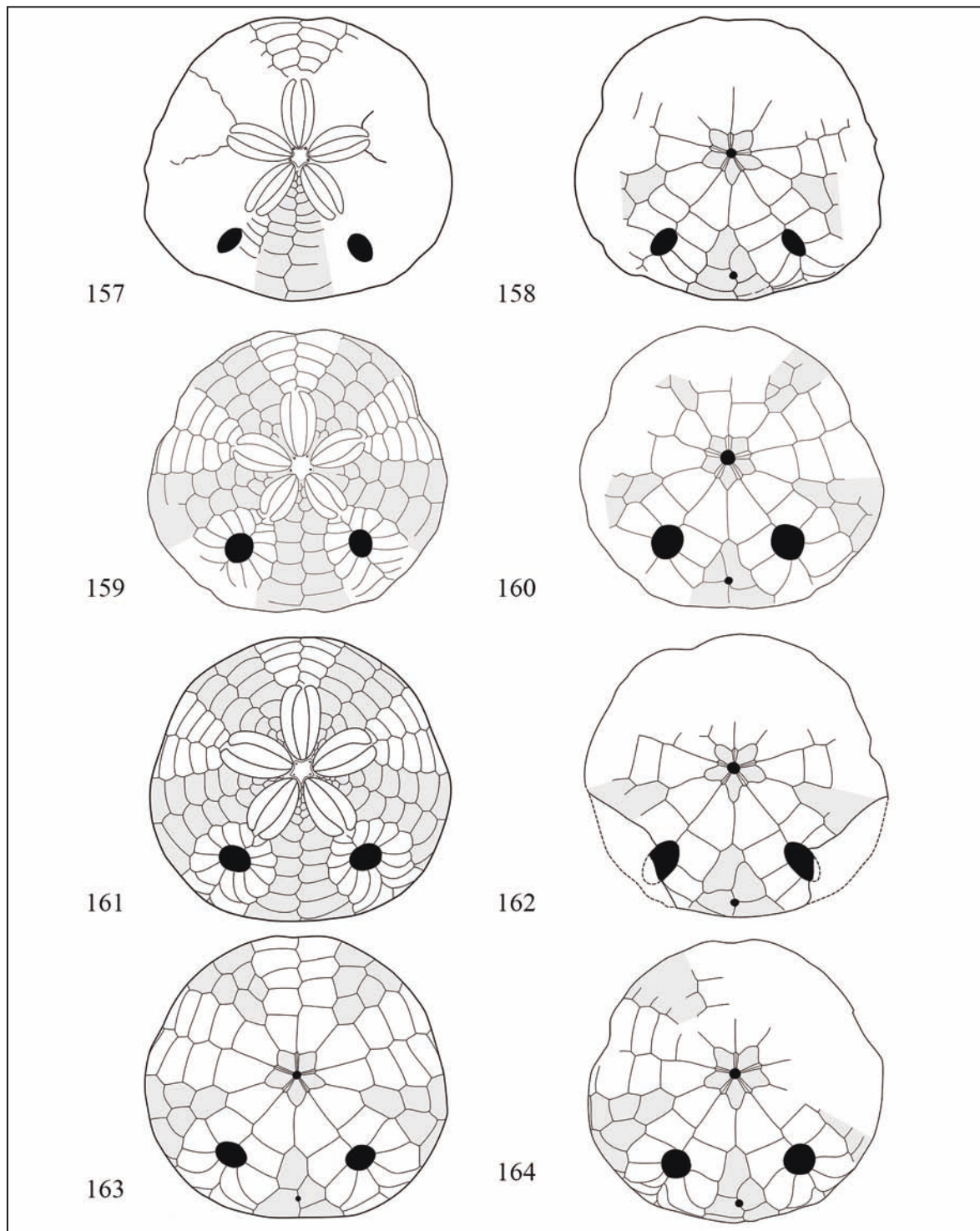
Figures 157–164. Oral and/or aboral plating schemes of two species belonging to *Amphiope* and two belonging to *Paraamphiope*. Figs. 157, 158: *Paraamphiope agassizi* (MNHN-F.A22688), from Montségur. Figs. 159, 160: *P. baquiei* (MNHN-F A22689-L18452), from Cucuron. Figs. 161, 163: *A. romani* n. sp. (MNHN-F.A57780.PL1669), from Channay-sur-Lathan. Fig. 162: *P. agassizi* (MNHN-F. A22687), from Pellegrue. Fig. 164: *A. romani turonensis* (MNHN-F.A22713. L.18482a), from Oisly.
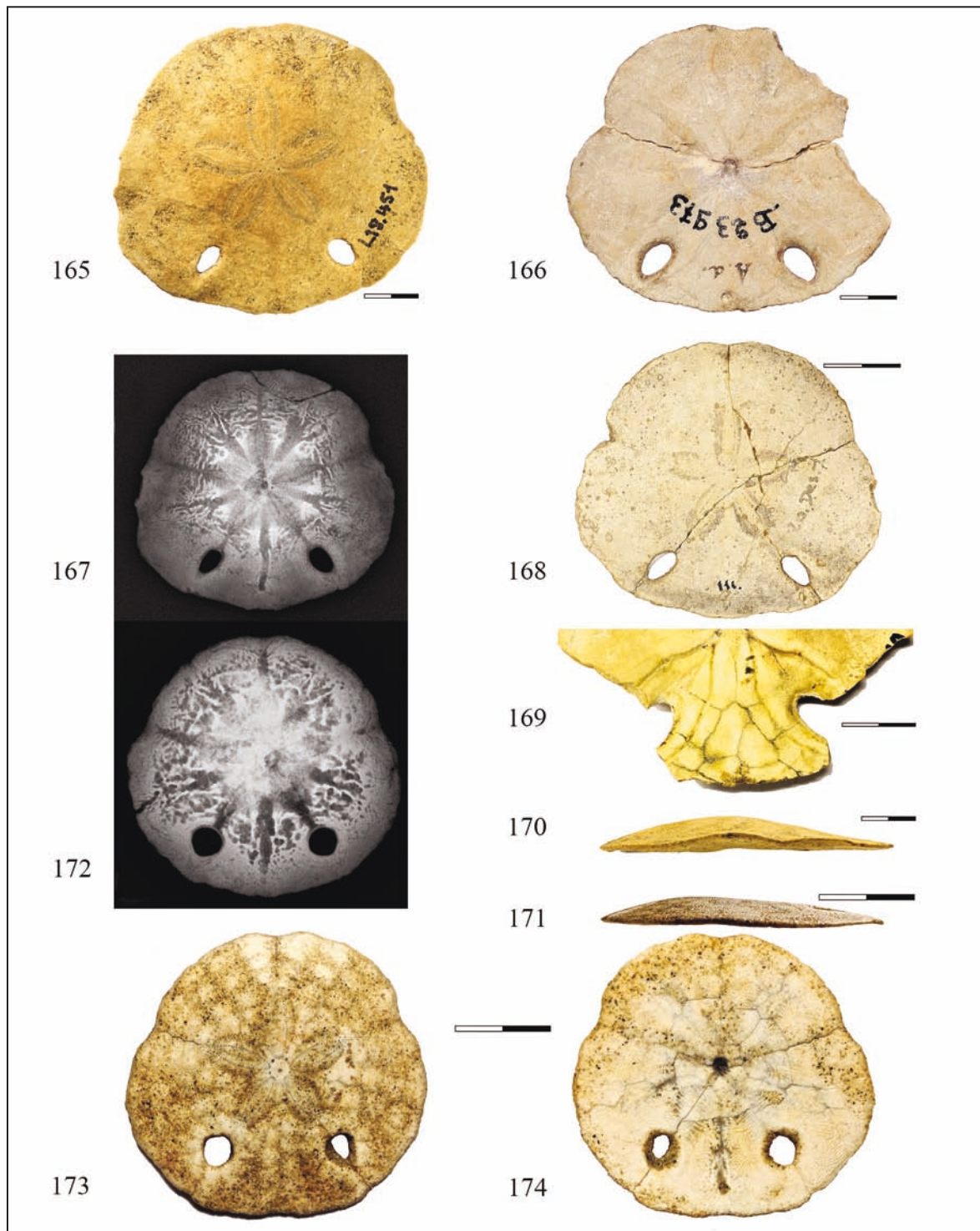
Figures 165–174. *Paraamphiope agassizi* (Figs. 165–170) and *P. baquiei* (Figs. 171–174). *Paraamphiope agassizi*, specimen MNHN-F.A22688.L18.451, from Montségur: aboral (Fig. 165) and lateral (Fig. 170) views and radiography (Fig. 167); syntype (MNHN-F. B23973) from Montségur (Gironde), oral view (Fig. 166); syntype (MHNBx 111 6.194) from S. Albert (Gironde) (Fig. 168); specimen MNHN-F.A22687.L18.450-sn2, from Pellegrue: oral view (Fig. 169) highlighting the almost paired first postbasicoronal plates in the interambulacrum 5. *Paraamphiope baquiei*, specimen MNHN-F.A22689.L18452, from Cucuron (France): lateral (Fig. 171), radiography (Fig. 172), aboral (Fig. 173) and oral (Fig. 174) views.
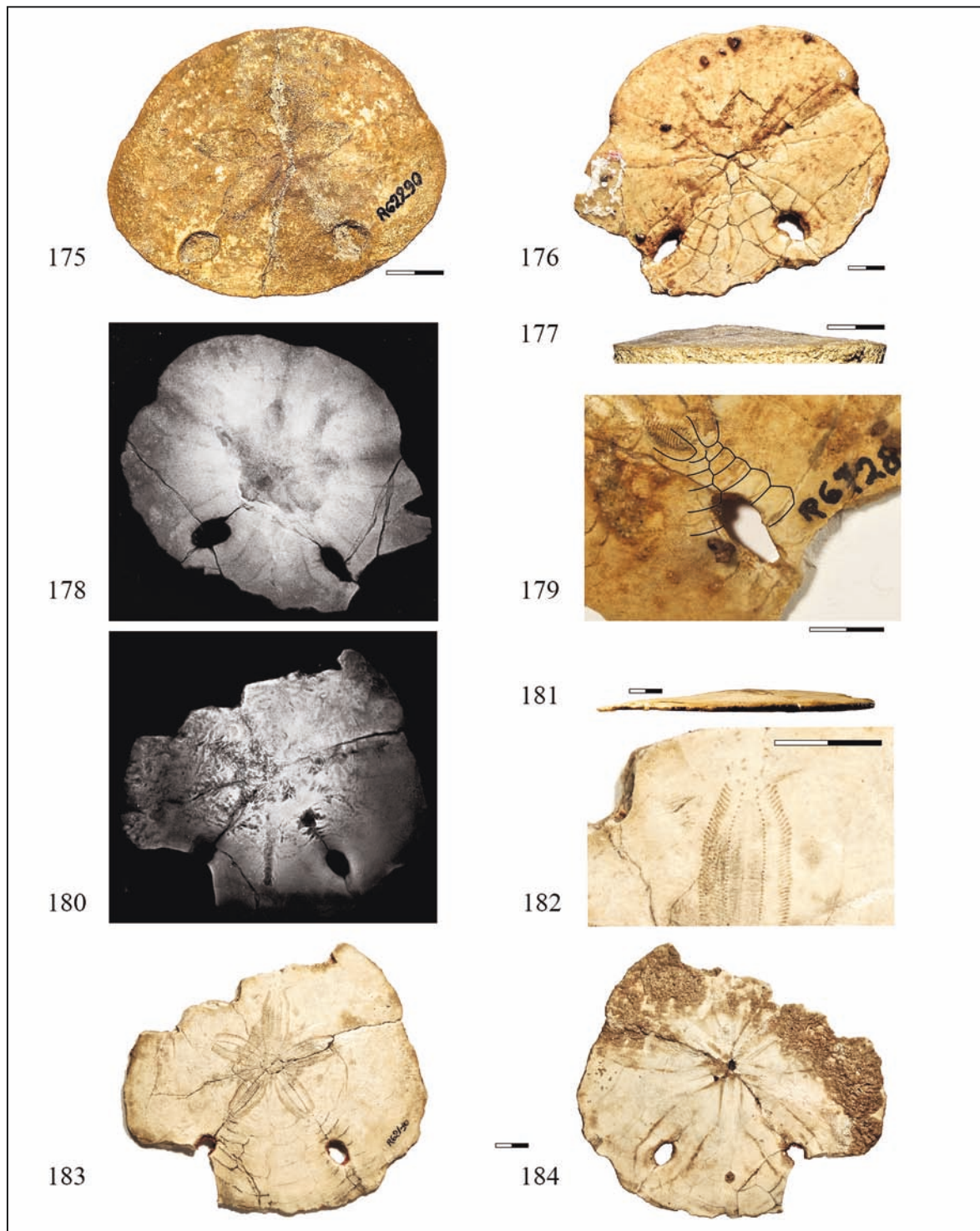
Figures 175–184. *Paraamphiope cherichirensis* (Figs. 175–179) and *Sculpsitechinus boulei* (Figs. 180–184). *Paraamphiope cherichirensis*, holotype (MNHN-F.R62290), from Djebel Cherichira (Tunisia): aboral (Fig. 175) and lateral (Fig. 177) views; specimen (MNHN-F.R62288) from Bou Golrine (Tunisia): oral view (Fig. 176), radiography (Fig. 178) and close up (Fig. 179) of the aboral face showing the plates between the petal tip and the lunule. *Sculpsitechinus boulei*, holotype (MNHN-F R62136), from Carry le Rouet (France): radiography (Fig. 180), lateral view (Fig. 181) and close-up of the left anterior paired front petal (Fig. 182); aboral (Fig. 183) and oral (Fig. 184) views.

Species	New arrangement / validity	Type locality	Stratigraphy	Type material
A. bioculata (Des Moulins, 1837)	valid	Sure, près Bollène (unknown locality)	unknown	sintype (MNHBX 2014.6.189)
		Lespignan (Hérault - France)	Langhian-Serravallian	neotype (MNHN-F.A57777)
A. perspicillata Agassiz, 1841	species inquirenda	Rennes (France)	unknown	wanting - repository unknown
A. elliptica Desor, 1847	valid	Carry Le Rouet (Bouche du Rhône - France)	late Aquitanian- early Burdigalian	holotype wanting
A. agassizi Des Moulins in Cotteau, 1865	recombined into Paraamphiope agassizi	La Réole and Montségur (Gironde - France)	Rupelian-Chattian (Oligocene)	n. 2 sintypes (MHNBX 111.6-194, MNHN B23973)
A. ovalifora (Des Moulins in Benoist, 1875)	valid	Gornac (Gironde - France)	early Aquitanian	n. 2 sintypes (MNHBx 2014.6.180.2)
A. hollandei Cotteau, 1877	valid	Bonifacio (Corsica - France)	Burdigalian	holotype (MNHN-F A22378. L18472)
A. arcuata Fuchs, 1882	recombined into Paraamphiope arcuata	Oasis Siouah (Egypt)	Middle Miocene	holotype illustrated, but its repository is unknown
A. truncata Fuchs, 1882	not belonging to Amphiope, not discussed here	Oasis Siouah (Egypt)	Middle Miocene	?
A. styriaca Hoernes, 1883	nomen dubium	Leibnitz (Austria)	Langhian	holotype (UGP 1880.XX.5)
A. palpebrata Pomel, 1887	valid	Algeria	Burdigalian	only a topo-typic specimen (MNHN. L18.478)
A. depressa Pomel, 1887	valid	Algeria	"Helvétien"	repository unknown
A. personnata Pomel, 1887	species inquirenda	Algeria	Burdigalian	repository unknown; type locality untraceable
A. villei Pomel, 1887	species inquirenda	Algeria	Burdigalian	repository unknown; type locality untraceable
A. fuchsi Fourtau, 1899	junior synonym of A. truncata not belonging to Amphiope not discussed here	unknown locality (Egypt)	Middle Miocene	?
A. cherichirensis Thomas & Gauthier, 1889	recombined into Paraamphiope cherichirensis	Djebel Cherichira (Tunisia)	Burdigalian	holotype (MNHN-F-R62290)
A. dessii Lovisato in Cotteau, 1895	species inquirenda	Nurri (Sardinia - Italy)	Burdigalian	type series lost in 1943 type locality unknown
A. lovisatoi Cotteau, 1895	valid	Chiaramonti (Sardinia)	late Burdigalian	neotype (MAC.PL1706)
A. koehleri Mortensen, 1905	not discussed here	?	?	?
A. neuparthi De Loriol, 1905	valid	Angola	Burdigalian	sintype (LNEG)
A. baquiei Lambert, 1907	recombined into Paraamphiope baquiei	Cucuron (Vaucluse - France)	Langhian-Tortonian	neotype (MRA 3.000.154)
A. lorioli Lambert, 1907	valid	St-Félix-de-Lodez (Hérault - France)	Langhian-Tortonian	(MNHN-F A22707-L 18472A)

Table 1/1. Summary list of the Astrilypeidae taxa examined in this work. Data concerning the taxonomic arrangement, type locality/type area, stratigraphy and repository of the type material have been updated, for each taxon, when possible.

Species	New arrangement / validity	Type locality	Stratigraphy	Type material
A. duffi Gregory, 1911	not belonging to *Amphiope* not discussed here	Cirenaica (Libya)	Oligocene	Two syntypes: (NHMUK CY66/E11350, Cy264/ E11349)
A. montezemoloi Lovisato, 1911	valid	S. Giorgio (Sardinia - Italy)	Burdigalian-early Langhian	neotype (MAC.PL1827)
A. sarasini Lambert, 1912	valid	Cruzy (Hérault - France)	Tortonian	syntype (MNHN-F J00985)
A. transversifora Lambert, 1912	valid	Saint-Paul-Trois-Châteaux (France)	Langhian	sintype (MNHN-F J01682)
A. deydieri Lambert , 1912	valid	Vaugines (Vaucluse - France)	Langhian-Serravallian	holotype (MRA 3.000.157)
A. laubei Lambert, 1912	nomen dubium *	Niederkreuzstetten (Austria)	late Burdigalian	holotype (NHMW 1849.XX. 39)
A. pallavicinoi Lovisato, 1914	valid	Ploaghe, the type-stratum crops out also at Bessude (Sardinia - Italy)	late Burdigalian-Langhian ?	type series lost - neotype MDLCA 23583
A. calvii Lovisato, 1914	species inquirenda	Torralba (Sardinia - Italy)	late Burdigalian-Langhian ?	type series lost type locality untraceable
A. boulei Cottreau, 1914	recombined into *Sculpsitechinus boulei*	Carry-le-Rouet (Bouche du Rhône - France)	Aquitanian	holotype (MNHN-F R62136)
A. ludovici Lambert, 1915	valid	Cucuron (Vaucluse - France)	Tortonian	n.2 sintypes (MNHN J00999 L18473, L18474)
A. bioculata aequipetala Lambert 1915	subspecies inquirenda.	Montréal (Gers - France)	Burdigalian-Serravallian ?	repository unknown
A. doderleini Lambert & Thiéry 1921	junior synonym of *Echinodiscus truncatus* (Agassiz L., 1841)	unknown	Recent	MNHN-F
A. labriei Lambert, 1927	species inquirenda	St-Félix-de-Lodez (Hérault - France)	unknown	repository unknown
A. dallonii Lambert, 1931	species inquirenda	Algeria	Middle Miocene	repository unknown
A.bioculata philodonax Lambert, 1927	subspecies inquirenda	Saucats (France)	Early Miocene	MHNBx 2014.6.189
A. bioculata pelatensis Fabre, 1933	subspecies inquirenda	France	Middle Miocene	repository unknown
A. bioculata bentivegnae Desio, 1934	subspecies inquirenda	Libya	Middle Miocene	repository unknown
A. tipasensis (Aymé & Roman, 1954)	valid	Tipasa (Algeria)	Pliocene	holotype (MNHN-F-R06930)

Table 1/2. Summary list of the Astrilypeidae taxa examined in this work. Data concerning the taxonomic arrangement, type locality/type area, stratigraphy and repository of the type material have been updated, for each taxon, when possible.

PAOLO STARA & ENRICO BORGHI
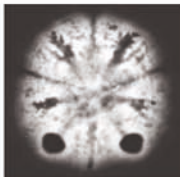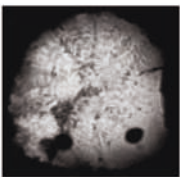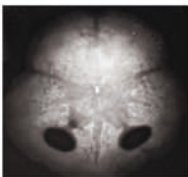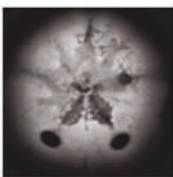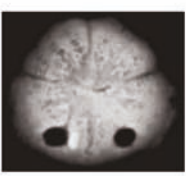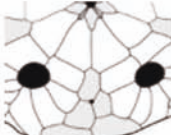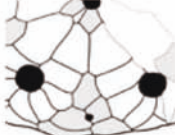
	A. bioculata	A. elliptica	A. lovisatoi	A. ovalifora	A. lorioli
TL (mm)	61	84.5	76	75	88
TH	16.5	17	10.1	13	11.7
TW	107	104	105.4	105	107
Internal structure (X-ray photographs)					
Shape and size of the central hollow	Subpentagonal-starring 50	Roundish -	Roundish to subpentagonal 50	Subpentagonal 46	Subpentagonal-starry 46
Internal test structure	**Very light** - large vacuoles also towards the margin	Light. denser towards the margin	Light very dense near the margin	**Dense**, almost massive towards the margin	Light
Apical disc position (L4)	57	56	62	55	58
Petalodium size (PL)	52	56	52	50	50
N (column a) N (column b)	2-3 3	2 3	2-3 3	2-3 3	2 3
N tot - interambulacrum 5	13-15	14-16	14-16	14-16	15-16
Length of plate 5.b.2	15.6 (27.8)	8 (17)	16 (29.5)	15.8 (25.5)	16 (29)
Lunules: WI SI	114 1.2	82 1.3	180 1,56	127 1.6	75 1.5
Lunules outline and distance from the posterior petals tips					
Periproct position (L11)	11.6	7	12	9.6	11.6
Oral scheme with the position of the periproct					
Remarks	Internal structure very light Plate 5.b.2 short	Basicoronal circlet large, L13=14% TL Plate 5.b.2 short	Margin sharp	Internal structure strong Basicoronal circlet very large (L13 up to 20% TL)	Lunules very small

Table 2/1. Comparison of the main morphological features of the species of *Amphiope* attributed to the informal bioculata group. If not otherwise indicated, the data report the mean value of the biometric measures expressed as % TL. N = number of post-basicoronal plates in the oral interambulacrum 5, N tot = whole number of plates in the interambulacrum 5. Red numbers = maximum values; blue numbers= minimum values.
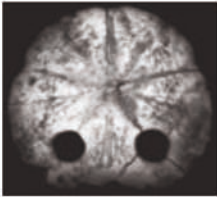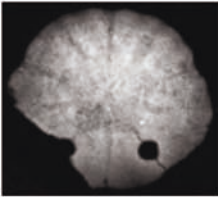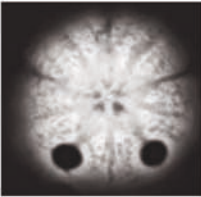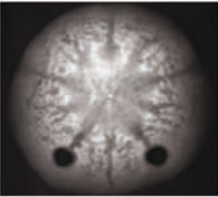
	A. montezemoloi	*A. ludovici*	*Amphiope* sp. 2	*A. romani* n. sp.
TL (mm)	**109**	**29**	**96 (up to 137)**	62
TH	9.8	9	12.3	15
TW	105.7	108	104.7	105
Internal structure (X-ray photographs)				
Shape and size of the central hollow	Subpentagonal-starring 47	Subpentagonal 49	sub-pentagonal 50	Subpentagonal-starring 49
Internal test structure	very light in all the structure	**Very dense** in whole body	well developed	**Very light** very dense near the margin
Apical disc position (L4)	59.3	59	59.7	57.5
Petalodium size (PL)	50	50	52	52
N (column a) N (column b)	2 3-4	2 2	2 3-4	2-3 2
N tot - interambulacrum 5	13+	10-11	14-15	13-14
Length of plate 5.b.2 (distance from the posterior edge of the occlusion point)	13.5 (28)	16 (23)	mean 15.6 (32.2)	16 (25)
Lunules: WI SI	295 1,2	100 1.1	250 1,3	123 1.2
Lunules outline and distance from the posterior petals tips				
Periproct position (L11)	12	4.6	13	5.6
Oral scheme with the position of the periproct				
Peculiar characters	Test and lunules very large	Test very small and low Very dense internal structure Very few plates in Iamb 5 Periproct very close to the posterior test margin	Test very large	Internal structure very light

Table 2/2. Comparison of the main morphological features of the species of *Amphiope* attributed to the informal bioculata group. If not otherwise indicated, the data report the mean value of the biometric measures expressed as % TL. N = number of post-basicoronal plates in the oral interambulacrum 5, N tot = whole number of plates in the interambulacrum 5. Red numbers = maximum values; blue numbers= minimum values.
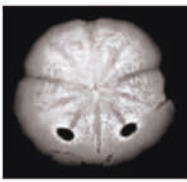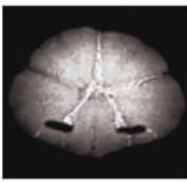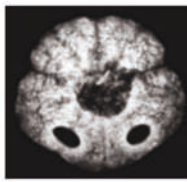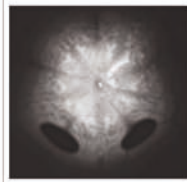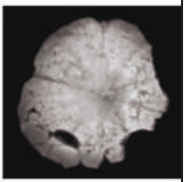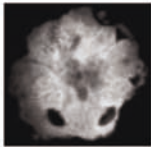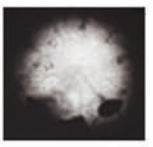
	A. sarasini	A deydieri	A. transversifora	A. nuragica	A. pallavicinoi
TL (mm)	72	51	46	93	100
TH	14	12.5	13	14	11
TW	108.5	122	110	106	111
Internal structure (X-ray photographs)					
Shape and size of the central hollow	Subpentagonal 46	roundish to star shaped	Roundish	Roundish	Subpentagonal
Internal test structure	Light - denser near the margin	Light	Light also near the margin	Strong and dense	Light - denser near the margin
Apical disc position (L4)	57	56	58	57	62
Petalodium size (PL)	49	53	55	53	59
N (column a) N (column b)	2 3	2 2	2 3	3 4	2 3
N tot -interambulacrum 5	13-14	10-11	13	16-20	15-16
Length of plate 5.b.2 (length of the post-basicoronal oral interambulacrum 5)	14.6 (28)	18 (25)	18 (27,5)	15 (30)	16,6 (25,4)
Lunules: WI SI	97 1.8	113.5 2.3	149 2	175 2.3	151 2,4
Lunules outline and distance from the posterior petals tips					
Peristome position (L12)	51	56	-	52	65
Periproct position (L11)	12	6-13	7.4	9	9
Oral scheme with the position of the periproct					
Peculiar characters	Very small lunules Strongly branched food grooves	Test very small Low whole number of plates in lamb 5	Test very small Lunules large (highest value of WI in this group)	Shell thick internal structure very strong Poriferous zones convex High number of plates in the oral Interambulacrum 5	Test low Petalodium very large

Table 3/1. Comparison of the main morphological features of the species of *Amphiope* attributed to the informal *A. bioculata* group. If not otherwise indicated, the data report the mean value of the biometric measures expressed as % TL. N = number of post-basicoronal plates in the oral interambulacrum 5, N tot = whole number of plates in the interambulacrum 5. Red numbers = maximum values; blue numbers= minimum values.
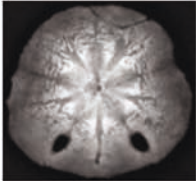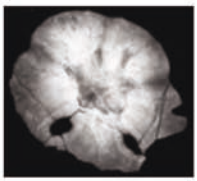
	A. depressa	A. palpebrata	A. tipasensis	A. hollandei	Amphiope sp. 1
TL (mm)	95.5	90	92	106	95
TH	16	14	13	6.5	20.7
TW	111	109	118	120	109
Internal structure (X-ray photographs)	-			-	
Shape and size of the central hollow	-	Subpentagonal to roundish	-	-	Subcircular to subpentagonal 47
Internal test structure	-	very light, it becomes denser towards the margin	-	-	Light; become denser near the margin
Apical disc position (L4)	51.5	55.5	-	58	53
Petalodium size (PL)	44	48-51	46	54	54.5
N (column a) N (column b)	-	>2 >2	3 4	3 3	2 3
N tot -interambulacrum 5	-	>14	15-17	14-15	14-16
Length of plate 5.b.2 (distance from the posterior edge of the occlusion point)	-	13.3 (25?)	13 (27,5)	13.2 (26)	15,8 (25)
Lunules: WI SI	57 1.9	91 2.1	99 2.1	72 7.3	184 2
Lunules outline and distance from the posterior petals tips	-				
Peristome position (L12)		-	50	60	48
Periproct position (L11)	13	8.7	12.5	12	13.8
Oral scheme with the position of the periproct	-				
Peculiar characters	Test very large Apical disc subcentral with 5 gonopores Petalodium small	Edge of the lunules salient	Test outline roundish High number of plates in the oral Interambulacrum 5	Test very low Lunules very long and narrow Frontal petal very long	Test very high Frontal ambulacrum much longer than the others Lunules close to the tips of the posterior petals

Table 3/2. Comparison of the main morphological features of the species of *Amphiope* attributed to the informal *A. bioculata* group. If not otherwise indicated, the data report the mean value of the biometric measures expressed as % TL. N = number of post-basicoronal plates in the oral interambulacrum 5, N tot = whole number of plates in the interambulacrum 5. Red numbers = maximum values; blue numbers= minimum values.
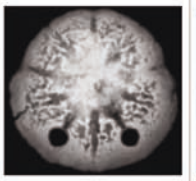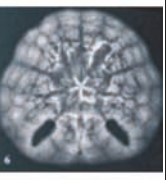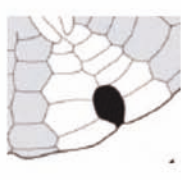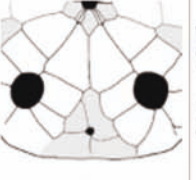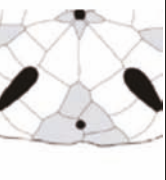
	P. agassizi	P. arcuata	P. cherichirensis	P. baquiei	P. raimondii
TL (mm)	46	54	75	29	53
TH	12.5	9	10	10	11
TW	110	102	123	110	109
Internal structure (X-ray photographs)		-			
Shape and size of the central hollow	Subpentagonal 48	-	Subpentagonal >46	Subpentagonal 46.5	Subpentagonal 47
Internal test structure	Rather light, denser posteriorly	-	Very dense	Rather light Very dense towards margin	Rather light dense towards margin
Petalodium size (PL)	48	44	50	46.5	42
N plates (column a) N plates (column b)	2-3 2-3	2 2-3	2-3 3	2 2	2 2
N tot - interambulacrum 5	14-15	-	-	10	-
Length of plate 5.b.2 (length of the post-basicoronal oral interambulacrum 5)	16 (26)	14 (24,7)	>18	17,5 (24,3)	15 (25)
Lunules: WI SI	106 1.6	80 1.6	140 1.4	140 1.2	133 2.8
Lunules outline and distance from the posterior petals tips					-
Peristome position (L12)	49.5	49	60	51	48
Periproct position (L11)	4.7	9.7	≈10	8.2	7
Oral scheme with the position of the periproct					
Peculiar characters	Basicoronal circlet very large (L13= 19% TL)	Test low	Test large Internal structure very dense	Test very small, lunule sub-rounded	Test outline rounded Lunules slit-like and very elongate (SI=3.2)

Table 4. Schematic comparison of the species attributed to the genus *Paraamphiope*. If not otherwise indicated, the data report the mean value of the biometric measures expressed as % TL. N = number of post-basicoronal plates in the oral interambulacrum 5, N tot = whole number of plates in the interambulacrum 5. Red numbers = maximum values; blue numbers= minimum values.

PALAEOECOLOGY

Amphiope, *Paraamphiope* and *Sculpsitechinus* were deposit feeders (Stara et al., 2012; Stara & Sanciu, 2014), well adapted to shallow water settings, with middle to high water energy and tropical climate (Stara & Borghi, 2014). They lived partially burrowed, with the petalodium emerging from the bottom. *Amphiope* is commonly found within sediments made of coarse sand and small rounded pebbles, typical of very shallow environments (Stara et al., 2012). Also *P. agassizi* has been cited by Chauzac & Roman (1994) from the late Oligocene of Aquitaine (France), within very shallow nearshore settings, based on the abundance of the tropical bivalve *Trisidos* Röding, 1798 (Arcidae), which is known to live at 2–10 m depth (Chauzac & Roman, 1994). The sediments embedding the fossils under study indicate that *Paraamphiope* and *Sculpsitechinus* were able to settle also finer substrates thus indicating somewhat deeper settings.

This matches with the ecology of the Recent *S. tenuissimus* and *S. auritus* which are known to live at 2-10 m (Lembeh, North Sulawesi, Indonesia, and Tulear, Madagascar, respectively) and, on the other hand, with *Sculpsitechinus* sp.1, which lives at 80 m (Stara & Sanciu, 2014). *Sculpsitechinus* cf. *auritus* is common at about 2 m depth at Ghubbet Soghra (Red Sea) but was found also down to 100 m depth (Dollfuss & Roman, 1981).

PHYLOGENESIS AND MIGRATION PATHWAYS

Phylogenesis

Notwithstanding the high number of species (and specimens) examined, the fossil record from Europe, North-Africa and Middle-East of *Amphiope*, *Paraamphiope*, *Echinodiscus* and *Sculpsitechinus* remains patchy, thus preventing to propose reliable hypothesis on the phylogenesis and migration pathways of these genera. Another problem affecting the phylogenetic reconstruction is the uncertainty about the stratigraphical position of a large part of the finding localities, as seen in previous chapter.

Amphiope was able to modify its morphology to adapt to environmental changes and to different set-

tings encountered along the migration pathways. These modifications, which were likely rather quick at the geologic scale, sometimes consisted of back-modifications, thus making difficult the comprehension of the evolutive trends. Also the main trends indicated in Stara & Borghi (2014), when studying *Amphiope* from Sardinia, must be used with caution, since they could be partially obliterated by the still unclear evolution of this genus. They were:

- increasing complexity and progressive reduction of the internal support system; in particular, the dense and strongly developed internal buttress and the thick shell of the late Oligocene-Aquitanian *A. nuragica* was regarded as a primitive character in *Amphiope* with transverse lunules;

- decreasing whole number of plates in the ambulacral (extra petals) and interambulacral columns;

- progressive migration of the periproct towards the peristome, from plates 5.b.3–5.a.3 in *A. nuragica*, to the distal part of the suture separating plates 5.a.2–5.b.3 in *A. lovisatoi* (Burdigalian), to the proximal part of 5.a.2-5.b.3 in *A. montezemoloi* and *Amphiope* sp. 2 (early Langhian).

The factors leading to the noticeable dimensional changes in the size of the petalodium (PL ranges from about 41 to 62% TL in *Amphiope*) are unclear (Stara et al., 2015). However, the differences observed between *A. nuragica* (PL=47–56 %TL) and the closely related species from the Tortonian of north Africa (Morocco, our observations) and Calabria (PL=40.5–46% TL) (Stara et al., 2015) have been interpreted as adaptations to different environmental and climatic changes. Interestingly, the main change in the petalodium size occurred mainly in the Late Miocene (Tortonian) of the southern Proto-Mediterranean area.

The first records of *Amphiope* are dated to the late Oligocene (Chattian)-early Aquitanian of Sardinia and the Early Miocene (Aquitanian) of the Gulf of Biscay, whereas *Echinodiscus pedemontanus* and *Paraamphiope agassizi* were already present in the Oligocene (Rupelian) of the Piedmont Basin and the Gulf of Biscay, respectively; thus they could be possible ancestors of *Amphiope*.

However, some cases point to a different and more complex history. *Paraamphiope agassisi* (Rupelian-Chattian), *A. ovalifora* (early Aquitanian) and *A. romani* n. sp. (Serravallian-Tortonian) are three species from western France, listed in the chronological order. *Amphiope ovalifora* has a

higher whole number of plates in the ambulacral and interambulacral columns than *P. agassizi*. The high number of plates was considered as a primitive feature in *Amphiope* by Stara & Borghi (2014), thus making unlikely a derivation of *A. ovalifora* from *P. agassizi*. *Amphiope ovalifora* shares many features with *A. bioculata* (Langhian-Serravallian of Hérault), notwithstanding the relevant geographic and chronological distance.

Amphiope ovalifora and *A. bioculata* differ by several aspects from *A. sarasini* and *A. lorioli*, which are stratigraphically more recent.

The most intriguing case in *Amphiope* is represented by *A. sarasini*, which shows some intermediate features between *Amphiope* and *Sculpsitechinus*. In the best preserved specimen, the food grooves are rather thin as in *A. bioculata* (Fig. 75), *A. ovalifora* (Fig. 72) and *A. lovisatoi* (Fig. 70) but they are much more branched.

In *Amphiope*, the highest number of post-basicoronal plates in the oral interambulacrum 5 is present (Stara & Borghi, 2014) in the "ancient" *A. nuragica*, with three and four plates in columns "a" and "b" respectively, rarely four and four (Fig. 36). It was also commonly observed that the number of plates decreased in the more recent species (Figs. 40, 42). However, *A. sarasini* has two or three plates in column "a" and three in column "b" (Fig. 44); since it was from the Serravallian-Tortonian, a lower number of plates would be expected. This is valid also for *A. tipasensis*, from the Pliocene of Algeria which has three and four plates in columns "a" and "b", respectively (Fig. 154). However, the morphological variability is not known yet in this species, as well as its apical disc.

In *A. sarasini*, *Amphiope* sp.1 from Valencia (Stara et al., 2015) (also in this case the apical disc is unknown), *A. lorioli* and *A. tipasensis* the mean distance of the periproct from the posterior test margin (L11) is about 12–13% TL, which represents an elevate value for *Amphiope* (*Amphiope* sp.1 from Valencia has L11=20) and is close to the lowest limit (L11>13) for *Sculpsitechinus*, which gets up to 26% TL (Stara & Sanciu, 2014).

On the other hand, in some Recent specimens of *Sculpsitechinus* the plate 5.b.2 in the oral interambulacrum is in contact with the two adjacent am-bulacral post-basicoronals. The occasional occurrence of this character, which is unusual for *Sculpsitechinus*, likely points to a possible relation-ship between this genus and the latest species of *Amphiope*, such as *A. sarasini*, *Amphiope* sp.1 from Valencia and *A. tipasensis*. All these observations likely indicate the presence of at least three evolutive lines in the genus *Amphiope*:

- *Amphiope elliptica* (Aquitanian-Burdigalian, south-eastern France) and similar species with roundish lunules from the western Proto-Mediterranean Basins (including *A. ovalifora*, *A. bioculata* and *A. romani* n. sp.).

- *Amphiope nuragica* (Chattian-Aquitanian of Sardinia) and its related forms with transversely elongate lunules.

- a group of species, including *A. sarasini*, *Amphiope* sp.1 from Valencia, *A. lorioli* and *A. tipasensis*, with small rounded or narrow lunules, three to four or more numerous post-basicoronal plates in the oral interambulacrum 5 and the periproct far from the posterior test margin (L11>12–13% TL); these forms likely shared a common ancestor with *Sculpsitechinus boulei*.

Paraamphiope agassizi (Oligocene) could be the ancestor of a series of species characterized by small-sized test, the structure in the interambulacrum 5 typical of this species, food grooves large and strongly branched: *P. cherichirensis*, *P. arcuata* (may be also its closely related species from Egypt and Libya), *P. baquiei* and the Recent *P. raimondii*.

Sculpsitechinus boulei (Aquitanian) is the earliest species so far known of this genus. However, likely it was not the common ancestor of all the recent species of *Sculpsitechinus* (Figs. 80, 81), since some specimens of *S. auritus* have a higher number of plates in the whole interambulacrum 5 and in its oral part (4/4) (Stara & Sanciu, 2014; pl. 11, figs. 1–4, 6–7). Therefore, the presence of an earlier taxon (from Oligocene?) is prospected, which was the common ancestor of *S. boulei*, *S. auritus* (with 4/4 plates and slit-like notches) and the group of species of *Amphiope*, including *A. sarasini* and *A. tipasensis*, with small transverse lunules and 4/4 plates in the oral interambulacrum 5.

However, only a cladistic analysis based also on the results of the other researches in progress in other peri-Mediterranean areas will help to clear the complex phylogenesis of this genus.

Migration pathways

The appearance of the first lunulate scutelliforms in the Atlantic-Europe and the Western Proto-

Mediterranean (sensu Stara & Rizzo, 2014) followed the great extinction occurred at the Eocene-Oligocene transition (see Miller et al., 2009, with references). The renewal of the scutelliform fauna after that critical period was likely the source of the ancestors of *Amphiope*, *Paraamphiope* and, maybe, also of *Echinodiscus* and *Sculp-sitechinus*.

Although the first citations of *Amphiope* date back to the Late Oligocene-Early Miocene in the area comprehending Sardinia, Gironde and Provence, the genus at that time was already well differentiated, thus pointing to an earlier origin well into the Oligocene. In fact, *A. nuragica* (late Chattian-early Aquitanian of Sardinia), *A. ovalifora* (early Aquitanian of Gironde) and *A. elliptica* (late Aquitanian of the Rhône Basin) were morphologically very different.

Amphiope diffused from that area towards the southern and eastern parts of the Proto Mediterranean (Fig. 1, pro parte) and western Africa (de Loriol, 1905; Dartevelle, 1953).

The investigation of the migration pathways is affected by the same problems seen in the phylogenetic analysis, that is patchy fossil record and uncertainty regarding the stratigraphic position of a part of the fossil material and finding localities. However, a useful tool for the investigation is provided by the palaeoecology of this echinoid: *Amphiope* was a strictly shallow water echinoid, thus its diffusion occurred only through nearshore settings and it was not able to cross large deep-water basins.

The case of Sardinia corroborates this hypothesis, since the species described from that area from late Chattian to the early Messinian (Stara & Borghi, 2014) were never recorded from other areas, thus indicating the isolation of that isle with regard to the local populations of *Amphiope*. Sardinia shifted away from the European plate starting from the end of the Oligocene - beginning of the Miocene (Stara & Rizzo, 2014, with references), and was transformed by the progressive marine ingression into an archipelago emerging from an epicontinental sea (Gattaceca et al., 2007). In that period *Amphiope* was represented in Sardinia by *A. nuragica* and *Amphiope* sp. 1, which were morphologically very different from *A. elliptica* living in the Provençal Basin during the Aquitanian, thus pointing to an earlier separation of the populations of the two basins. In the Middle Miocene Sardinia was surrounded by a deep sea which increased the

geographic isolation, favoring the development of new species, such as *A. pallavicinoi*, *A. lovisatoi*, *A. montezemoloi* and *Amphiope* sp. 2 from the Burdigalian-early Langhian of the Calcari di Mores Formation, which were different from the coeve species in south-eastern France. In particular, small to medium-sized forms prevailed in the French basins, whereas the average size was much larger in Sardinia (TL up to 170 mm). These differences were likely due to more favorable environmental conditions for *Amphiope* present at that time in Sardinia.

Data regarding the Balearic Islands, the Spanish coasts and the Kabylies were not available to this study and the plate patterns in *Amphiope* from Sicily (Garilli et al., 2010) must be improved; however, a new research is in progress on these arguments.

The diffusion of *Amphiope* starting from the original area was rather quick, since in the ?Burdigalian it was already present in Angola (de Loriol, 1905) and in the Paratethys (Hoernes, 1883). Also in the eastern Proto-Mediterranean, specimens attributable to the *Amphiope nuragica* group were collected from the Burdigalian of Erzincan (MNHN-F, R67283, collection Pinar), along the Turkish southern coast of the Black Sea, and from the Mut Basin (southern Turkey; Kroh & Nebelsick, 2003).

Some specimens of *Amphiope* from Mosul (Iraq, NHMUK.E73263) and the Gulf of Aqaba (Jordan, NHMUK.EE534-8) and those from the Qom Formation in Central Iran (Khaksar & Moghadam, 2007), indicate the presence of populations attributable to the *Amphiope nuragica* group in the Early Miocene of eastern Asia. Those forms certainly migrated when the connection between the Paratethys or the eastern Proto Mediterranean and the Indian Ocean was still active, that is before the definitive closure of that channel occurred in the Middle Miocene between 17 and 11 Ma (Hüsing et al., 2009). In particular, the specimens of *Amphiope* from Iran were dated to the late Aquitanian (Khaksar & Moghadam, 2007), thus indicating a quick arrival from the original area.

The diffusion of *Amphiope* from the western towards the eastern part of the Proto Mediterranean was controlled by the Alpine orogeny which periodically opened peri-Alpine channels connecting the two parts of the Basin, during the Early Mio-

cene. Some studies (e.g. Rögl et al., 1998; Harzhauser et al., 2007) affirmed that during the Oligo-Miocene the connection between the western and eastern parts was wide and continuous. However, a different theory suggests that the two parts of the Basin were only occasionally connected (Rosembaum et al., 2002; Stara & Rizzo, 2013; 2014).

The citation of a single species (*A. tipasensis*) from the Pliocene of western Mediterranean, represented by a sole and incomplete specimen, indicates that *Amphiope* survived the Messinan crisis, likely along the western Atlantic coasts, and re-entered the Mediterranean though with a strong reduction of diversity. The citation of a number of *Amphiope*-bearing outcrops from the Atlantic coast to the Taza-Guercif basin of the Morocco Late Miocene gateway (Lacointre, 1952; Flecker et al., 2015) and a study in progress on some specimens (MNHN-F R67286) from the Middle-Late Miocene of the Guercif area, corroborate this hypothesis.

A more accurate reconstruction will be provided by the results of the investigations in progress on unpublished fossil findings from southern and central Italy, Spain (including the Balearic Basin), Portugal, Morocco, Algeria and Libya.

CONCLUSIONS

Recent studies (e.g. Stara & Borghi, 2014) pointed out that a revision by modern methods of the earlier species attributed to *Amphiope* was needed to clear the largely unresolved taxonomy of this genus. In particular, the distinctive characters of the type species, *A. bioculata* (Des Moulins, 1837), were so far unclear and the type locality was unknown. The Serravallian of the surroundings of Nissan (Hérault, France) has been here considered as the type locality for *A. bioculata*, following the opinion of earlier studies (de Loriol, 1902; Cotteau, 1914; Lambert, 1912a; 1915a). Since the existing type was badly preserved, the re-description of the type-species has been based on a sample made of 11 well preserved topo-typic specimens from Lespignan and Nissan.

The type material of several species of *Amphiope*, examined in public institutions, and new topo-typic specimens, studied using statistical biometrical analyses and with emphasis on the test structure, enabled comparison between a relevant part of the earlier species attributed to this genus.

On the whole the research indicated that apparently similar forms in this genus could turn out to have a different structure and, consequently, to represent well distinct species; therefore, the high morphological variability, which is objectively typical of *Amphiope*, cannot justify the institution of new species, based only on external characters.

As a result (Table 1), 17 species have been confirmed as valid and maintained in the genus *Amphiope*; *A. romani* n. sp. has been instituted on the basis of a group of specimens from the late Serravallian-early Tortonian of Channay-sur-Lathan, Touraine (France). Three species previously assigned to *Amphiope* have been transferred to the genus *Paraamphiope* (Stara & Sanciu, 2014), since they have radially elongate lunules separated by at least three to four plates from the posterior petals tips, small or rather small petalodium and strongly branched oral food grooves. Another species with very branched food grooves, radially elongate lunules separated from the posterior petals by four plates and with a oral interambulacral plating consistent with that of *Sculpsitechinus tenuissimus*, has been transferred to the genus *Sculpsitechinus* (Stara & Sanciu, 2014). *Amphiope arcuata* Fuchs, 1882 have been recently transferred to the genus *Paraamphiope* by Stara & Sanciu (2014); the generic placement of three similar species from the Miocene of Libya and Egypt, *A. truncata* Fuchs, 1882, *A. fuchsi* Fourtau, 1899 and *A. miocenica* Ali, 1998, remains uncertain since no plating schemes were provided in the original descriptions. The attribution of these species to *Paraamphiope* seems more probable, due to their close similarity with *P. arcuata*. For an overview, the results of this work have been condensed in Tables 2–4.

The original description of a number of other species attributed to *Amphiope* did not provide reliable distinctive characters and in some cases information on the repository of the type material and on the type localities was not reported. This was the case with *A. perspicillata* Agassiz, 1841, *A. styriaca* Hoernes, 1883, *A. personnata* Pomel, 1887, *A. villei* Pomel, 1887, *A. dessii* Lovisato in Cotteau, 1895, *A. laubei* Lambert, 1912, *A. calvii* Lovisato, 1914, *A. labriei* Lambert, 1915 and *A. dallonii* Lambert, 1931, which are here considered as *species inquirendae*.

New morphological acquisitions regarding the characters of *Amphiope* and *Paraamphiope* are:

- almost the same whole number of plates is present in each column of the interambulacrum 5 and the ambulacra I and IV (sometime one o two plates of difference).

- the species represented by large samples from a single locality often show a rather wide morphological variability regarding above all shape and size of test, petals and lunules, whereas the patterns and the features of the internal support system are almost constant.

The last point indicates the need of basing the study of these astriclypeids on samples made of a significant number of specimens. Only in a few cases we accepted the validity of species represented by a sole specimen (e.g. *A. hollandei* and *A. transversifora*), since the types showed peculiar features and looked well characterized. It would be desirable, however, that new topotypic material could clear the morphological variability of these two species, which remains so far unknown.

Notwithstanding the news provided by the present research, the fossil record of *Amphiope* and the other closely related genera, *Paraamphiope*, *Echinodiscus* and *Sculpsitechinus*, remains patchy, thus preventing to propose exhaustive hypothesis about the phylogenesis and the migration pathways of these astriclypeids. For this purpose, new studies are needed to clear the partially unresolved stratigraphy of a large part of the finding localities examined in this work. Studies in progress dealing with the populations of *Amphiope* from Italy (Calabria, Campania and Tuscany), Spain, Portugal and north Africa (Algeria, Morocco) and of *Sculpsitechinus* from Iran will likely provide new useful data.

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