

Distribution of two *Amphiope* L. Agassiz, 1840 (Echinoidea Clypeasteroidea) morphotypes in the Western-Proto-Mediterranean Sea

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ABSTRACT

Several species belonging to the genus *Amphiope* L. Agassiz, 1840 (Echinoidea Astriclypeidae) from the Mediterranean Oligo-Miocene have been synonymised with *A. bioculata* (Des Moulins, 1835), the type-species of the genus, based on the interpretation given by Philippe (1998) as a taxon characterized by a large amount of morphological variability. A recent study introduced the characters of the internal test structure and the plating patterns as taxonomic tools in this genus. That paper indicated the occurrence of at least five different species in the examined sample from the Oligo-Miocene of Sardinia, thus pointing to a previous over-estimation of the variability-range of the type-species and to the need of a review of the largely unresolved taxonomy of *Amphiope*. According to a recent study, *Amphiope* is considered as a shallow-water echinoid, inhabiting sandy bottoms with high hydrodynamic energy; so it represents a coastline marker, useful for the study of the paleo-geographic changes occurred in the Proto-Western-Mediterranean during the Miocene. The diffusion and speciation of *Amphiope* were highly influenced by those changes. In particular, the speciation rate of this genus was likely favored by the occurrence of isolated populations created when islands (e.g.: Balears, Calabria, Corse, Kabylies, Sardinia) separate from the mainland, above all in the western part of that Basin, because of the opening of the Balearic Basin during the Late Oligocene-Early Miocene and of the Tyrrhenian Sea during the Burdigalian-Tortonian (references in this work). Two main morphotypes of *Amphiope* sensu Stara & Sanciù (2014), developed in the Western Mediterranean from the late Oligocene to the late Miocene. They are herein called the “*bioculata*” group, characterized by roundish to broad elliptical lunules with major diameter/minor diameter ratio (SI) < 1.59, and the “*nuragica*” group, with more or less narrow lunules and SI > 1.6. According to this authors, most Miocene forms with narrow elliptical lunules would derive from *A. nuragica* (Comaschi Caria, 1955), late Oligocene-early Miocene of Sardinia, the most archaic form so far known of this genus. The forms belonging to the “*bioculata*” group likely derived from a different common ancestor bearing round to broad ovoidal lunules. “*A. bioculata*” described by Cottreau (1914), from the Burdigalian (Philippe, 1998) of Saint Cristol (Nissan, Hérault, France), is so far the most ancient known form belonging to this group. This work proposes a possible speciation sequence of the “*nuragica*” group.

KEY WORDS

Amphiope; Western-Proto-Mediterranean Sea; Paleogeography.

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INTRODUCTION

Paleogeography and paleoecology

Amphiope L. Agassiz, 1840 (Echinoidea Astri-
clypeidae) is considered as a shallow-water echin-
oid, typical of sandy settings characterized by high
hydrodynamic energy (Stara et al., 2012). According
to Stara & Rizzo (2013, 2014) and Stara & Sanci-
u (2014) it represents also a valid coastline marker.

On the basis of the fossil record and the avail-
able paleoecological data it is herein hypothesized
that the diffusion of *Amphiope* was highly influ-
enced by the paleogeographic (Doglioni et al.,
1998; Rosenbaum et al., 2002; Carminati et al.,
2012, Stara & Rizzo, 2014) and paleoecological
(Popescu, 2009) changes occurred in the Western
Proto-Mediterranean during the Miocene. In partic-
ular the opening of the Balearic and Ligurian Basins
during the Late Oligocene-Early Miocene and
of the Tyrrhenian Sea during the Burdigalian-
Messinian (Doglioni et al., 1998; Rosenbaum et al.,
2002; Carminati et al., 2012) originated islands
(e.g.: Balears, Calabria, Corse, Kabylies, Sardinia)
separated by deep water, thus leading to the occur-
rence of isolated populations and favoring speci-
ation within this Astri-*clypeid* genus.

The orogenetic trend in the Mediterranean area
mainly derived from the differential movement
between the Adria microplate, belonging to the
African plate, and the European one.

The geodynamic and paleogeographic evolution
of the Western Mediterranean may be divided into
two distinct phases: the first occurred during the
Chattian-Burdigalian, the second started in the
Burdigalian and it is still active today.

First phase - The migration of the Sardinia-
Corsica microplate and the Calabrian block, with
respect to the more stable European plate, likely
began 25-23 My ago, with a general translation
towards SE. This drift was accompanied by a 45°
counterclockwise rotation of the Sardinia-Corsica
microplate between 20.5 and 15 Ma, with a broad
oceanic domain in the Liguro-Provençal basin (up
to 400 km in the southern part) between 20.5 and 18
Ma (Gattacceca et al., 2007). These evidences
firstly improved the presence of a connection
between the Liguro-Provençal Basin and the Valencia
trough before 20.5 Ma, then the connection between
the Alboran and the Algerian basins. Based on the

available paleontological data it is here hypothes-
ized that the transcurrent belt located to the north
of the Sardinia-Corsica microplate and the
Calabrian block led to the formation of a neritic sea,
occasionally connecting for short periods the
Ligurian-Provençal Sea to the Po Basin.

Second phase - Further translation towards SE,
with a rotation of about 15° of the Calabrian block
(Gueguen, 1995), led to the opening of the Tyrrhe-
nian Basin, in the Late Miocene. As a result of these
changes the Mediterranean began to take on an
appearance more similar to the current one.

Doglioni et al. (1998) has affirmed that the Apen-
nine orogenetic front kept on migrating towards E
leading to the emersion of the Apennine Chain, thus
separating the Tyrrhenian Sea from the Adriatic after
the Burdigalian. On the other hand, based on the
opinion by Rosenbaum et al. (2002) and on the
available macro-paleontological data (Stara &
Rizzo, 2013; 2014), it seems likely that the connec-
tion between the Tyrrhenian and the Adriatic basins
had been realized in the Plio-Pleistocene when the
Calabrian block reached the Apennine Arc, with the
exception of the Ligurian Channel (the Val Bormida
Channel of Stara & Rizzo, 2013). The crustal
thinning of the back-arc areas located W to the
Sardinia-Corsica microplate led to extensive flows
of basaltic lava (indicated by magnetic field anom-
alies) in the Balearic and the Tyrrhenian basins; both
of them were deep water seas with a maximum
depth of 3000 and 3700 m, respectively.

Kotsakis et al. (2004) prospected the occurrence
of a Sardinia-Tuscany bio-paleoprovince during the
Serravallian, on the basis of the close similarity of
the vertebrate fauna present in these areas. This
would imply the existence of landmass bridges or
shallow water basins separating lands, important
factors conditioning the diffusion of *Amphiope*
between the two sides of the Tyrrhenian Basin.

MATERIAL AND METHODS

The studied material consists of 78 *Amphiope*
specimens, preserved as whole coronas deprived of
the spines, from 5 Oligo-Miocene localities of
Western-Mediterranean Basin. 44 *A. lovisatoi*
Cotteau, 1895 (inventory code: (PL1301-03,
PL1317, PL1413, PL1418- 20, PL1422-24, PL1427,
PL1429, PL1567-70, PL1572-80, PL1583, PL1585-

87, PL1692-99, PL1700-07, PL1709-14, PL1715-18, PL1720-23, PL1726) from Chiaramonti (Sassari province); 1 *Amphiope* sp. from Capo Frasca (Medio Campidano Province); 19 *A. nuragica* from Cuccuru Tuvullao (Cagliari Province) MAC (PL1590-91, PL1678-80, PL1684, PL1727, PL1820, PL1829; PL1835-44); 1 *A. montezemoloi* Lovisato 1901 from Bonnanaro, Sassari; 5 *Amphiope* sp. from Calabria (Vibo Valentia Province, Italy), no code; 2 from Alicante (unknown locality); 1 from Torrent, Valencia Province (Spain) are housed at the Museo di Storia Naturale “Aquilegia” (MAC code) of Cagliari; the Holotype of *A. nuragica*, at the University of Cagliari Sardinia (Italy), UNICA code, inventory 9CC.8-10504. 10 *Amphiope* specimens from Calabria (Vibo Valentia Province, Italy) number 104/E 101-110, are housed at the Civico Museo Paleontologico di Ricadi (Vibo Valentia province), Calabria, Italy. 3 specimens from Torrent, Valencia Province (Spain) were studied in private collections. One syntype of *A. bioculata* from Sure-Pres-Bollène today “Suze-la-Rousse” near “Bollène”, France, housed at the Muséum d’Histoire Naturelle of Bordeaux (code MHNb), France, inventory number MHNbX 2014.6.317.

The plate pattern of the syntype of *A. bioculata*, variety A of Des Moulins (1835), is not visible, but the two lunules are clearly rounded, as described by the author (“*foraminibus subrotundis*”).

Morphological abbreviations (Fig. 1) TL = test length; TW = test width; TH = test height; PL = petalodium length; L1 = lunule length; L2 = lunule width. The measure of TL is reported in mm; other data in % TL; SI= lunule shape index ($L2/L1$); WI= lunule width index ($(L1+L2)/2$).

Biometric analyses were carried out and data analyzed using the software PAST-version 3.2 (2014) (Hammer, 2014), to help the interpretation of the samples collected from Sardinia and Calabria. Systematic palaeontology follows Kroh & Smith (2010).

TWO MAIN AMPHIOPE MORPHOTYPES

The genus *Amphiope* sensu Stara & Sanciu (2014) developed from the end of the Oligocene to the late Tortonian-early Messinian in the Proto-Western-Mediterranean Sea.

A. nuragica (Comaschi Caria, 1955), from the Oligo-Miocene of Sardinia, is the more ancient species so far known belonging to this genus (Stara & Borghi, 2014), though the genus *Amphiope* looked like already well differentiated in the Aquitanian.

Based on the phylogenetic hypothesis proposed by Stara & Borghi (2014) most forms with narrow transversely elongate lunules derived from *A. nuragica*, whereas those with sub-rounded to broad elliptical lunules as *A. bioculata* (including “*A.*

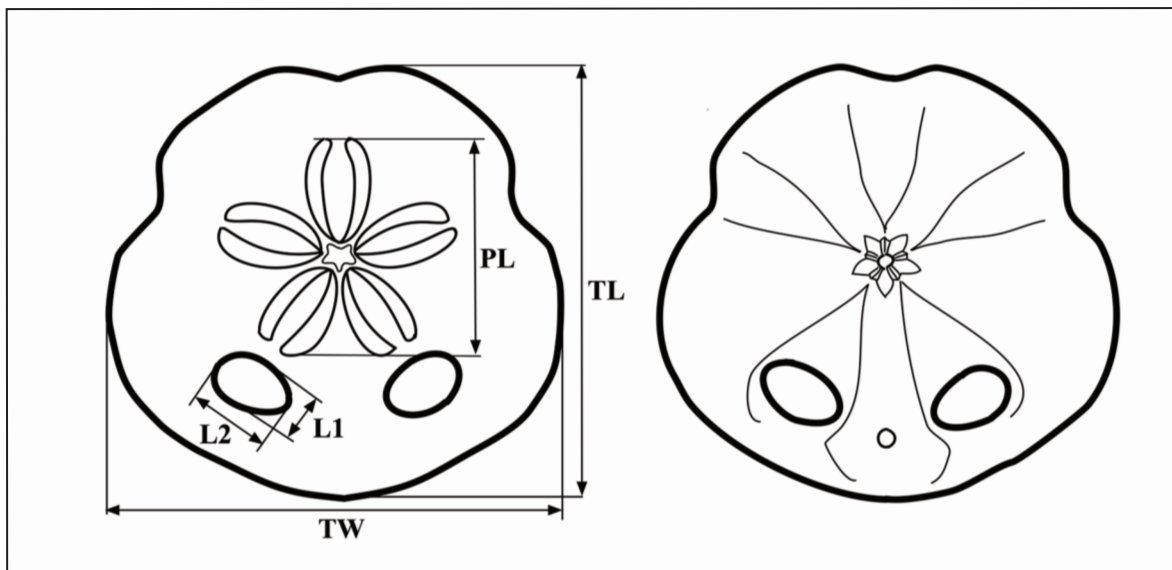


Figure 1. Set of morphometric measurements used in this work.

bioculata” from the Aquitanian of Carry, France, as interpreted by Cottreau, 1914 and Philippe, 1998) originated from a different common ancestor.

Two main morphotypes of the genus *Amphiope* are here proposed: the “*nuragica*” group (Pl. 1 Figs. 3-4), characterized by narrow transversely elongate lunules with $SI > 1.6$, and the “*bioculata*” group (Pl. 1 Figs. 1-2), with roundish to broad ovoid lunules and $SI < 1.59$. Both these groups are well represented in the study area, however in this paper we’ll go deep into the “*nuragica*” forms only, since clear structural data are so far available only for this group.

DISTRIBUTION OF THE TWO MAIN MORPHOTYPES IN THE WESTERN MEDITERRANEAN

Amphiope has been recorded from more than 30 localities both in Sardinia (Comaschi Caria, 1955, 1972; Stara et al, 2012) and in the Rhône Basin (France) (Cottreau, 1914; Philippe, 1998). This echinoid has been cited in Italy also in Tuscany (Gianini, 1957; present paper), Campania (Barbera & Tavernier, 1989), Calabria (Cottreau, 1914; Carone & Domning, 2007), Sicily (Garilli et al., 2010). In Spain *Amphiope* was recorded in Catalogna (Lambert, 1928), Mallorca (Llompert, 1983), Valencia (personal communication of Bajo Campos, July

2012) and Alicante (present paper). *Amphiope* has also been recorded from Algeria (Pomel, 1887-88 and Cotteau et al., 1891) and Corse (Cotteau, 1877).

The finding localities corresponding to these records are reported in Table 1 and figure 2, with the attribution to the “*nuragica*” or to the “*bioculata*” group. The asterisk marks the species not directly examined by the authors.

The syntype of *A. bioculata* from the Bollène area has the $SI = 1$; the sample of *A. bioculata* described by Cottreau (1914) has a mean value of $PL = 53$ and SI ranges from 0.95 to 1.47, with a mean of 1.22. The studied sample of *A. nuragica* from Sardinia has a similar mean value of PL (51), however SI ranges from 2 to 3 with a much higher mean value (2.4) than that of *A. bioculata* sensu Cottreau (1914).

Based on its small sized petalodium ($PL = 40-47$, with a mean value of 43.3) the sample from the Tortonian of Calabria clearly differs from all the others belonging to the “*nuragica*” group (Fig. 3), with the exception of the few specimens from the Tortonian of Valencia (mean $PL = 44$).

In the sample from Calabria SI ranges from 2.4 to 4.3, with a mean value of 3.

A specimen from Sicily shows the lowest value for the “*nuragica*” group ($SI = 1.6$), whereas a specimen of *A. hollandei* Cotteau, 1877 (the holotype) from Corse has the highest value ($SI = 6.5$).

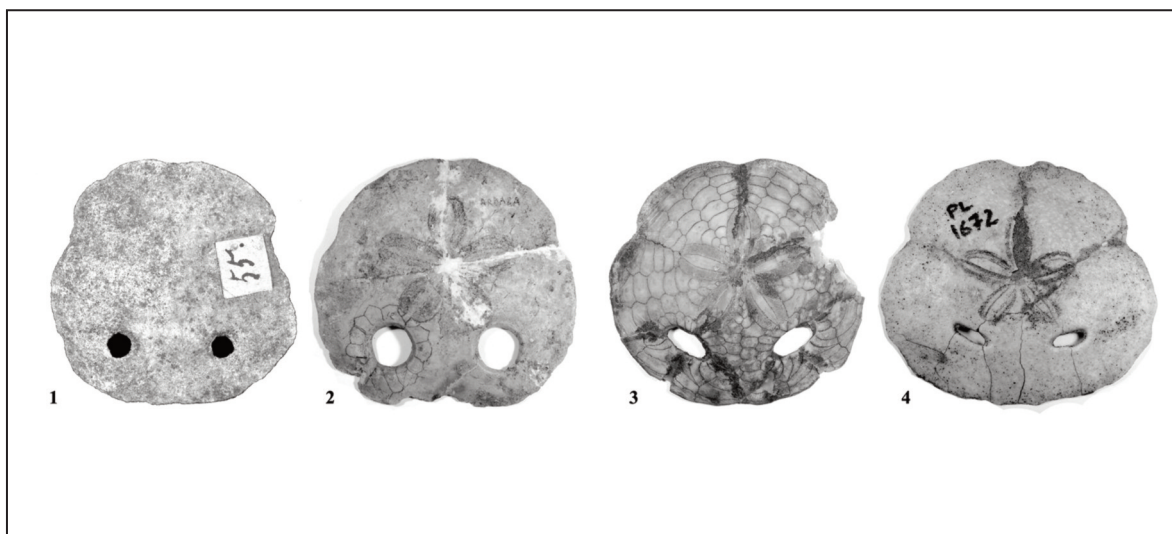


Plate 1. Main *Amphiope* morphotypes. Figure 1-2, “*bioculata*” group; Figure 1: *A. bioculata* syntype MHNBx 2014.6.317; Figure 2: *A. montezemoloi* MAC.PL1676. Figure 3-4, “*nuragica*” group; Figure 3: *A. nuragica* MAC.PL. 1680; Figure 4. *Amphiope* sp. from Calabria, MAC.PL1672.

TYPE	PL % TL	L1 % TL	L2 % TL	WI	SI
<i>Amphiope bioculata</i> , sintype MHNB2014.6	—	10	10	10	1
<i>A. cf. bioculata</i> (in Cottreau, 1914)*	53			10.2 (9-12.6)	1.22 (0.95-1.47)
<i>A. montezemoloi</i> , San Giorgio	-	16.8	16	16.4	0.95
<i>A. nuragica</i> , holotype	51			13.5 (11.5-15)	2.4 (2-3)
<i>A. sp.</i> , Sicilia	56	9	15	12	1.6
<i>A. deyrieri</i> , France*	? 47	5.5	15.5	10.5	2.8
<i>A. sp. 1</i> , Calabria	44	5	13	9	2.6
	41	5.5	14	9.7	2.5
	45	5.5	18	11.7	3.3
	44	6	17	11.5	2.8
	47	5	16	11.5	3.2
<i>A. sp. 2</i> , Calabria	44	4	14.5	9.2	3.6
	43	4.5	14	9.2	3.1
	40	5	12	8.5	2.4
	42	3.5	15	9.2	4.3
<i>A. sp. 1</i> , Valencia	42	5	13	9	2.6
	44	4.5	11	7.7	2.4
<i>A. depressa</i> , Algeria*	44	5	10	7.5	2
<i>A. sp.</i> , Capo Frasca	54	7.5	16	11.7	2.1
<i>A. sp. 2</i> , Valencia	55	5	14	9.5	2.8
<i>A. sp.</i> , Alicante	52	4	17	10.5	4.5
<i>A. hollandei</i> , Corsica*	54	3	20	11.5	6.6
<i>A. sarasini</i> , France*	50	6	13	9.5	2.1
<i>A. palpebrata</i> , Algeria*	52	6.5	14	10.2	2.1

Table 1. Data PL, L1, L2, WI and SI of species included in the "nuragica" group, present in the area under study. For comparison, in the first three rows are reported the data of syntype of *A. bioculata* and two other forms of the group.

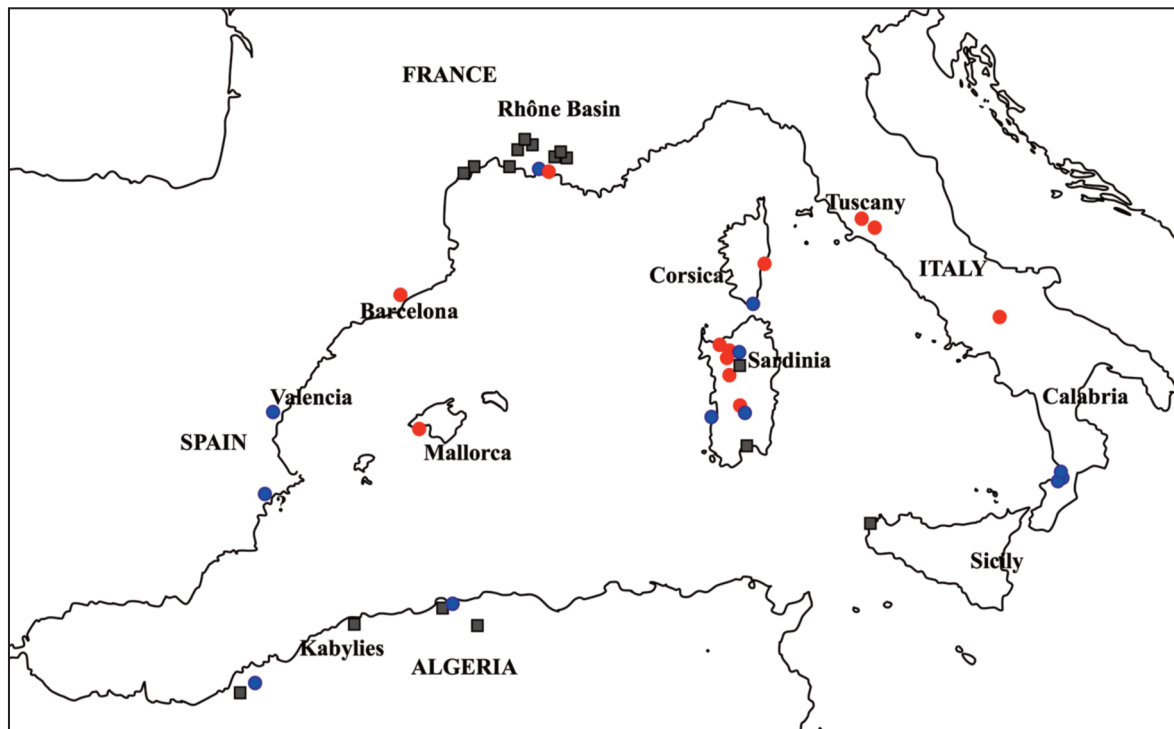


Figure 2. Distribution of two main morphotypes in the Western Mediterranean basin. Red dot = “*bioculata*” group; blue dot = “*nuragica*” group; square dot = insufficient data.

However the last two are border-line cases represented by single specimens; additionally the specimen from Corse is poorly preserved (*vide* Cottreau, 1914) and the drawing may be not reliable.

The shape index of lunules is not discriminant between the forms of the “*nuragica*” group, however comparison based on the values of L1 and L2 is more significant. In the large sample from Sardinia (Stara & Borghi, 2014) the range of L1 is 6-16.7 (6-11.2 in *A. nuragica*), that of L2 is 11-23.5 (14.1-23.5 in *A. nuragica*). The samples from Calabria and Valencia show much lower values of the lunule length (L1 ranges from 3.5 to a maximum of 6), L2 ranges from 11 to 18.

Based on these observations the sample from Calabria is characterized by:

1. the smallest petalodium so far known for the genus *Amphiope*; only some specimens from Valencia and *A. depressa* Pomel, 1887, from Algeria show similar values of PL (see Fig. 3)

2. lower values of L2, WI and above all L1 when compared to the species described from Sardinia by Stara & Borghi (2014): *Amphiope lovisatoi* and *A. nuragica* (Fig. 4). A larger sample

is needed to confirm the same results also for the examined specimens from Valencia.

CONCLUSIONS

This preliminary study indicates clear morphological differences within the “*nuragica*” group, with respect to the size of the petalodium (PL) and of the lunules. In particular the samples from the late Miocene of Calabria (Southern Italy) and Valencia (Spain) show much smaller petalodium and smaller lunules when compared to the other known species belonging to this group.

It is presumable that in some nearshore areas of the Mediterranean (e.g. along the coasts of Calabria, Balearic, Kabilyes, Sardinia, Corsica), separated by deep water, different species of *Amphiope* developed independently, adapting to the environmental changes occurred through the Miocene, mainly climate, due also to the latitudinal migration of lands, and ecology.

On the other hand, during the Miocene *Amphiope* showed also structural modifications

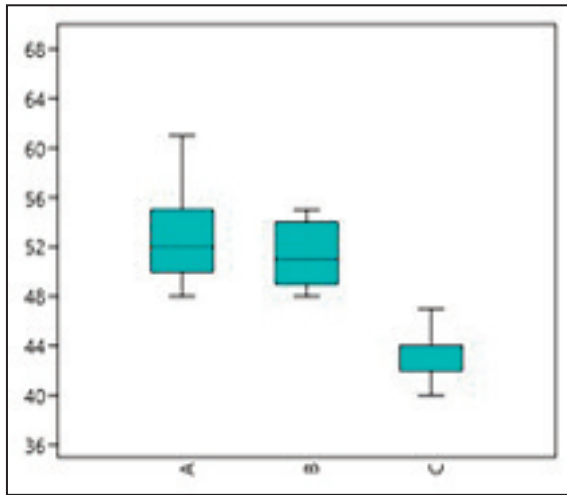


Figure 3. Petalodium comparison data on some species belonging to the “*nuragica*” group (PL in% TL). A = *A. lovisatoi*; B = *A. nuragica*; C = *Amphiope* sp. Calabria.

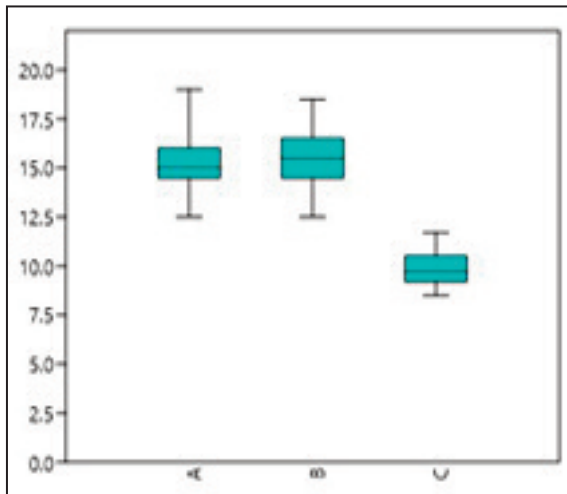


Figure 4. Size of lunules (WI) comparison on some species belonging to the “*nuragica*” group. A = *A. lovisatoi*; B = *A. nuragica*; C = *Amphiope* sp. Calabria.

common to almost all of the Mediterranean forms, such as the decreasing number of plates and a progressive lightening of the test-structure (Stara & Borghi, 2014; Stara & Sanciu, 2014).

Future studies focusing on paleoecology will be probably able to explain these dynamics and in particular why some populations underwent significant morphological modifications (e.g. the decreasing in the petalodium size seen in the samples from Calabria and Valencia).

The results of this study indicate the occurrence of different species in the “*nuragica*” group, that is *Amphiope* characterized by narrow and transversely elongate lunules. All these forms likely derived from a common ancestor living in the Archipelago formed during the Oligocene-Miocene boundary between the Provençal and the Sardinian-Corsica coasts.

A similar differentiation is expected to be also in the “*bioculata*” group and also this argument will be the object of future studies.

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