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MONOGRAPH

Paleogeography and diffusion of astriclypeids (Echinoidea Clypeasteroida) from Proto-Mediterranean basins

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ABSTRACT In this paper, the authors retrace the geological changes that during the Neogene have modified the paleogeography of the Western Mediterranean up to its current set-up. It is assumed that migration and probably also speciation of the involved astriclypeids (particularly *Amphiope* L. Agassiz, 1840 and *Echinodiscus* Leske, 1778) are closely related to those changes.

KEY WORDS Paleogeography; Astriclypeidae; Oligo-Miocene; Mediterranean Sea.

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INTRODUCTION

Currently we are dealing with investigations on the Miocene echinoids of Sardinia and their relationship with the echinological paleofaunas that during the Cenozoic have migrated from, or towards, the Proto-Mediterranean seas. In particular, great attention is given to the genus *Amphiope* Agassiz, 1841 (family Astriclypeidae Stefanini, 1912), which is common in the Oligo-Miocene marine deposits of Sardinia (Comaschi Caria, 1955; Stara et al, 2012; Mancosu & Nebelsick, 2013; Stara & Borghi, 2014) and its relationship both with congeners of peri-Mediterranean regions and the phylogenetically closest genera such as *Echinodiscus* Leske, 1778.

The clypeasteroids appeared at the end of the Mesozoic or in the early Cenozoic. According to Smith (2001), the oldest clypeasteroid genus is *Togocyamus* Oppenheim, 1915, from the end of the Paleocene of Senegal, Togo and Nigeria. It is assumed that they evolved from the cassiduloids, which were already present in the Maastrichtian, at the end of the Cretaceous or in the early Paleocene, and then spread and diversified through the world oceans (Smith & Kroh, 2011). The large number of fossil records from the Eocene of United States, Europe, Middle East, Taiwan, Japan and Africa, confirms this wide diffusion and diversification of clypeasteroids, raising doubts as to whether all this could have happened in a tens of millions of years as assumed by Kier (1982). Wang (1984) argued that *Echinodiscus tiliensis* was already present in the late Paleocene or early Eocene in Taiwan, although the remains of this species were poorly preserved and their stratigraphic occurrence was uncertain. Because of paucity of the fossil record available for study, the discussion on the phylogenetic position of many of these fossils is still open.

Many genera of clypeasteroids lived in the Proto-Mediterranean and/or peri-Mediterranean basins, from Eocene to Miocene, as *Sismondia* Desor, 1857, *Clypeaster* Lamarck, 1801, *Scutella* Lamarck, 1816, *Parascutella* Durham, 1953, *Amphiope* L. Agassiz, 1840 (Cottreau, 1914; Smith & Kroh, 2011); few of these survived there until the Pliocene, such as *Clypeaster* (Giannini, 1957; Cotteau et al., 1876-1891). In Sardinia, in particular, *Amphiope* appeared in the Chattian-Aquitanian and disappeared in the Tortonian-Messinian age (Comaschi Caria, 1955, 1972; Stara et al., 2012a).

Nowadays, a number of clypeasteroid genera inhabit wide areas that include environments ranging from tropical to temperate, with some species extending even further polewards, such as *Echinarchnius* Gray, 1825; they adapted to different ecological niches, with preference for the inter-tropical zone (Ghiold & Hoffmann, 1984, 1986).

Several members of the Astriclypeidae family, found the ideal habitat in more or less limited geographic regions. *Astriclypeus* Verrill, 1867 has been adapted from Oligocene to the present, in Japan, China and Cambodia seas (Smith & Kroh, 2011). *Echinodiscus* (herein assumed as a monophyletic group) spread from the Oligo-Miocene throughout the Indo-Pacific, as far as Australia and South Africa, including the Red Sea and the Persian Gulf; *Amphiope* and all other echinoids belonging to the family Astriclypeidae, are absent from the present Mediterranean Sea. Different scientists did not agree on the generic attribution of astriclypeids with two lunules aligned with the rear ambulacra, and about the size and shape of the lunules variability in *Amphiope* (Stara & D. Fois, 2014).

In the North-Western Mediterranean, *Amphiope* (bearing transverse or rounded lunules) is recorded from Chattian-Aquitanian to Tortonian–Messinian, and it occurs in about thirty localities of the Rhône Basin, south-eastern France (Philippe, 1998) and in other thirty sites of Sardinia (Italy) (Stara et al., 2012a; Stara & Borghi, 2014).

Furthermore, in the Tyrrhenian Basin *Amphiopeis* reported in Corsica (Cotteau, 1877) and in some Italian regions: Tuscany (Giannini, 1957), Campania (Barbera & Tavernier, 1989), Calabria (Cottreau, 1914, Carone & Domning, 2007; our observations) and Sicily (Garilli, 2010); further, to the West it is found in some regions of Spain [Barcelona (Lambert, 1928a); Valencia and Alicante (our collections); Mallorca and Menorca Islands (Llompart, 1983)] and Algeria (Pomel, 1887-1888; Cotteau et al., 1891). Along the Atlantic-European coasts *Amphiope* is reported in Portugal [Lisbon, etc. (De Loriol, 1896; Pereira, 2010)] and in France [Aquitaine (Lambert, 1928b) and Touraine (our collections)]; along the Atlantic-African coasts *Amphiope* is found in Angola (De Loriol, 1905). To the East, *Amphiope* is reported in both the Central Paratethys [Austria and Hungary (Kroh, 2005)], in the eastern basins [Turkey (Nebelsick & Kroh, 2002)] and from the Middle East regions [Egypt (Kroh & Nebelsick, 2003), Arabia, Iraq (our observations) and Iran (Khaksar & Moghadam, 2007)] to the Indian coasts (Mooi, 1989). Atypical forms of "*Amphiope*" with axial lunules are mentioned, but they are less frequent and mainly consist of Oligocene species found in France [Aquitaine (Lambert, 1915)], Italy [Liguria-Piedmont (Airaghi, 1899, 1901), North Africa [Tunisia (Gauthier, 1899), Libya and Egypt (Gregory, 1911; Fourtau, 1899, 1904)] and in the Aquitanian of the Rhône Basin, France (Cottreau, 1914; Philippe, 1998). In the Miocene of some regions of the Middle East both forms are recorded (Kier, 1972) (Fig. 1).

NOTES ON THE EXAMINED ASTRICLYPEIDS ECOLOGY

The ecology and life styles of some clypeasteroids have been studied in the past: among others, Merrill & Hobson (1970) observed *Dendrasterex centricus* populations along the Pacific coast of California and Mexico; Kang & Choi (2002) studied a population of *Astriclypeus manni* from the Cheju island of South Korea, Nebelsick & Kampfe (1994) examined, from a taphonomic point of view, some populations of *Echinodiscus auritus* and *Clypeaster humilis* in the Bay of Safaga, Red Sea, Egypt. Kleitman (1941) observed that some clypeasteroids can live at temperatures ranging from 10°C to 30°C, with best conditions between 24°C and 26°C; Nebelsick (1999) observed that most species of astriclypeids lived in near-shore to infralittoral sandy environments, with high to medium-high wave energy and deep currents. The discovery of Pliocene fossils of *Echinarachnius* at Lituya Bay (North West Coast of Alaska) in the Arctic Circle, corresponding to 59° north latitude (Merte, 1930) and Late Miocene *Amplaster* and *Monophoraster* along the Atlantic coast of the Province of Chubu in Argentina, at 45°South (Martinez & Mooi, 2005), indicates that some clypeasteroids were and are able to adapt to significant differences in tem-

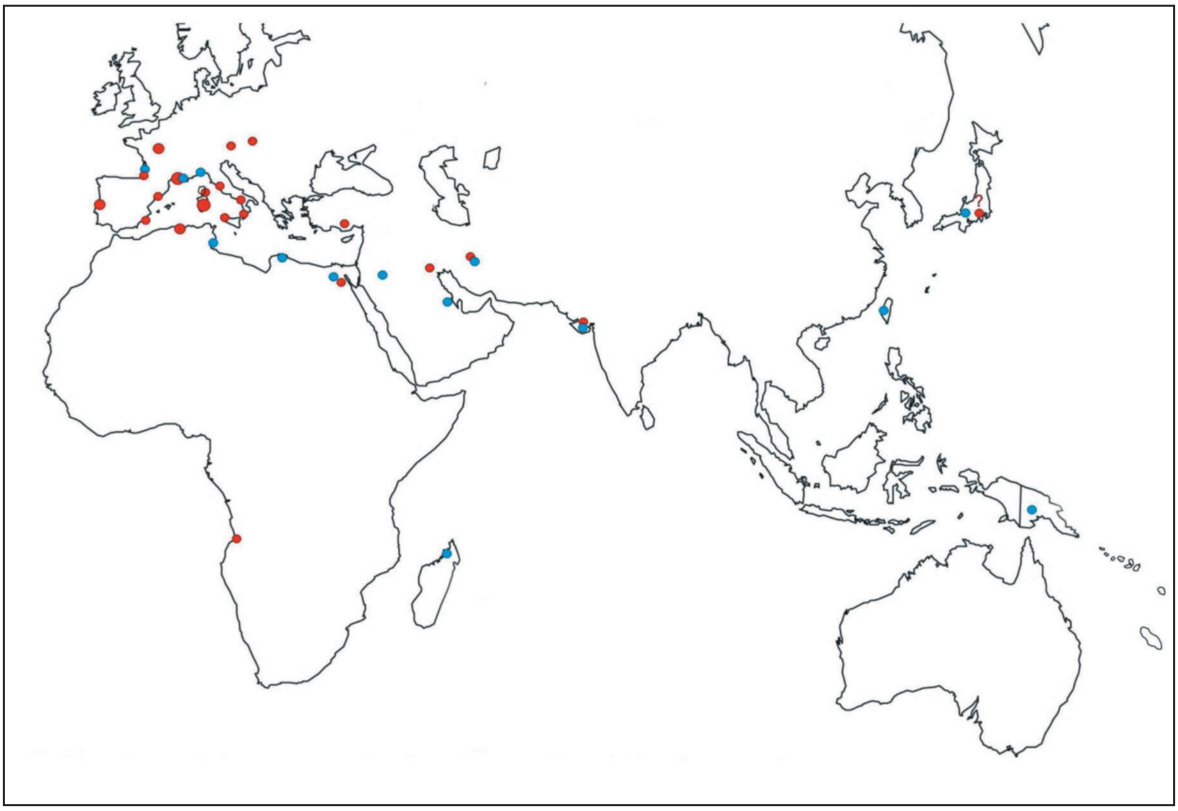


Figure 1. Oligo-Miocene distribution of the the main morphotypes.

perature and salinity conditions. Stara et al. (2012), comparing the sediments of 15 Sardinian sites of Miocene *Amphiope* with those of 5 present beaches observed that those populations live in environment characterized by sandy bottoms and shallow water.

As summarized by Kroh & Nebelsick (2003), *Mellita*, *Encope*, *Leodia* and *Echinodiscus* are all shallow borrowers, whereas *Dendrasterex centricus*, that maintains a partially exposed vertical position in the sediment is a suspension feeder (see Merrill & Hobson, 1970).

In particular, with regard to the bathymetric range of *E. auritus*, Dollfus & Roman (1981) observed it at 1–2 meters in depth in the Red Sea, but also dredged a number of specimens between 10 and 15 meters in depth; the samples studied from Bohol (Philippines), were collected at about 50 meters in depth and Mazzetti (1893) during the dredging session carried out in the Red Sea by the ship "Scilla" in 1891-92, at Goubet Soghra, collected several specimens between 40 to 100 meters in depth.

PALAEOGEOGRAPHY AND PHYLOGENETIC RECONSTRUCTIONS

In order to better understand the relationships between these echinoids, we need to reconstruct their migration pathways. As noted by Stefanini (1912), the "scutellidi" always spread in a relatively limited geographical area. We suppose that this fact depends on their lifestyles, linked to nearshore sandy environments.

Probably, their larval dispersal was not very wide and needed to find sandy bottoms near roosts. This seems justified by the fact that their spread seems to have proceeded along the coast or through basins of limited depth.

In the paleo-biogeographic reconstruction, however, one of the keystones is the completeness of the knowledge of the paleofauna of the period under study.

Unfortunately, as stated also by Harzhauser et al. (2007), only some areas have been deeply investigated and therefore are well known.

DIFFUSION OF THE ASTRICLYPEIDS FROM PROTO-WESTERN MEDITERRANEAN BASINS

An interesting contribution on the temporal and spatial distribution of “scutelliformes" was published by Stefanini (1912), who assumed that the North Ocean was a spreading center for these groups of echinoids, where several species were already present during the Eocene and Oligocene. A further contribution came from Cottreau (1914), who made a summary on the diffusion and evolution of echinoids (among others, also *Amphiope*) in the context of the Mediterranean Neogene.

By using the latest knowledge of geology and paleobiogeography, as we shall see later, it is possible to better define the temporal distribution of the two basic morphotypes, that are the main object of this study. The first is "*Amphiope*" and “*Echinodiscus*” with axial lunules (Figs. 2, 3), appeared during the Rupelian in Italy (Piedmont and Liguria), Libya and perhaps also in Tunisia, and subsequently diffused in the Middle Oligocene (late Rupelian-Early Chattian) of the Bay of Biscay (France). In the Aquitanian, a similar morphotype is present in the Basin of the Rhône and then in the Early Miocene of Tunisia, Libya, (Burdigalian) Egypt. In the Middle Miocene the diffusion area shifted decisively towards the East. There are no citations of this morphotype in the Western Proto-Mediterranean basins, along the Atlanto-European coasts (from the Bay of Biscay to down) and along the Atlanto-African coasts (Fig. 1).

The second morphotype, *Amphiope* with round or transverse lunules (Figs. 4, 5), appeared in the Chattian-Aquitanian in Sardinia and in the Aquitanian of France and Kabylies; it was widespread during the Miocene in the Western Mediterranean Basin, along the Atlanto-European and Atlanto-African coasts, in the Paratethys, in the Middle East, as for as India and perhaps to Japan (Fig. 1), and went extinct during the Tortonian-Messinian in Sardinia (Philippe, 1998; Smith & Kroh, 2011; Stara et al., 2012). Another morphotype (Fig. 6), characterized by small rounded lunules rather far from the petaloid tips (Fig. 7), firstly appeared in Libya during the Miocene; it showed some features of both the previous main morphotypes.

Echinodiscus cf. *auritus* (Fig. 3) is already widespread from the Gulf of Suez to the Indo-Pacific coasts in the Plio-Pleistocene. This morphotype is recorded in the Plio-Pleistocene of Suez (Fourtau, 1899), in the Isle of Kharak (current Khark Island) of the Persian Gulf (Duncan & Sladen, 1883) and of the Aru Islands in Indonesia (Currie, 1924), in the late Pliocene and Pleistocene of Java (Jeannet & Martin, 1937). Lastly, it appeared in Pleistocene-Holocene sediments near Hurghada (Red Sea, Egypt) accompanied by other forms of *Echinodiscus*. Lindley (2001) cited a similar morphotype characterized by axial and medium-sized lunules, in the Middle Miocene (Langimar beds) of the province of Morobe (Papua New Guinea), but he assigned it by mistake to *Echinodiscus bisperforatus*.

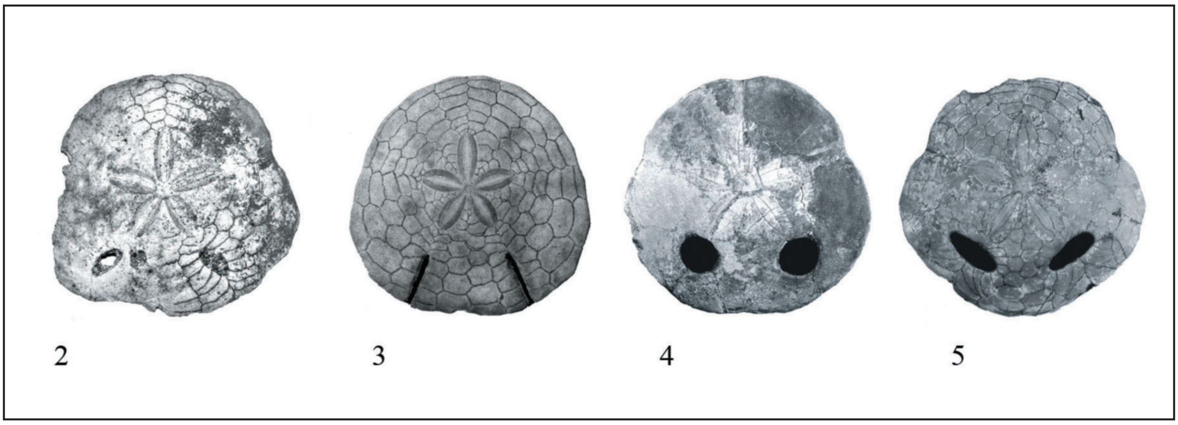
Currently *Echinodiscus* cf. *auritus* seems to be the astriclypeid with the widest spread surpassing the lines of the two tropics, 30°North to 35°South. Their presence is ascertained along the East African coast of Mozambique and South Africa and along the coasts of Madagascar. To the North it is ascertained along the Red Sea, to the Gulfs of Suez and Aqaba, (Dollfus & Roman, 1981) the Persian Gulf and along the northern shores of the Indian Ocean (Sakthivel & Fernand, 2014). Lastly, to the East, it is widespread in the Malay Archipelago (Indonesia), Thailand (Putchakam & Sonchaeng, 2004), Philippines, along the Gulf of Siam, China (Lane et al., 2000) and Japan, reaching the Northern and Western coasts of Australia and perhaps New Caledonia (Fig. 8).

Echinodiscus bisperforatus shows a similar distribution: it was present in the Middle Miocene of Makamby island, Northern Madagascar (Collignon & Cottreau, 1927) and in the Pleistocene-Holocene sediments of Hurghada in the Red Sea (our collections), but some morphotypes showing features similar to those of *E. bisperforatus* (*E. formosus* Yoshiwara and *E. yeliuensis* Wang), were maybe already present in the Middle Eocene and certainly in Miocene of Taiwan.

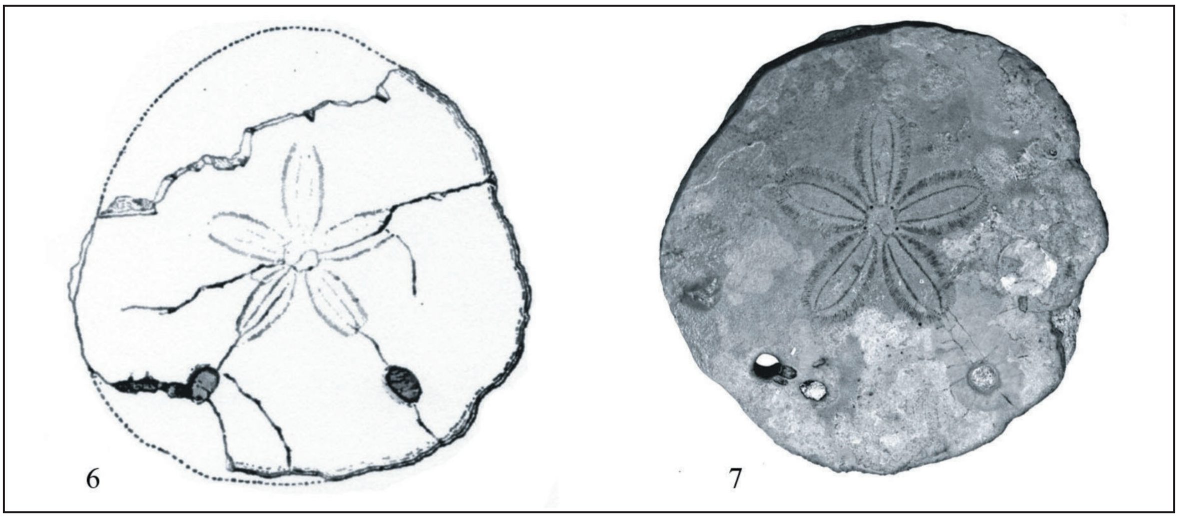
Finally, the "*E. tenuissimus*" group seems to have a limited distribution in northern latitudes of the Indian Ocean to Oceania, but today it would be absent from the eastern and southern coasts of Africa (Fig. 8).

In the reconstruction proposed by Stara & Rizzo (2013), the similarity between the echinoid faunas of North Atlantic and Western Mediterranean would have been facilitated by the opening of the pre-Pyrenean Corridor, which took place between Middle Eocene and Middle Oligocene (Fig. 9), allowing direct exchanges between the Atlantic faunas of the Bay of Biscay and those of the Alpine Tethys or intra-AlKaPeCa basins (this is an acronym used by Bouillin et al. (1986) to indicate the micro-continent that moving away from the European plate, would have given rise to different regions of the actual Western Mediterranean). After the closure of the pre-Pyrenean Corridor, which probably has occurred during the Middle Oligocene, the two faunas began to differentiate.

In addition, the almost complete separation between the Alpine Tethys (from which the Proto-Western-Mediterranean was born) and the Western Neotethys basins (according to the reconstructions of Stampfli et al. (2002), or basins resulting from detachment of the AlCaPeKa micro-plates, according to Carminati et al. (2012), also justifies a lot of the differences observed between the Miocene faunas of the Western Mediterranean and of the Eastern Mediterranean (see Figs. 9-14). For example, in the first area, "*Amphiope*" with axial lunules and



Figures 2–5. Morphotypes based on the shape of rear ambulacral lunules/slits. First morphotype, bearing axial lunules or slits notching the posterior margin: Figure 2. “*Amphiope*“ pedemontana, Oligocene, Val Bormida, Liguria and Piedmont, Italy. Figure 3. “*Echinodiscus*”cf. *auritus*, Recent, Mangili, Tulear, Madagascar; Second morphotype, bearing rounded or transverse lunules: Figure 4. *Amphiope* sp., Oligo-Miocene, Duidduru, Sardinia, Italy. Figure 5. *A. nuragica*, Oligo-Miocene, Cuccuru Tuvullao, Sardinia.



Figures 6, 7. Morphotype with small lunules far from the petal tips: 6 “*Amphiope*” *boulei*, Aquitanian, France (from Cottreau, 1914). Fig. 7. “*Amphiope*” sp., “Miocene”, Libya (NMHUK collections).

Scutella were absent, whereas in the second area both these genera were widespread. Indeed, in the Western Mediterranean, only *Amphiope* and *Parascutella* are known (A. Kroh, personal communication, June 2012).

According to Stara & Rizzo (2013), from the Sardinian-Provençal basins, derived from the fragmentation of the micro-continent AlKaPeCa, at least three waves of migration of lunulate scutellids may have originated: two from the East and one from West. The first wave would have taken place during the Oligocene through the corridor of the Bormida Valley (Piedmont and Liguria) (Fig. 10), the second at the beginning of the Miocene, through the corridor of the Alpine Paratethys, the third was a result of the fragmentation, the detachment and their drift towards the south, of micro-plates, from the continental margin of the Ibero-Provençal crust.

The second of these migration has been already recognized by Kroh (2007), who stated that the majority of the echinoid fauna of the Central Paratethys is immigrant from the western Mediterranean and partly shows similarities with that of the Atlantic region. This migration took place in three phases: the first wave would have started at the beginning of the Miocene from the Rhône Basin through the Alpine Tethys, the second and the third, much later, according to Kroh (2007) took place through the trans-Tethys Dinarids Corridor that led to the Adriatic Neotethys. Some species wich immigrated during the first phase had Atlanto-Mediterranean affinities, those joining the second and third phases were more closely related to the faunas of the Eastern-African coasts.

The migration along the Val Bormida Corridor has been hypothesized by Stara & Rizzo (2013), based on the presence of a series of *Scutella* and "*Amphiope*" *pedemontana* rich beds that crop out in the Rupelian of Liguria and Piedmont. The hypothesized migration is in accordance with the similarity of some characters that these "*Amphiope*" share with those of Rupelian from the coast of Libya and those of the Middle Oligocene (Late Rupelian-Early Chattian?) of the Gulf of Biscay. In addition, this step is also traced by the spread of *Heterobrissus* Manzoni et Mazzetti, 1878. This

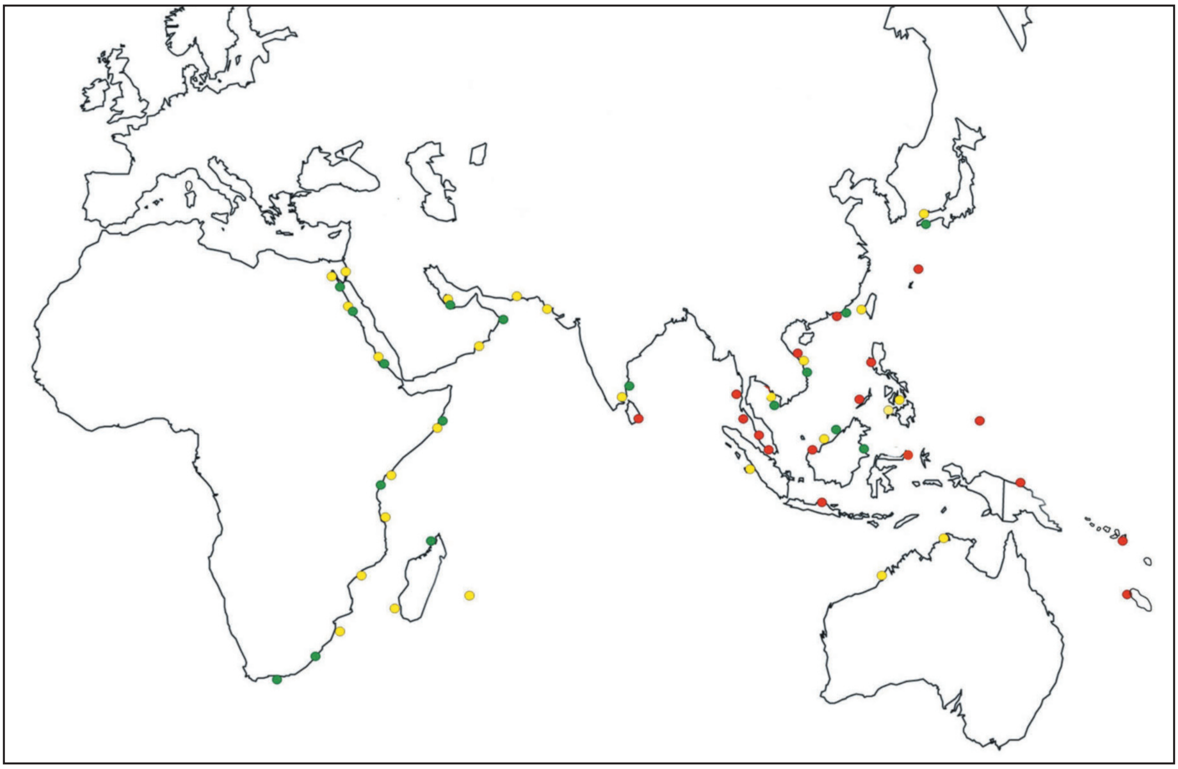
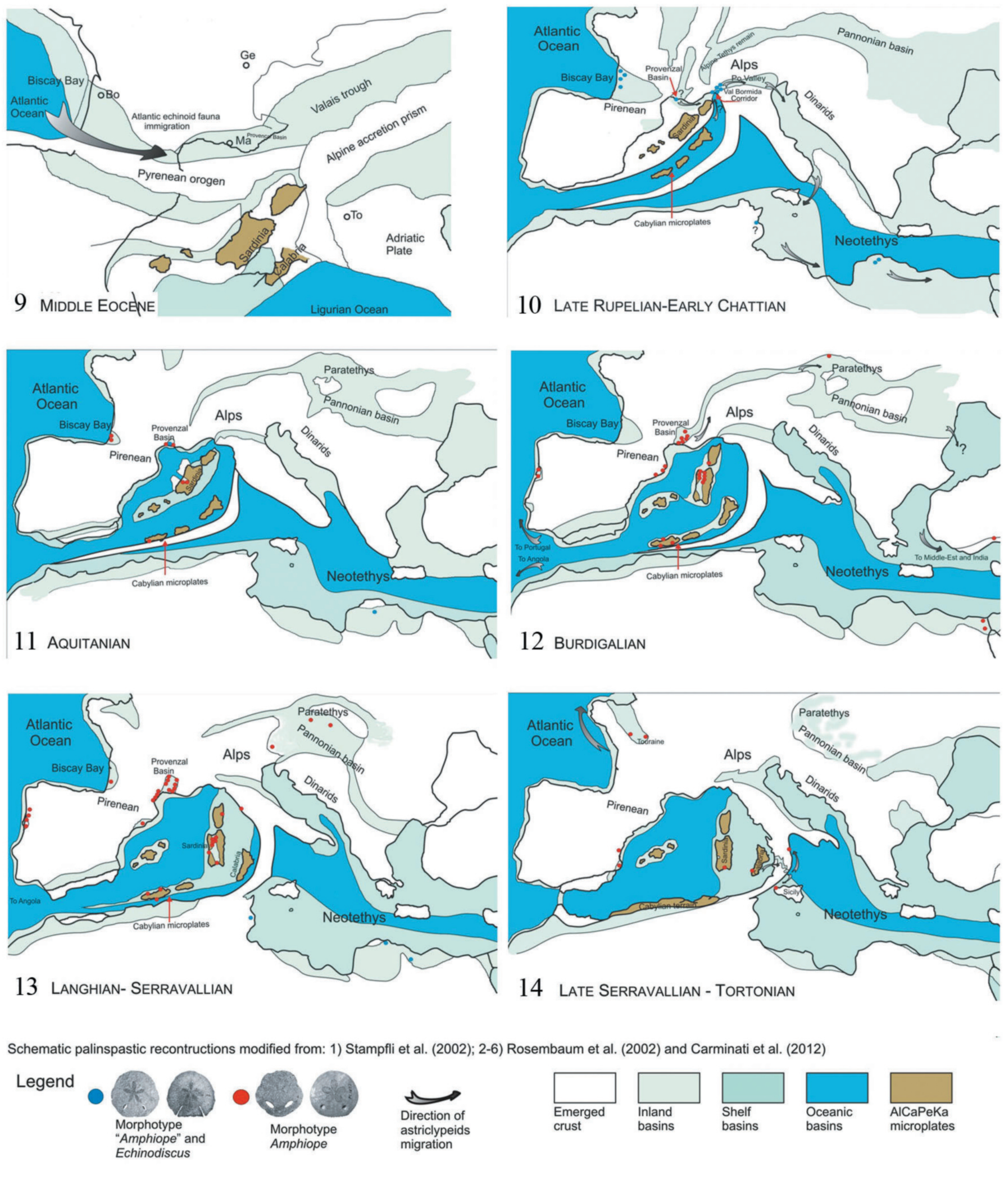


Figure 8. Distribution of extant main morphptypes of "*Echinodiscus*" genus. Yellow dots: "*Echinodiscus*" cf. *auritus* group. Green dots, *Echinodiscus bisperforatus* group. Orange dots: "*Echinodiscus*" *tenuissimus* group.



Schematic palinspastic recontructions modified from: 1) Stampfli et al. (2002); 2-6) Rosembaum et al. (2002) and Carminati et al. (2012)

Figures 9–14. Time scanning of *Amphiope* diffusion in the proto-Mediterranean basins. Figure 9. Middle Eocene-Lower Oligocene connection between the Atlantic-Gulf of Biscay and the Provençal Basin. Figure 10. Morphotype 1 populations begin their eastward Oligocenic migration through the Val Bormida Corridor. Figure 11. Starting from a single distribution center, located between the Biscay and the original intra-AlCaPeKa basin, morphotype 2 populations begin their Oligo-Miocenic spread. Figure 12. Morphotype 2 is already widespread from Atlantic coasts to the far east; morphotype 1 is no longer present in the western basins. Figure 13. Morphotype 2 reaches its peak in the Rhône Basin and in Sardinia; morphotype 1 has spread from the Middle East to India. Figure 14. At the end of the Middle Miocene, morphotype 2 begin to extinguish, whereas morphotype 1 has colonized the Indian Ocean and the Western Pacific Ocean. Based on the paleogeographic data from Stampfli et al., 2002; Rosenbaum et al. 2002; Carminati et al., 2012.

genus is present in the Oligocene of Caribbean Islands (Jackson, 1922), in the Early Miocene of Sardinia (Stara et al., 2012b), in the Middle Miocene of Emilia and San Marino (Manzoni & Mazzetti, 1878), lastly in the Serravallian of Cyprus (Currie, 1935; Smith & Gale, 2009), and today it is widespread in the seas of China and South Eastern Asia (Lane et al., 2000). So, the basins of the Middle East suffered at least two waves of migrants from N-NW, the first one through the Adriatic Tethys during Oligocene and the second one through the eastern Paratethys between the end of the Early Miocene and the Middle Miocene.

In summary, from the Late Oligocene to the Early Miocene, the Val Bormida Corridor had already closed as a result of Apennines orogeny, while the Alpine Tethys Corridor shut at the end of Burdigalian as a result of the Alpine orogeny. The closing of these two corridors led to the isolation or, at least, to a drastic reduction of the exchanges between the eastern and western faunas of the Tethys (or Proto-Mediterranean basins). This new situation probably allowed the differentiation of the Oligo-Miocene "*Amphiope*" with axial lunules from the North-African and Middle-Eastern coasts. During the Burdigalian, *Amphiope* with rounded or transverse lunules was already present in the central Paratethys and in Egypt. However, while it seems clear that it arrived in the Paratethys crossing West to East the canal north-Alpine, is not yet clear how it arrived in Egypt. In fact, there is no evidence of these echinoids, nor *Parascutella*, along the Miocene Adriatic and Ionian seashores, favoring the continuity of their migration through the eastern basins, already during the Middle-Early Miocene, to other marine faunas. In any case, as a result of their migration, *Amphiope* went to Turkey, Egypt, Saudi Arabia, Iran and finally to India and also in Iraq (our observations). Finally, Harzhauser et al. (2007) suggest that the complete disconnection between the Proto-Mediterranean basin and the Indian Ocean basin occurred at the end of the Burdigalian, when the two faunas where already differentiated.

The apparent diachrony should be clarified when the astriclypeids of the eastern regions faunas will be studied. In fact, it is possible that faunas from the West (as we assumed), but also from the East, met in the Middle East area, since different forms of “*Echinodiscus*” were already present (doubtfully) in the Middle Eocene, but certainly in the Lower Miocene, respectively, in the islands of Taiwan and Japan.

Regarding the Mediterranean, according to Rögl (1998), during the Miocene the two sides of the Mediterranean were in full connection, while according to Stampfli et al. (2002), these were completely separate. Much evidence is needed, however, we argue in favor of this second hypothesis. The reconstruction made by Stampfli et al. (2002) suggests that the complete connection between the Eastern and the Western Mediterranean would have occurred much later, when the Calabrian microplate reached the Italian Apennines, at the end of the Miocene or during the Pliocene. Although the precise date of the disconnection between the basins of the eastern Neotethys and the Indian Ocean is still under discussion, Harzhauser et al. (2007) agree with the development of different biota for these two regions during the beginning of the Middle Miocene.

THE SPREAD OF *AMPHIOPE* WITH TRANSVERSE OR ROUNDED LUNULES TO THE WEST-SOUTH-WEST

In the North-Western Mediterranean sedimentary basin, Chattian-Aquitanian to Tortonian-Messinian fossils of *Amphiope* with rounded or transverse lunules have been found in many localities in the Rhône Basin (Philippe, 1998), and Sardinia (Stara et al., 2012a; Stara & Borghi, 2014).

In detail, starting from density of *Amphiope* deposits existing in a specific region, we can assume that *Amphiope* appeared in a fairly restricted area within the archipelago formed between the Basin of the Rhône and Sardinia, from the end of the Oligocene to the beginning of Miocene. According to Rosenbaum et al. (2002) and Gattacceca et al. (2007), in this period different microplates began drifting towards the South forming that archipelago (Figs. 11–14). The shift of these microplates to the current position point lasted about 7 million years, and during this time the fauna could (in some cases) differ from the original giving rise to new species, as it happened for example in Sardinia, where 3 species [*Amphiope nuragica* (Comaschi Caria, 1955); *Amphiope lovisatoi* Cotteau, 1895, and *Amphiope montezemoloi* Lovisato, 1911] were confirmed and for the first time, another two new ones have been described (Stara & Borghi, 2014).

At the end of the Burdigalian the Sardinia-Corsica microplate had completed its route after an anticlockwise rotation, stopping more or less in its current position; Calabria located in the East of Sardinia, and it reached its current position only in the Pliocene, the Kabylies had almost welded with North Africa, the Betic-Rifian microplates were still in the Alboran Sea, while the Balearic Islands were more or less in the current position.

A part of Sardinia-Corsica and Balearic Islands now detached itself, the other microplates, each with its own specific fauna, to the contact with the North African margin (for example the Kabylies) or southern Europe (Iberia) were able to create further migrations, which most likely occurred along the sandy beaches adjacent to shallow depths (Stefanini, 1912).

Pomel (1883, 1887-8) and Cotteau et al. (1876-1891) reported the presence of *Amphiope* in the Early Miocene of Cherchell and in the Middle Miocene of Mléta, Oran, as well as in other places of Kabylies (Algeria). Most likely, as suggested by Stefanini (1912), starting from the Kabylies, *Amphiope* populations reached the Atlantic Ocean to continue towards South to colonize the area of Bom Jesus (Angola, West Central Africa) during the Middle Miocene. It is uncertain if the presence of *Amphiope* in the region of Alicante and Valencia during the Tortonian is due to a direct migration from the North, since its presence is also reported in the Middle Miocene in the region of Barcelona. It seems logical that, starting from the South of the Iberian Peninsula *Amphiope* has continued its coastal migration as far as the Atlantic Ocean and back along the coast of Portugal (Fig. 12). Pereira (2010) reports: "The echinoid fauna of mainland Portugal is closely related to that of the Mediterranean region. In fact, the biogeographic investigation of the Portuguese echinoid fauna shows that a major part of the Portuguese species is composed by Portuguese immigrants from the Mediterranean area (42.9% of the fauna in the Burdigalian and 60.9% in the Middle Miocene). Endemism is low during Miocene, with endemic species not exceeding 25% of total Portuguese echinoid fauna".

Following its migration toward the North, *Amphiope* reached the French coast until the Bay of Biscay, where it has been reported in the Serravallian deposits; its migration toward the North seems to stop in the great inland sea that covered the Touraine, where different sites related to Middle-Late Miocene (Serravallian-Tortonian) are reported. However, after the closure of the pre-Pyrenean Corridor, in Aquitaine an endemic fauna probably developed independently and directly from the original Aquitanian *Amphiope ovalifora* Fallot, 1903.

In conclusion, along the Italian peninsula, *Amphiope* was found in the Middle Miocene of Tuscany (Giannini, 1957) and Campania (Barbera & Tavernier, 1989); in the first case it is unclear whether the migration is linked to the movement of microplates along the Mediterranean, or if it occurred directly from North along the peninsula coasts. However, the presence of *Amphiope* in the Middle Miocene of Campania and in the Tortonian of Sicily (Garilli et al., 2010), can be connected with the approach of the Calabrian microplate (Fig. 14). During the Burdigalian this microplate moved to the East bringing the original fauna, as stated by the findings in the Tortonian deposits of Cessaniti near Vibo Valentia (Cottreau, 1914).

CLIMATE CHANGE, LIMIT OF THE DIFFUSION

To understand the diffusion of scutelliforms living nearshore, we need to consider the trend of climate change from the Cretaceous on to the Miocene, and how it conditioned the life of organisms inhabiting the continents and oceans of the northern hemisphere and Southern Africa. As summarized by Harzhauser et al. (2007), the warm climate of the Cretaceous continued into the Early Palaeogene, with a distinct optimum that characterized the Paleocene-Eocene transition. Starting in the Late Eocene, a gradual decrease in temperature culminated around the Eocene-Oligocene boundary, leading to the formation of the first Antarctic ice cap. From the late Oligocene times, the trend of increasing temperature continued intermittently until the Middle Miocene, when it reached its maximum (Climate Optimum).

Around 14.2 Ma began the transition of the Middle Miocene climate, characterized by the cooling of surface waters and the expansion of the East-Antarctic ice cap (Shevenell et al., 2004), and during this time the extinction of *Parascutella* and *Amphiope*, began, thus stopping their diffusion to the south. Only for "*Echinodiscus*" migration will continue in the Indian Ocean and along the coast of South Eastern Europe to settle in the current positions.

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