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BIOLOGICAL OCEANOGRAPHY AT THE TURN OF THE MILLENIUM. *J.D. ROS, T.T. PACKARD, J.M. GILI, J.L. PRETUS and D. BLASCO (eds.)*

The present-day Mediterranean brachiopod fauna: diversity, life habits, biogeography and paleobiogeography*

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SUMMARY: The present-day brachiopods from the Mediterranean Sea were thoroughly described by nineteenth-century workers, to the extent that Logan's revision in 1979 listed the same 11 species as Davidson, almost 100 years earlier. Since then recent discoveries, mainly from cave habitats inaccessible to early workers, have increased the number of species to 14. The validity of additional forms, which are either contentious or based on scanty evidence, is evaluated here. Preferred substrates and approximate bio-depth zones of all species are given and their usefulness for paleoecological reconstruction is discussed. A previous dearth of material from the eastern Mediterranean has now been at least partially remedied by new records from the coasts of Cyprus, Israel, Egypt, and, in particular, Lebanon and the southern Aegean Sea. While 11 species (79 % of the whole fauna) have now been recorded from the eastern basin, *Terebratulina retusa*, *Argyrotheca cistellula*, *Megathiris detruncata* and *Platidia* spp. appear to be less common than in the western basin. *Lacazella mediterranea*, *Tethyrhynchia mediterranea* and *Gwynia capsula* have not yet been recorded from the eastern Mediterranean, but whether this is due to a west-east faunal impoverishment or insufficient collecting is uncertain. *L. mediterranea* and *T. mediterranea* may be endemic to the Mediterranean. The Messinian (Late Miocene) salinity crisis caused most species to disappear from the ancestral Mediterranean Sea. *T. mediterranea* may be a paleoendemic that has survived in marine refuges mostly located on the outer margin of the western basin, while other species either entered or re-entered the Mediterranean from the Atlantic after the Miocene.

Key words: Mediterranean, Recent, brachiopods, diversity, life habits, biogeography, paleobiogeography.

RESUMEN: LA FAUNA ACTUAL DE BRAQUIÓPODOS DEL MEDITERRÁNEO: DIVERSIDAD, MODOS DE VIDA, BIOGEOGRAFÍA Y PALEOBIOGEOGRAFÍA. – Los Braquiópodos actuales del mar Mediterráneo fueron descritos con detalle por los investigadores del siglo XIX, hasta el punto que en la revisión de Logan (1979) se citaban las mismas 11 especies que indicaba Davidson (1886-1888) casi un siglo antes. Desde entonces, descubrimientos recientes, en su mayor parte procedentes de hábitats de cuevas, inaccesibles a los primeros investigadores, han aumentado el número de especies hasta 14. Aquí se evalúa la validez de las formas adicionales, que son disputadas o bien se basan en escasas pruebas. Se dan los sustratos preferidos y las zonas batimétricas aproximadas de todas las especies, y se comenta su utilidad para la reconstrucción paleoecológica. La escasez previa de material procedente del Mediterráneo oriental se ha solventado al menos parcialmente mediante nuevos registros de las costas de Chipre, Israel, Egipto y, en particular, Líbano y el mar Egeo meridional. En la cuenca oriental se han registrado ahora 11 especies (el 79% de toda la fauna), pero *Terebratulina retusa*, *Argyrotheca cistellula*, *Megathiris detruncata* y *Platidia* spp. parecen ser menos comunes que en la cuenca occidental. *Lacazella mediterranea*, *Tethyrhynchia mediterranea* y *Gwynia capsula* no se han encontrado todavía en el Mediterráneo oriental, pero no está claro si ello se debe a un epobrecimiento de la fauna en el sentido oeste-este o a una recolección insuficiente. *L. mediterranea* y *T. mediterranea* pueden ser endémicas del Mediterráneo. La crisis de salinidad del Messiniense (Mioceno tardío) hizo que muchas especies desaparecieran del mar Mediterráneo ancestral. *T. mediterranea* puede ser un paleoendemismo que sobrevivió en refugios marinos situados en su mayor parte en el borde externo de la cuenca occidental, mientras que otras especies entraron o volvieron a entrar desde el Atlántico después del Mioceno.

Palabras clave: Mediterráneo, Reciente, braquiópodos, diversidad, tipos de vida, biogeografía, paleobiogeografía.

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INTRODUCTION

Although individual species were first described by various authors in the eighteenth and nineteenth centuries, the first systematic account of modern brachiopods as a whole was by Davidson (1886-88). Included in his 3-part monograph, which brought all previous records together, were 11 species of brachiopods from the Mediterranean Sea and adjacent regions, with accompanying descriptions, illustrations, ecological information, geographical distribution and geological records. So comprehensive was this work that almost a century later a revision of the Recent Mediterranean brachiopods by Logan in 1979 (summarised in Benigni and Corselli, 1981) did not add any new species to those recognized by Davidson. Since then, however, more collections of Recent Mediterranean brachiopods have been studied (Llompart, 1983, 1988; Logan and Noble, 1983; Templado and Luque, 1986; Ruggiero, 1985, 1990, 1994, 1996, 2000; Brunton, 1989; Logan and Zibrowius, 1994; Simon and Willems, 1999; Logan and Long, 2001; Logan *et al.*, 2002; Logan, in press), resulting in one new species *Tethyrhynchia mediterranea* by Logan and Zibrowius (1994) and one new record for the Mediterranean, that of *Gwynia capsula* (Jeffreys) by Simon and Willems (1999), plus the re-validation of *Novocrania turbinata* (Poli) as a species by Brunton (1989) and Logan and Long (2001). Two additional species, which we consider to be contentious, are *Megerlia monstruosa* (Scacchi) discussed by Brunton (1989) and *Frenulina sanguinolenta* (Gmelin) described by Ruggiero (2000).

Older records of brachiopods from Tertiary and Quaternary rocks of the Tethyan (ancestral Mediterranean) region by Davidson (1864, 1870) and Fischer and Oehlert (1891) have been supplemented by newer records which document the geological ranges of many extant and extinct forms (Pajaud, 1970; Pedley, 1976; Brebion *et al.*, 1978; Llompart and Calzada, 1982, Llompart, 1983; Ruggiero, 1983; Gaetani and Saccà, 1984; Bitner, 1990, 1993; Vazzana, 1996; Bitner and Pisera, 2000).

In this paper we review the main substrate and bio-depth zone preferences of those 14 species which we consider unequivocal, give our opinion on those that we regard as contentious or incorrectly cited for the region and, on the basis of recent discoveries in the eastern Mediterranean (Logan *et al.*, 2002), discuss the biogeography of living species in the region. Finally, we summarise the Tertiary and Quaternary paleobiogeography and geological history of both extant and extinct brachiopods throughout the Mediterranean-Paratethys region.

DIVERSITY, SUBSTRATE AND BIO-DEPTH ZONE PREFERENCES

Logan (1979) discussed the distribution and ecology of the 11 species of Recent Mediterranean brachiopods recognized at that time. The 14 species of brachiopods which we now consider to be valid for the present-day Mediterranean, along with their preferred substrates and bio-depth zones, are shown in Table 1. Not surprisingly, recent investigations, mainly by divers in submarine cave habitats inaccessible to early workers, have yielded new species (Logan and Zibrowius, 1994) or forms new to the Mediterranean (Brunton, 1989; Simon and Willems, 1999). Any new discoveries in the future are likely to be made in these environments, although bathyal zone substrates may also provide promising hunting grounds.

Logan (1979) divided the Mediterranean brachiopods into two depth groups: those typically found in shallow water (shelf species ranging down to about 200 m, occasionally deeper, belonging to *Argyrotheca*, *Megathiris* and *Lacazella*) and eurybathic species which may occur on the shelf but are more typical of the bathyal zone at depths of about 600 m or more (*Novocrania*, *Gryphus*, *Terebratulina*, *Platidia* and *Megerlia*). This scheme has basically been retained here, except that *Novocrania* is moved to the shallow water group, because even though it ranges greatly in depth, it is found most commonly in shallow caves less than 50 m in depth. Precise depth ranges for all brachiopods in the Mediterranean are difficult to establish, as Recent brachiopods generally have wide depth tolerances and should be used with caution when reconstructing paleobathymetry (Fischer and Oehlert, 1891; Cooper, 1977; Logan, 1979; Emig, 1988). As an example, Bitner and Pisera (2000) attempted to reconstruct the paleobathymetry of Miocene brachiopods from south-eastern Poland using the published depth ranges of their modern Mediterranean descendants as analogues but, in the end, were forced to use sediment characteristics and the more precise depth ranges of other biota. Bottom type is clearly the dominant limiting factor in modern brachiopod distribution as a whole, most species requiring hard substrates for their settlement.

TABLE 1. – Information on life habits and geological range of the fourteen species of Mediterranean Recent brachiopods, compiled from many sources but mainly from Davidson (1864, 1870, 1886-8), Fischer and Oehlert (1891), Pajaud (1970), Pedley (1976), Brebion *et al.* (1978), Logan (1979), Llompart and Calzada (1982), Llompart (1983), Ruggiero (1983), Gaetani and Saccà (1984), Bitner (1990, 1993), Vazzana (1996) and Bitner and Pisera (2000). Recent references to descriptions and illustrations of Mediterranean brachiopods are indicated by a superscript number after the species in the left-hand column, as follows: [1] Logan (1979); [2] Logan and Long (2001); [3] Simon and Willems (1999); [4] Logan and Zibrowius (1994).

Species	Preferred substrate and bio-depth zone	Recent and Tertiary occurrences in Mediterranean, Tethys and Paratethys
Novocrania anomala (Müller 1776)[1]	Cemented to cave walls and roofs; boulders; coralligène; mainly shallow, infralittoral-bathyal	**Recent**: NE Atlantic, Mediterranean
Novocrania turbinata (Poli 1776)[2]	Cemented to cave walls and roofs; boulders; coralligène; mainly shallow, infralittoral-circalittoral	**Recent**: NE Atlantic, Mediterranean; **Miocene**: Italy
Gryphus vitreus (Born 1778)[1]	Pedicle attachment to rock; gravel clasts; eurybathic; circalittoral-bathyal	**Recent**: NE Atlantic, Mediterranean; **Pleistocene**: Italy; **Pliocene**: Italy
Terebratulina retusa (Linnaeus 1758)[1]	Pedicle attachment to rock; gravel clasts; eurybathic; circalittoral-upper bathyal	**Recent**: NE Atlantic, Mediterranean, **Pleistocene**: Italy, Spain; **Pliocene**: Italy, France, Algeria, **Miocene**: Italy, Morocco
Argyrotheca cistellula (Searles-Wood 1841)[1]	Pedicle attachment to cave walls and roofs; boulders; coralligène; shallow; infralittoral-circalittoral	**Recent**: NE Atlantic, Mediterranean; **Pleistocene**: Greece; **Pliocene**: Italy
Argyrotheca cuneata (Risso 1826)[1]	Pedicle attachment to cave walls and roofs; boulders, coralligène; shallow; infralittoral-circalittoral	**Recent**: NE Atlantic, Mediterranean; **Pleistocene**: Italy; **Miocene**: Italy, Poland, Bulgaria
Argyrotheca cordata (Risso 1826)[1]	Pedicle attachment to cave walls and roof; boulders, coralligène; infralittoral-circalittoral	**Recent**: NE Atlantic, Mediterranean, **Pliocene**: Italy, Spain; **Miocene**: Poland, Austria, Ukraine, France, Hungary, Bulgaria
Megathiris detruncata (Gmelin 1790)[1]	Pedicle attachment to cave walls and roofs; boulders; coralligène; shallow; infralittoral-circalittoral.	**Recent**: N.E. Atlantic, Mediterranean, Caribbean; **Pleistocene**: Italy; **Pliocene**: Italy, Spain; **Miocene**: Poland, Italy, Austria, Ukraine, France, Hungary, Spain; **Eocene**: Italy
Gwynia capsula (Jeffreys 1859)[3]	Pedicle attachment to cave walls and roofs; shallow; infralittoral-circalittoral	**Recent**: NE Atlantic, Mediterranean (Croatia)
Tethyrhynchia mediterranea (Logan 1994)[4]	Pedicle attachment to cave walls and roofs; shallow; infralittoral-circalittoral	**Recent**: Mediterranean (France, Tunisia, Croatia)
Platidia anomioides (Scacchi and Philippi 1844)[1]	Pedicle attachment to rock and shell substrates; eurybathic; circalittoral-bathyal	**Recent**: SW and E. Atlantic, Mediterranean; Caribbean, Indian Ocean, Antarctic; **Pleistocene**: Italy; **Miocene**: Poland
Platidia davidsoni (Deslongchamps 1855)[1]	Pedicle attachment to rock and shell substrates; eurybathic; circalittoral-bathyal	**Recent**: SW and E. Atlantic, Mediterranean, Caribbean, Indian Ocean; **Pleistocene**: Italy
Megerlia truncata (Linnaeus 1767) (includes *M. monstruosa* auct.)[1]	Pedicle attachment to rock and shell substrates; shallow but more typically eurybathic, infralittoral-upper bathyal	**Recent**: NE Atlantic, Mediterranean, Indian Ocean; **Pleistocene**: Italy; **Pliocene**: Italy, France, Spain; **Miocene**: Poland, Italy, Austria, Ukraine, Hungary, Bulgaria, Spain, Malta
Lacazella mediterranea (Risso 1826)[1]	Cemented to cave walls and roofs; boulders; coralligène; shells; shallow; infralittoral-circalittoral	**Recent**: SW Mediterranean; **Pliocene**: France, Spain, Algeria, Italy; **Miocene**: Malta, France, Italy; **Oligocene**: Austria, Italy; **Eocene**: Italy

CONTENTIOUS FORMS

Megerlia truncata (Linnaeus) var. *monstruosa*

The common Mediterranean brachiopod *Megerlia truncata* is typically characterized by a biconvex shell ornamented with radial costae which are occasionally slightly nodulose (Logan, 1979). Dall (1919, 1920) proposed the genus *Pantellaria*, with type species *Terebratula monstruosa* Scacci, and type locality of Naples, Italy, for specimens similar to *Megerlia truncata* (Linnaeus) but with an amphithyridid instead of submesothyridid foramen and a flat or slightly concave dorsal valve lacking radial sculpture. This recognition of *Pantellaria* as a genus separate from *Megerlia* was followed by Thomson (1927), Hatai (1965), Cooper (1981b, 1982), Llompart (1988) and Zezina (2000). However, others believed that these differences were, at best, specific and included *monstruosa* within the genus *Megerlia* but separated it from *truncata* (Fischer and Oehlert, 1891; Atkins, 1961; Ruggiero, 1983; Brunton, 1989; Anadón, 1994). However, there are those (Jeffreys, 1878; Davidson, 1887; Logan, 1979; Bitner 1990, 1993) who regard *monstruosa* as merely a variety or ecomorph of *M. truncata*, because the shape of the shell and the nature of the foramen is influenced by the angle of attachment to the substrate. In the case of specimens whose dorsal valve happens to be adpressed to the substrate, the imprint of the latter may partially or completely obliterate the radial costae. While these differences of opinion may eventually be resolved by molecular studies, we here maintain the varietal status of *monstruosa* and cite as support the following observations from an exhaustive study of over 2500 examples of fossil *M. truncata* from the Miocene of Poland by Bitner (1990). She states (op. cit., p. 146): "In the studied material .. there are many intermediate forms, thus specimens having the irregular, noncostate, only with irregular growth lines as an ornamentation, flat or slightly concave brachial valve but with the foramen submesothyridid or slightly amphithyridid (occur). Sometimes one may observe a patch with preserved ornamentation on the brachial valve. There are also specimens which are biconvex with normal ornamentation on the brachial valve but having an amphithyridid pedicle opening, or specimens having (the) ventral umbo badly worn. Thus, the present author's observations also confirm that *P. monstruosa* and *M. truncata* are conspecific, and differences between them are caused only by ecological factors."

Frenulina sanguinolenta **(Gmelin)**

While the genus *Frenulina* Dall is Indo-Pacific in distribution, the type-species *F. sanguinolenta* (Gmelin) has been recorded only from shallow, low-latitude Pacific localities where it is not uncommon (Davidson, 1887; Dall, 1920; Cooper, 1978). It is externally very distinctive in being ornamented with red stripes, while internally the deltidial plates are disjunct and the brachial loop and its developmental stages are characteristic (Cooper, 1973). Ruggiero (2000) described and illustrated a single living specimen of this species from the Ionian Sea at a depth of 70 m attached to *Corallium rubrum*. Although the loop is somewhat obscured by the remains of the lophophore, its developmental stage, disjunct deltidial plates and shell colour pattern are typical of *F. sanguinolenta*.

However, the origin of this specimen is puzzling, to say the least. Ruggiero (2000) suggests three possibilities: 1) the depth at which the specimen was collected makes it difficult to confirm by diving whether the species is common there or just forms a small, isolated population; 2) it might have arrived with other organisms imported for aquaculture or any other purpose; 3) it is a "Lessepsian migrant", recently arrived in the Mediterranean from the Red Sea through the Suez Canal.

If the species forms a viable population there, then it might be widespread in the Mediterranean but has escaped attention. However, harvesting of the precious red coral *Corallium rubrum* has a long tradition in the Mediterranean, so that most of the small and cryptic species attached to its colonies were already described in the 19th century (e.g. Delle Chiaje, 1822; Costa, 1861). The continued occurrence of a Pacific taxon in the present-day Mediterranean means that it has been living there since late Miocene, when the Mediterranean and the Indo-Pacific separated (Bianchi and Morri, 2000), but no fossil record of this genus is known from the Mediterranean region. As to the second possibility, it is difficult to imagine what species of aquacultural interest might have been the carrier of a brachiopod found at 70 m depth within a red coral population. Species passively introduced by maritime traffic usually settle in shallow-water, often in harbours, estuaries or coastal lagoons rather than in open-sea and comparatively deep environments (Zibrowius, 1983). No other brachiopod species is known to have been passively introduced anthropogenically (Zibrowius, 1992). The third possibility is the most interesting and would explain why the species has never been found on red coral, which has been studied almost exclusively in the western Mediterranean (Zibrowius, 1979). The Ionian Sea is one of the areas of the Mediterranean Sea that are presently receiving many Lessepsian migrants (Por, 1978). However, no other record of *Frenulina sanguinolenta* is known for the whole Eastern Mediterranean (Logan *et al.*, 2002) or for the Red Sea (Dall, 1920), although the closely related species *Frenulina cruenta* Cooper, which is larger, with a different arrangement of red stripes, conjunct deltidial plates, and a more advanced loop stage, occurs off the coast of Somalia at the entrance to the Gulf of Aden (Cooper, 1973).

There is a fourth possibility that must be considered - that there has been confusion about the origin of the specimen studied by Ruggiero (2000). Ruggiero (*in litteris*, 2001) said that she was given the specimen by the late Professor P. Parenzan, who in turn received it from a professional red coral harvester and trader for jewellery. Parenzan's biological collection was vast and heterogeneous (Fanelli and Rubino, 2000). We know neither the name of the donor nor when and where the piece of coral with the brachiopod attached was collected, nor indeed whether the Ionian locality from which the brachiopod reportedly came is regularly or only occasionally exploited for coral harvesting. Since most of the precious coral presently worked in Italy is actually imported from Taiwan and other Pacific localities (Liverino, 1984), it cannot be discounted that collections of Ionian Sea coral have somewhere been inadvertently mixed with similar material of Pacific origin. The Pacific *Corallium japonicum*, for example, can be mistaken for *C. rubrum* because they share the same intense red colour. Only the discovery of further specimens of *Frenulina sanguinolenta* from the Mediterranean will resolve this dilemma.

ERRONEOUS CITATIONS

We believe the following are erroneous citations of species from the Mediterranean, providing classical examples of initial errors perpetuated by later authors.

Eucalathis tuberata (Jeffreys)

This common northeastern Atlantic species was listed by Brunton and Curry (1979) as occurring in the south-west Mediterranean, but we believe this to be incorrect for the following reason. Jeffreys (1870) stated that he had access to an example of this species collected by Lovén from Josephine Bank, off the Straits of Gibraltar, dredged at a depth of between 620-780 m. It is more than likely that the position of the bank was later thought by Brunton and Curry (1979) to be in the Mediterranean, rather than the Atlantic about 800 km west of the Straits of Gibraltar. The species is not listed from the Mediterranean by Fischer and Oehlert (1891) or Dall (1920).

Dallina septigera (Lovén)

Fischer and Oehlert (1891) reported that this species is only represented by a few separated valves ("valves isolées") obtained by "Travailleur" from dredge 1 in 1881 from 555 m in the Gulf of Lions, France. We believe these specimens are derived from late Pleistocene sediments in the area, since no living specimens have been found. Dall (1920) does not list this species from the Mediterranean. Pérès (1964) clearly listed *Magellania septigera* from the southwest part of Gorringe Seamount at 510 m depth, collected in 1958, but we maintain that subsequent authors, such as Fredj (1974), Benigni and Corselli (1981) and Templado and Luque (1986) were misled into believing that *M. septigera* (or *septata*) had been collected by Pérès from the Alborán Sea (western Mediterranean), because the precise title of his publication "Contribution à l'étude des peuplements benthiques du Golfe Ibéro-Marocain" is preceded by general information on the cruise from which the paper is a result: "Campagne de la Calypso en mer d'Alboran et dans la baie Ibéro-Marocaine (1958)". In fact Gorringe Bank is located in the Atlantic about 500 km west of the Straits of Gibraltar.

Macandrevia cranium (Müller)

Like the previous species this form was also recorded by Fischer and Oehlert (1891) as "valves isolées" from the Gulf of Lions, but again we believe these are Pleistocene in age. Dall (1920) listed a single example of this species from south of Sicily in the collection of the U.S. National Museum, dredged by the Porcupine Expedition at about 400 m depth. This specimen is probably from the Pleistocene, since Jeffreys (1870, 1878), writing on the brachiopods collected by this expedition, makes no mention of live specimens of this species from the Mediterranean. Cooper (1977, 1981), likely following Fischer and Oehlert and Dall, notes that the genus *Macandrevia* is rare in the present-day Mediterranean but more common in Mediterranean Tertiary deposits. Brunton and Curry (1979) also follow these authors in listing this species from the Mediterranean, but Brunton (*in litteris*, 2001) now believes this citation to be erroneous, an opinion with which we concur.

EASTERN MEDITERRANEAN MATERIAL

A previous dearth of documented occurrences of Recent brachiopods from the eastern Mediterranean relative to the more widely explored western basin has resulted in uncertainties in reconstructing the biogeography of Mediterranean brachiopods as a whole. This has now been at least partially remedied by new records from the coasts of Cyprus, Israel, Egypt, and, in particular, Lebanon and the southern Aegean Sea (Logan *et al.*, 2002). Eleven species, representing 79 % of the whole Mediterranean brachiopod fauna recognized here, have now been recorded from the eastern basin. *Lacazella mediterranea*, *Tethyrhynchia mediterranea* and *Gwynia capsula* have not yet been recognized, but whether this is due to a genuine west-east faunal impoverishment or insufficient collecting has not yet been resolved. The species *Terebratulina retusa, Argyrotheca cistellula*, *Megathiris detruncata* and the two species of *Platidia* appear to be less common in the eastern than in the western basin, based in part on the latest material obtained from the eastern area, but this needs to be confirmed by more collecting.

ENDEMICS

Endemism in Mediterranean species was reviewed by Pérès (1985) who suggested that there are very few, if any, species which are true endemics and that genera rather than species are the true relicts of Tethyan forms. Only two brachiopod species are likely to be endemics: *Tethyrhynchia mediterranea* and *Lacazella mediterranea*. However, the two species may have different origins. According to Bianchi and Morri (2000) Mediterranean endemics belong to one of two categories: paleoendemics and neoendemics. Paleoendemics are derived directly from Tethyan ancestors that may have survived the Messinian salinity crisis in refuge areas on the outer margin of the western basin, such as southeastern Spain (Montenat *et al.*, 1980), while neoendemics are derived from Atlantic species that re-entered the Mediterranean during the Pliocene. *Lacazella mediterranea*, whose closest relative is the sub-tropical Atlantic species *L. caribbeanensis* Cooper (Logan, 1979), may be an example of a neoendemic species. Its present distribution in the southwestern area of the Mediterranean (Logan, 1979), along the main path of the incoming Atlantic current, supports this interpretation. *Tethyrhynchia mediterranea* has not been recorded from the Atlantic and may be a Mediterranean paleoendemic, notwithstanding its enigmatic taxonomic affinities, being the only species of the genus and belonging to the separate family Tethyrhynchidae. The species has probably evolved by neoteny and, at present, is only known from the dark parts of submarine caves (Logan and Zibrowius, 1994). There is little, if any, evidence of recent speciation in Mediterranean submarine caves (Riedl, 1966; Bianchi *et al.*, 1996). Such caves commonly harbour preadapted species derived from cryptic or deep habitats (Balduzzi *et al.*, 1989; Harmelin and Vacelet, 1997) but may also act as "refuges" for archaic forms of Tethyan origin (Harmelin *et al.*, 1985). Recent investigations on larval brooding and development of Adriatic examples of this species by Lüter (2001) indicate a low dispersal ability, mitigating against recent colonization and suggesting that its present biogeography may represent relict populations of a wider distribution in the Mesozoic Tethys. Further searching for this species from cryptic and deep habitats within and outside the Mediterranean, and its possible ancestors in Cenozoic rocks in the region, will help clarify its origin.

TERTIARY AND QUATERNARY HISTORY OF MEDITERRANEAN BRACHIOPOD GENERA

The Tertiary and Quaternary occurrences of the 14 species of brachiopods, belonging to 10 genera, that presently inhabit the Mediterranean Sea is shown in Table 1. The biogeographic history of 11 of these species was discussed by Logan (1979), who concluded that they are an impoverished group compared to the pre-Messinian brachiopod fauna. It appears that the late Miocene Messinian salinity crisis was responsible for an extensive (but perhaps not complete) decimation of the marine fauna (Bianchi and Morri, 2000), so that most present-day brachiopods are re-immigrants to the Mediterranean from the Atlantic, where their closest affinities lie. If so, then species belonging to several genera were unable to re-establish themselves permanently in the Mediterranean after the Miocene. While 8 of the 10 genera are found fossil in Tertiary and Quaternary rocks in the Mediterranean region, the following additional genera from Tertiary and younger strata in the ancestral Mediterranean (Tethys) and Paratethys areas, are no longer represented in the present-day sea: *Ancistrocrania, Cryptopora, Hemithyris, Phapsirhynchia, Aphelesia, Terebratula, Ceramisia, Dallina, Fallax, Macandrevia, Dyscolia, Sphenarina,* and *Thecidellina* (Davidson, 1864, 1870, 1886-8; Fischer and Oehlert, 1891;

Tavani, 1969; Pajaud, 1976; Pedley 1976; Brebion *et al.*, 1978; Llompart and Calzada, 1982; Ruggiero, 1983; Gaetani and Saccà, 1984; Bitner, 1990, 1993; Vazzana, 1996; Bitner and Pisera, 2000). Following earlier authors, both Logan (1979) and Gaetani and Saccà (1984) related the disappearance of some of these forms to the progressive development of the Gibraltar sill in the early Pleistocene, causing the gradual extinction of those bathyal forms, dependent on cold deep Atlantic waters, in the western Mediterranean. Remnants of some of these may be the specimens of *Dallina* and *Macandrevia* found by Fischer and Oehlert (1891) from Late Pleistocene (Würmian) deposits in the Gulf of Lions.

More difficult to explain is the biogeography of the thecideid brachiopods. Absent from the Mediterranean is the shallow water thecideid *Thecidellina*, a cementing form present in the modern Caribbean (Cooper, 1977), Cape Verde area (Logan, 1988b; 1993) and the Tertiary of Paratethys and Italy (Thomson, 1927; Bitner, 1993). Assuming oceanic currents in the North Atlantic to have been constant since the Pleistocene, Logan (1993) attributed its absence from Bermuda to a migration route north of the islands and its absence from the Azores, Madeira and the Canary Islands to the close proximity to the African coast of the southward-moving gyre in the northeastern Atlantic, by-passing the islands north of Cape Verde. One might imagine that, having colonized Paratethys in the Middle Miocene, the genus would have re-colonized Mediterranean and adjacent waters from the Atlantic after the Messinian crisis. Perhaps competition from the already-established *Lacazella* in their preferred habitat precluded this re-colonization. The latter genus, also a cementing thecideid, has been found in the Recent and Tertiary of the Caribbean (Cooper, 1977, 1979; Logan, 1987) and Mediterranean (Pajaud, 1970) but on none of the islands in between, although a closely-related genus *Pajaudina* was described from the Canary Islands by Logan (1988a).

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