

Upper Oligocene (Chattian) brachiopod fauna from the Aquitaine Basin, southwestern France and its paleoenvironmental implications

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ABSTRACT

Brachiopods from the Upper Oligocene (Chattian), Aquitaine Basin, southwestern France comprise nine species in seven genera: *Novocrania* Lee & Brunton, 2001, *Terebratulina* d'Orbigny, 1847, *Megathiris* d'Orbigny, 1847, *Argyrotheca* Dall, 1900, *Joania* Álvarez, Brunton & Long, 2008, *Megerlia* King, 1850, and *Lacazella* Munier-Chalmas, 1880. One megathyridid is described as a new species, *Joania peyrerensis* n. sp., characterized by ornamentation of 6-8 distinct, sharp ribs and by triangular, plate-like teeth. With the exception of *Megathiris detruncata* (Gmelin, 1791) and *Lacazella mediterranea* (Risso, 1826), all species are recorded for the first time from the Oligocene of the Aquitaine Basin. In taxonomic composition this brachiopod fauna displays close affinity with the Miocene faunas of the Mediterranean Province and Central Paratethys. The dominance of micromorphic megathyridids and thecideides in the Peyrière assemblage, characteristic of cryptic habitats suggests the presence of submarine caves and/or crevices, thus supporting the previous interpretations of this faunistic assemblage as a cave biocenosis. Frequency of gastropod drillings observed on the investigated brachiopods is low (4%) as is in most Cenozoic brachiopod populations. The paleotemperatures calculated from the $\delta^{18}\text{O}$ values of brachiopod shells (21 to 24°C) correspond well to a paleoenvironmental interpretation based on paleoecology of other taxonomic groups.

KEY WORDS

Brachiopoda,
Upper Oligocene,
Chattian,
stable isotopes,
Aquitaine Basin,
France,
new species.

RÉSUMÉ

La faune de brachiopodes de l'Oligocène supérieur (Chattien) du Bassin d'Aquitaine, sud-ouest de la France et ses implications paléoenvironnementales.

Les brachiopodes de l'Oligocène supérieur (Chattien) du Bassin d'Aquitaine (France) comprennent neuf espèces appartenant à sept genres, à savoir *Novocrania* Lee & Brunton, 2001, *Terebratulina* d'Orbigny, 1847, *Megathiris* d'Orbigny, 1847, *Argyrotheca* Dall, 1900, *Joania* Álvarez, Brunton & Long, 2008, *Megerlia* King, 1850 et *Lacazella* Munier-Chalmas, 1880. Un Megathyrididae nouveau est décrit : *Joania peyrerensis* n. sp. Cette espèce est caractérisée par une ornementation comprenant de six à huit côtes fortes et aiguës, et par des dents triangulaires ressemblant à des plaques. À l'exception de *Megathiris detruncata* (Gmelin, 1791) et de *Lacazella mediterranea* (Risso, 1826), toutes les espèces sont signalées pour la première fois dans l'Oligocène aquitain. Dans sa composition taxonomique, cette faune de brachiopodes présente des affinités étroites avec celles du Miocène de la province méditerranéenne et de la Paratéthis centrale. La domination des Megathyrididae micromorphiques et Thecideidae à Peyrère, caractéristiques des habitats cryptiques, indique la présence de nombreuses grottes sous-marines et/ou de crevasses, appuyant ainsi les interprétations précédentes sur l'environnement de ces dépôts. La fréquence de la prédation de gastéropodes observée sur les brachiopodes étudiés est basse (4%) comme elle l'est dans la plupart des populations de brachiopodes cénozoïques. Les paléotempératures calculées des valeurs $\delta^{18}\text{O}$ obtenues des coquilles de brachiopodes (de 21 à 24°C) correspondent bien à l'interprétation paléoenvironnementale basée sur la paléoécologie des autres groupes.

MOTS CLÉS

Brachiopoda,
Oligocène supérieur,
Chattien,
isotopes stables,
Bassin d'Aquitaine,
France,
espèce nouvelle.

INTRODUCTION

Although brachiopods have lost importance in the Cenozoic and their taxonomic diversity is low, they are a stable, locally even dominant, element of the benthic fauna in European Tertiary deposits. Eocene brachiopods are well known and described from the whole of Europe, and although their taxonomic composition in particular assemblages can differ significantly, many species have a very wide geographical distribution from Great Britain to Ukraine. Miocene brachiopods are also well known in the whole of Europe, being especially studied from the Paratethyan and Mediterranean provinces, and they are predominantly micromorphic forms.

By contrast, very little is known about Oligocene brachiopods of Europe. They have been

reported from northern Italy (Sacco 1902; Fabiani 1913; Venzo 1941; Mandruzzato 1970; Altichieri 1992) where *Terebratula* Müller, 1776, *Terebratulina* d'Orbigny, 1847 and *Lacazella* Munier-Chalmas, 1880 were recorded. *Terebratulina* was also reported from the Oligocene of Belgium (Vincent 1893, 1923). Sandberger (1862-1863) described a rich brachiopod fauna from the Lower Oligocene of the Mainz Basin, southern Germany. He recognized *Terebratula*, *Terebratulina* and few species of megathyridid brachiopods. This fauna, however, needs re-examination and re-description using modern taxonomy; one species, *Argiope subradiata* Sandberger, 1862 has been revised and transferred into the genus *Bronnothyris* Popiel-Barczyk & Smirnova, 1978 (see Bitner & Kroh 2011). The

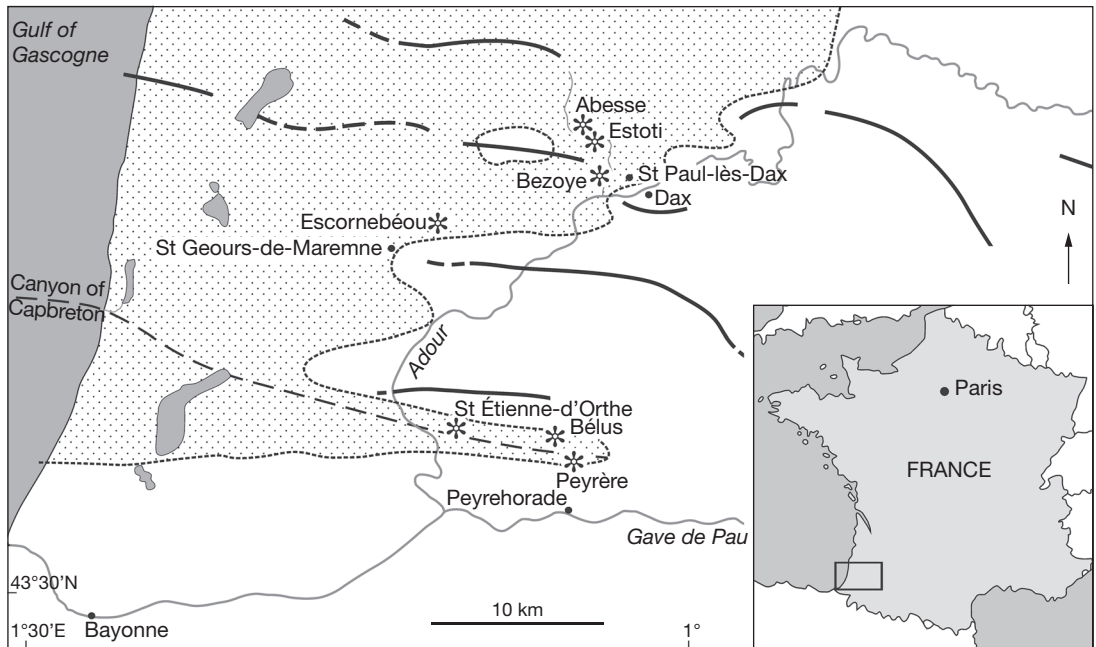


FIG. 1. — Map of the Aquitaine Basin, SW France showing the extension of the Chattian marine deposits (dotted line) and the localities of brachiopod fauna; heavy lines denote anticlinal ridges (simplified after Cahuzac *et al.* 1995).

inarticulate discinid species *Discinisca steiningeri* Radwańska & Radwański, 1989 was described from the Upper Oligocene of Austria (Radwańska & Radwański 1989).

From the Oligocene of Hungary Meznerics (1944) described three genera, *Lingula* Bruguière, 1797, *Terebratulula* and *Terebratulina*. Recently, a rich collection of Oligocene brachiopods from Hungary was also reported by Dulai (2010b). He recognized ten species belonging to nine genera; megathyrids dominate but *Novocrania* Lee & Brunton, 2001, *Gryphus* Mühlfeldt, 1811, *Terebratulina* and *Megerlia* King, 1850 also were present.

A new Lower Oligocene brachiopod fauna was briefly described from north-eastern Germany (Müller 2011a, b). This fauna contains one inarticulate genus, *Discinisca*, six terebratulides, *Terebratulula*, *Terebratulina*, *Orthothyris* Cooper, 1955, *Megathiris* d'Orbigny, 1847, *Argyrotheca* Dall, 1900 and *Megerlia*, and the thecideide *Lacazella*.

It is worth mentioning that the brachiopod assemblage from northern Germany described as Lower Oligocene by von Koenen (1894) has been found to be Upper Eocene in age (see De Geyter *et al.* 2006).

The present paper deals with a rich Upper Oligocene (Chattian) brachiopod fauna from the Aquitaine Basin (SW France) that belongs to the Atlantic Province. Brachiopods, in majority excellently preserved, with more than 1400 specimens are represented by nine species belonging to seven genera. Although so rich, this fauna has never been fully described before, however, the presence of the genera *Megathiris*, *Argyrotheca* and *Lacazella* was mentioned by several researchers (Peyrot 1932; Pajaud 1974; Lozouet 2004). Interestingly, brachiopods were described from the Aquitaine Basin from the younger, Miocene, deposits where inarticulate *Lingula* and *Discradisca* Stenzel, 1964, and micromorphic rhynchonellide *Cryptopora* Jeffreys, 1869 were recognized (Bitner & Cahuzac 2004, 2013; Emig *et al.* 2007).

GEOLOGICAL SETTING

Marine Upper Oligocene deposits crop out only in the south-western part of the Aquitaine Basin (Fig. 1; Cahuzac *et al.* 1995; Lozouet 2004). They are of transgressive character, having been deposited after a major regression related to the global sea-level fall at the Lower-Upper Oligocene boundary (Vail *et al.* 1977; Dolin *et al.* 1985). On the basis of the calcareous nannoplankton these deposits are referred to the zones NP24 and NP25 that correspond with the Chattian (Cahuzac *et al.* 1995). Moreover, based on neritic larger foraminifera abundant in these levels, they are attributed to the SBZ 23 biozone (Shallow Benthic Zone) of Cahuzac & Poignant (1997). They contain a rich benthic fauna, composed chiefly of gastropods, bivalves, corals, serpulids, bryozoans, and brachiopods, and are interpreted as having been deposited under tropical/subtropical conditions (Lozouet 2004).

Brachiopods were found at several localities (Fig. 1) in the Chattian deposits represented by various facies (Cahuzac *et al.* 1995; Lozouet 2004). In the north, in the vicinity of Dax (Bezoye, Estoti, Abesse) shallow-water calcareous facies with coral reefs occur. At Escornebéou the Upper Oligocene is represented by sandy marls and calcareous sands. The localities of Peyrère, Bélus and St-Étienne-d'Orthe are situated in the area that is considered to be originally a submarine canyon (Kieken 1973). The incision of the paleocanyon which is several hundred meters deep, may be related to the significant drop of sea-level (Dolin *et al.* 1985; Lozouet 2004). At the head of the paleocanyon (Peyrère, Bélus) the infralittoral to circalittoral facies with dominance of marls occur. To the west the facies become deeper-water and are represented by circalittoral to epibathyal marls and muddy sands at St-Étienne-d'Orthe.

LOCALITIES

Abesse: Landes, St-Paul-lès-Dax (Abesse);
Bezoye: Landes, St-Paul-lès-Dax (Bezoye);
Escornebéou: Landes, St-Geours-de-Maremne;
Estoti: Landes, St-Paul-lès-Dax (Estoti);
Marcon: Landes, Bélus (Marcon);

Peyrère: Landes, Peyrehorade (Peyrère);
Ruisseau de l'Église: Landes, St-Étienne-d'Orthe.

MATERIAL AND METHODS

The investigated brachiopods come from seven outcrops, namely Peyrère, Bélus, St-Étienne-d'Orthe, Escornebéou, Bezoye, Estoti and Abesse, in the Aquitaine Basin, SW France (Fig. 1). The material comprises mostly specimens obtained from the bulk samples washed and wet-sieved. The larger fraction was sorted in the field, while finer fractions were picked manually under the binocular microscope at the laboratory. There are also some specimens from the collections of the University of Bordeaux-1. Total number of specimens is 1466 (697 articulated specimens and 769 separate valves).

For isotope analysis, samples were taken by micro-drilling from the inner surface of shells. The analyses were done using a Finnigan MAT Delta Plus gas isotope mass spectrometer at the Light Isotope Laboratory of the Institute of Geological Sciences, Polish Academy of Sciences, Warsaw. The carbonate powder was reacted with 100% orthophosphoric acid under vacuum at 70°C in the KIEL IV carbonate device, which was coupled online to a Finnigan MAT Delta Plus gas isotope mass spectrometer. Isotope values are reported as parts per mil in the usual δ -notation relative to the PDB standard (defined via NBS 19). The spectrometer external error amounts to less than ± 0.08 . We took 20 samples from 20 specimens of two most common species, *Megathiris detruncata* and *Lacazella mediterranea*. Additionally two samples were also taken from the third commonest species, *Terebratulina retusa*. The isotopic paleotemperatures were calculated from the $\delta^{18}\text{O}$ values using the equation:

$$T (^{\circ}\text{C}) = 16.9 - 4.2 (\delta_c - \delta_w) + 0.13 (\delta_c - \delta_w)^2$$

where δ_c means the $\delta^{18}\text{O}$ values of brachiopod samples relative to the PDB standard and δ_w means the $\delta^{18}\text{O}$ values of seawater relative to the SMOW standard (see Nehyba *et al.* 2008).

The SEM micrographs were taken in the SEM laboratory of the Institute of Paleobiolo-



FIG. 2. — **A-D**, *Novocrania anomala* (Müller, 1776), Upper Oligocene; **A, B**, outer and inner views of ventral valve, Peyrère, MNHN.FA46481; **C, D**, inner views of dorsal valves, Abesse, MNHN.FA46483 and MNHN.FA46484; **E-H**, *Terebratulina retusa* (Linnaeus, 1758), Upper Oligocene, Peyrère; **E**, dorsal view of young complete specimen, MNHN.FA46485; **F**, inner view of dorsal valve to show a brachial skeleton, young individual, SEM, MNHN.FA46486; **G, H**, dorsal and lateral views of complete specimen, MNHN.FA46487. Scale bars: A-D, 2 mm; F, 500 µm; G, H, 5 mm.

gy (Warszawa) using a Philips XL-20 scanning microscope.

The investigated material is deposited in the paleontological collection in the Muséum national

d'Histoire naturelle, Paris (MNHN.F, Lozouet coll.), and in the University of Bordeaux-1 (nos 1498 and 1499 of the Peyrot Collection; Nolf-Cahuzac Collection; Larralde Collection; Buisson Collection).

TABLE 1. — Measurements (in mm) of *Novocrania anomala* (Müller, 1776).

Locality	Length	Width
Abesse	14.1	15.6
Abesse	12.0	13.8
Abesse	11.4	12.4
Peyrère	7.1	7.2
Peyrère	5.5	5.7

SYSTEMATIC PALEONTOLOGY

Phylum BRACHIOPODA Duméril, 1805
 Subphylum CRANIIFORMEA
 Popov, Bassett, Holmer & Laurie, 1993
 Class CRANIATA
 Williams, Carlson, Brunton,
 Holmer & Popov, 1996
 Order CRANIIDA Waagen, 1885
 Superfamily CRANIOIDEA Menke, 1828
 Family CRANIIDAE Menke, 1828

Genus *Novocrania* Lee & Brunton, 2001

TYPE SPECIES. — *Patella anomala* Müller, 1776, by original designation of Lee & Brunton (1986: 150).

Novocrania anomala (Müller, 1776)
 (Fig. 2A-D; Table 1)

Patella anomala Müller, 1776: 237.

Crania anomala — Logan 1979: 27-31, text-fig. 4, 5; pl. 1, figs 1-10. — Taddei Ruggiero 1985: 365-366, pl. 1, figs 1-6.

Neocrania anomala — Taddei Ruggiero 1994: 205, 206, pl. 2, fig. 7; 1996: 200, 201, fig. 5. — Logan 1998: 552, fig. 2A-C. — Logan & Long 2001: 74, fig. 8.3/1-8.

Novocrania anomala — Álvarez & Emig 2005: 105-107, figs 14, 57, 58A-I.

MATERIAL EXAMINED. — Peyrère: one ventral MNHN.FA46481 and two dorsal valves MNHN.FA46482. — Abesse: nine dorsal valves MNHN.FA46483, A46484.

OCCURRENCE. — In the fossil record this species is known from the Neogene of the Mediterranean region. Today

it lives in the eastern North Atlantic and the Mediterranean Sea, having a wide depth range from 3 to 1665 m (Logan 1979, 1998; Logan & Long 2001).

REMARKS

Novocrania anomala is rare (12 specimens) in the studied material, found only in two localities. The material is poorly preserved, both outer and inner surfaces are usually worn but it corresponds well with that hitherto described (Logan 1979, 1998; Logan & Long 2001; Álvarez & Emig 2005). The shell is small with maximum length 15.6 mm, subcircular in outline, wider than long. The posterior adductor muscle scars are large, subcircular, situated near posterior margin in both valves. The anterior adductor muscle scars are oval, elevated. On some specimens mantle canals can be observed (Fig. 2C, D). This is the only inarticulate brachiopod in the investigated assemblage.

Subphylum RHYNCHONELLIFORMEA

Williams, Carlson, Brunton,
 Holmer & Popov, 1996
 Class RHYNCHONELLATA
 Williams, Carlson, Brunton,
 Holmer & Popov, 1996

Order TEREBRATULIDA Waagen, 1883
 Suborder TEREBRATULIDINA Waagen, 1883
 Superfamily CANCELLOTHYRIDOIDEA
 Thomson, 1926
 Family CANCELLOTHYRIDIDAE
 Thomson, 1926
 Subfamily CANCELLOTHYRIDINAE
 Thomson, 1926

Genus *Terebratulina* d'Orbigny, 1847

TYPE SPECIES. — *Anomia retusa* Linnaeus, 1758, by subsequent designation of Brunton *et al.* (1967: 176).

Terebratulina retusa (Linnaeus, 1758)
 (Fig. 2E-H; Table 2)

Anomia retusa Linnaeus, 1758: 701, no. 191.

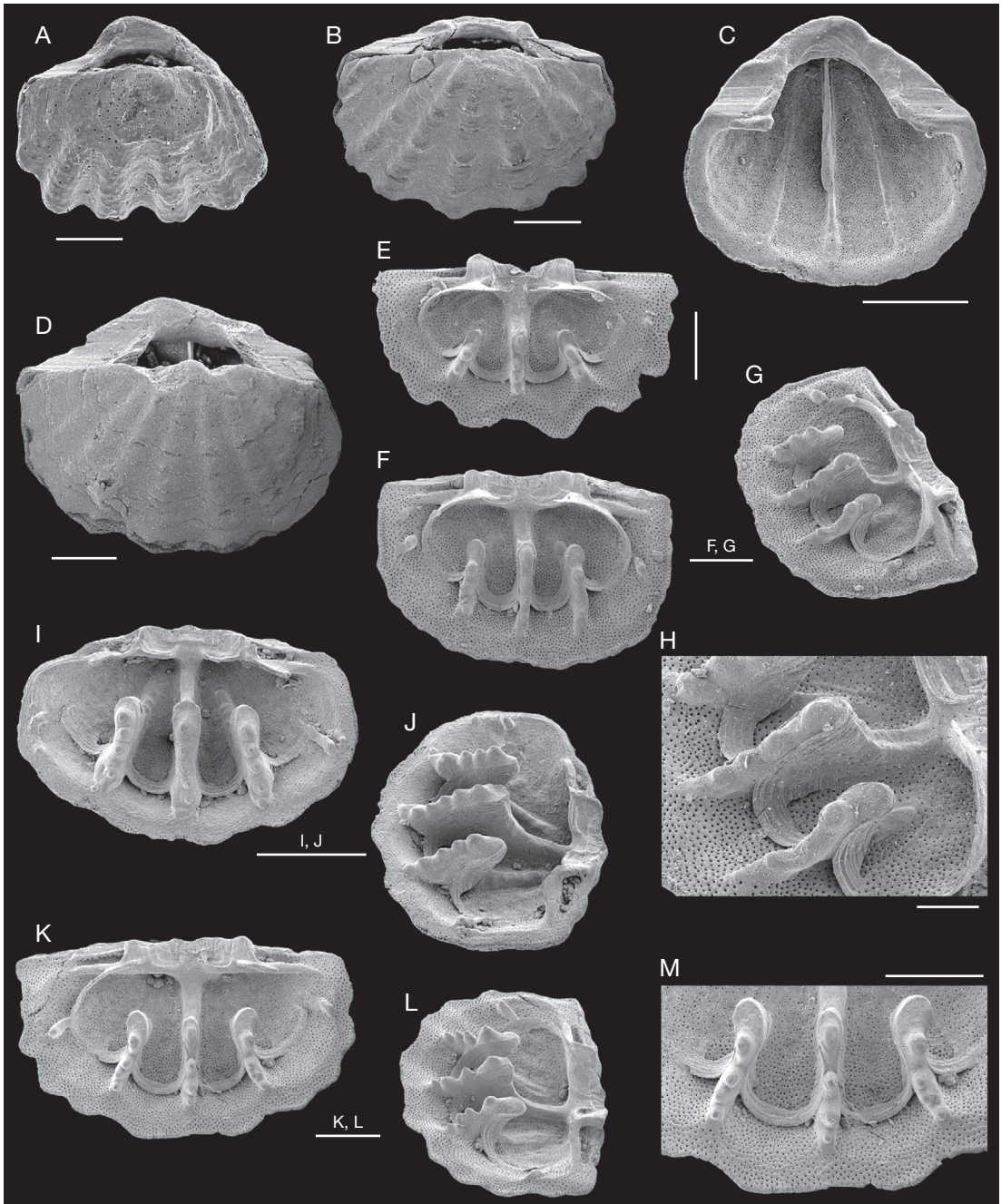


FIG. 3. — *Megathiris detruncata* (Gmelin, 1791), Upper Oligocene, Abesse: **A, B, D**, dorsal views of complete specimens, MNHN.F.A46491-A46493; **C**, inner view of ventral valve, MNHN.F.A46494; **E**, inner view of dorsal valve of young individual, MNHN.F.A46495; **F-M**, inner and oblique views of dorsal valves, and enlargements (**H, M**) to show details of septa and loop, MNHN.F.A46496-A46498. All SEM. Scale bars: A, H, 500 µm; B, D-G, K-M, 1 mm; C, I, J, 2 mm.

TABLE 2. — Measurements (in mm) of *Terebratulina retusa* (Linnaeus, 1758).

Locality	Length	Width	Thickness
Peyrère	14.8	12.1	–
Peyrère	10.0	6.4	–
Peyrère	18.1	15.7	7.7

TABLE 3. — Measurements (in mm) of *Megathiris detruncata* (Gmelin, 1791).

Locality	Length	Width	Thickness
Peyrère	6.5	7.3	3.4
Peyrère	5.6	6.2	3.0
Peyrère	4.9	6.5	2.9
Bélus	5.9	6.7	3.2
Abesse	3.2	4.6	2.1

Terebratulina retusa – Logan 1979: 37-43, text-fig. 8, pl. 3, figs 1-18. — Gaetani & Saccà 1985: 15-16, pl. 7, figs 5-10; pl. 9, figs 6-9. — Taddei Ruggiero 1985: 367-369, pl. 2, figs 1-7, pl. 3, figs 1-8, pl. 4, figs 1-7; 1994: 208, pl. 2, figs 1-3. — Bitner & Moissette 2003: 472, fig. 6A-E. — Bitner & Dulai 2004: pl. 3, fig. 1. — Álvarez & Emig 2005: 139, 140, figs 24D-E, 27D, 27E, 28, 53B, 54E-F, 61.

MATERIAL EXAMINED. — Peyrère: 74 complete specimens, 11 ventral and 15 dorsal valves, and many fragments MNHN.FA46485-A46488 and A46555. — Bélus: five complete specimens, two ventral and one dorsal valves MNHN.FA46489. — St-Étienne-d'Orthe: one ventral valve MNHN.FA46490.

OCCURRENCE. — This species is well known in the Neogene deposits of the Mediterranean province but rare in the Central Paratethys (Dreger 1889; Bitner & Dulai 2004), and it is present in the Aquitaine Middle Miocene (Bitner & Cahuzac 2004). Today it occurs in the north-eastern North Atlantic and the Mediterranean Sea (Logan 1979; Brunton & Curry 1979; Curry 1982). Its depth range is from 18 to 2157 m (Logan 2007).

REMARKS

This species has been found in three localities but only in one, Peyrère, it is numerous. The investigated specimens, although often crushed and/or damaged, are consistent with those hitherto described having, however, smaller size (Logan 1979; Taddei Ruggiero 1985; Gaetani & Saccà

1985; Álvarez & Emig 2005). The shell is ovate to subpentagonal, biconvex, covered with numerous, fine ribs that are coarser and strongly beaded in young individuals (Fig. 2E). The cardinalia are typical for the genus with prominent inner socket ridges and deep dental sockets. The loop is preserved only in a young specimen, with crural processes not yet united (Fig. 2F).

Suborder TEREBRATELLIDINA Muir-Wood, 1955

Superfamily MEGATHYRIDOIDEA Dall, 1870 Family MEGATHYRIDIDAE Dall, 1870

Genus *Megathiris* d'Orbigny, 1847

TYPE SPECIES. — *Anomia detruncata* Gmelin, 1791, by subsequent designation of Dall (1920: 331).

REMARKS

Dall (1920) showed that the first binominal valid name given to this species was *Anomia detruncata* Gmelin, 1791, and this should therefore be used for the type species (see also Thomson 1927: 213).

Megathiris detruncata (Gmelin, 1791) (Fig. 3A-M; Table 3)

Anomia detruncata Gmelin, 1791: 3347.

Megathiris decollata – Peyrot 1932: 485, 486, pl. 17, figs 11-13.

Megathiris detruncata – Logan 1979: 55-59, text-figs 15, 16; pl. 6, figs 1-13. — Gaetani & Saccà 1985: 17, 18, pl. 9, figs 10-12; pl. 10, figs 11-14. — Taddei Ruggiero 1985: 369-371, pl. 5, figs 1-9; pl. 6, figs 1-6; pl. 7, figs 1-9, 14; 1994: 208, pl. 3, figs 6-9; 1996: 202. — Bitner 1990: 135-138, text-figs 3, 4; pl. 3, figs 1-8; pl. 6, figs 1-7. — Bitner & Moissette 2003: 473, 474, fig. 6G, H. — Kroh 2003: 147, 148, pl. 1, figs 4-6. — Bitner & Dulai 2004: 74, 76, pl. 3, figs 11-15; 2008: 35, 36, fig. 5.1-4. — Álvarez & Emig 2005: 147, 148, figs 25C, 63-66. — Dulai 2007: 2, 3, fig. 2.1-2; 2010a: 26, pl. 3, fig. 1a, b. — Bitner & Schneider 2009: 127, fig. 6A-C.

MATERIAL EXAMINED. — Peyrère: 120 complete specimens, 32 ventral and 42 dorsal valves, MNHN.FA46502 and

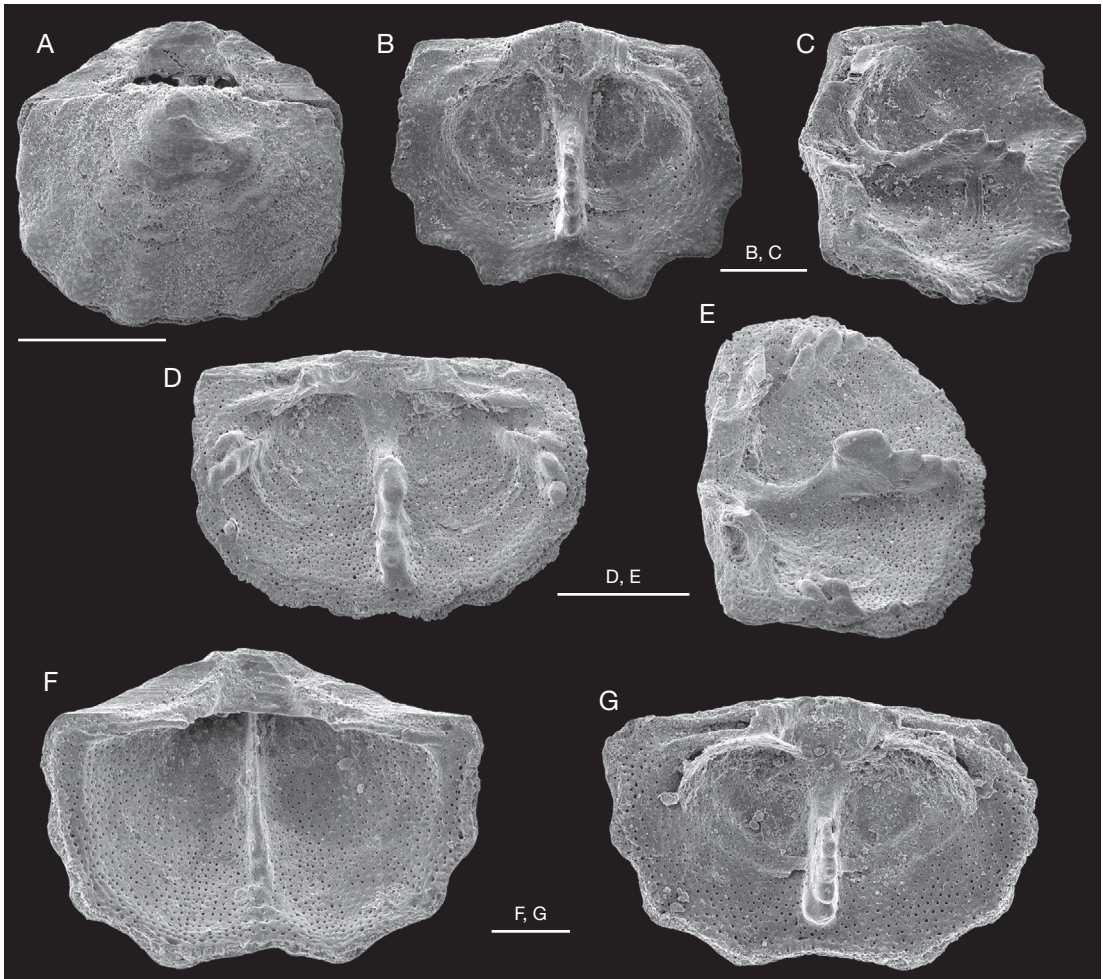


FIG. 4. — *Argyrotheca cuneata* (Risso, 1826), Peyrère, Upper Oligocene; **A**, dorsal view of complete specimen, MNHN.FA46507; **B-E**, inner and oblique lateral views of dorsal valves MNHN.FA46508-A46509; **F, G**, ventral and dorsal interiors of one specimen, MNHN.FA46510-A46511. All SEM. Scale bars: A, D, E, 1 mm; B, C, F, G, 500 µm.

A46554. — Abesse: 12 complete specimens, 72 ventral and 101 dorsal valves MNHN.FA46491-A46501. — Estoti: five ventral valves, MNHN.FA46503. — Bezoye: four complete specimens, three ventral and 17 dorsal valves, MNHN.FA46504. — Bélus: ten complete specimens, three ventral and five dorsal valves, MNHN.FA46505 and A46506.

OCCURRENCE. — This species is known in the fossil record since the Eocene and lives today in the Mediterranean and the north-eastern North Atlantic at the depth from 5 to 896 m (Logan 2007). Its occurrence in the Caribbean Sea reported by Cooper (1977) is questionable (see also Logan 2007).

REMARKS

Megathiris detruncata is one of the most common species (more than 400 specimens) in the investigated assemblage, found in five localities. It was already recorded from the studied area (Peyrot 1932; Lozouet 2004). The specimens from the Aquitaine Basin correspond well to those hitherto described (e.g., Logan 1979; Taddei Ruggiero 1985; Bitner 1990; Bitner & Schneider 2009). The shell is small (our largest specimen is a dorsal valve 7.0 long and 8.1 mm wide), transversely ovate in outline, covered with few wide, rounded ribs. The

TABLE 4. — Measurements (in mm) of *Argyrotheca cuneata* (Risso, 1826).

Locality	Length	Width	Thickness
Peyrère	3.0	3.2	–
Peyrère	2.3	3.0	1.3
Peyrère	2.2	2.3	1.2

foramen is large, triangular, bordered by two narrow deltidial plates. Internally, this species is characterized by the presence of three septa on a dorsal valve what makes it an easily recognizable species.

Genus *Argyrotheca* Dall, 1900

TYPE SPECIES. — *Terebratulina cuneata* Risso, 1826, by original designation of Dall (1900: 44).

Argyrotheca cuneata (Risso, 1826) (Fig. 4A-G; Table 4)

Terebratulina cuneata Risso, 1826: 388, pl. 12, fig. 179.

Argyrotheca cuneata – Logan 1979: 45-49, text-figs 11, 12; pl. 4, figs 1-12. — Bitner 1990: 138-140, text-fig. 5-6, pl. 4, figs 1-9; 1993: 149-150, pl. 2, figs 1-6; pl. 3, figs 1-6. — Taddei Ruggiero 1996: 202. — Bitner & Pisera 2000: 9, pl. 1, figs 1-7. — Kroh 2003: 148, pl. 1, figs 1-3. — Bitner & Dulai 2004: pl. 3, figs 2-6. — Bitner & Kaim 2004: 196, fig. 2A-C. — Álvarez & Emig 2005: 149-153, figs 25A-B, 27A, C, E, 44, 45, 67-69. — Dulai 2007: 4, fig. 3.1-7.

MATERIAL EXAMINED. — Peyrère: six complete specimens, six ventral and three dorsal valves, MNHN.FA46507-A46512.

OCCURRENCE. — This species is very common in the Miocene of the Central Paratethys and Neogene of the Mediterranean region. Today it lives in the Mediterranean Sea and North Atlantic (Brunton & Curry 1979; Logan 1979, 1983, 1988), having depth range of 5 to 645 m (Logan 2007). *Argyrotheca* cf. *cuneata* was also recorded from off Brazil (Simões *et al.* 2004).

REMARKS

Argyrotheca cuneata is rare in the studied assemblage and was found in only one locality. The shell is small,

rectangular with greatest width usually at hinge line. The shell surface is covered with 6-8 single, low and rounded ribs. The foramen is large, triangular with a wide pedicle collar supported by a septum. The teeth are widely separated lying parallel to the hinge line. The dorsal median septum is high, triangular in profile with 3-4 serrations.

Argyrotheca cuneata can be distinguished from a second *Argyrotheca* species, *A. bitnerae* Dulai, 2011 and *Joania cordata* (Risso, 1826) in rectangular outline and ribbed surface. Additionally, *A. cuneata* differs from *J. cordata* in lacking tubercles on the inner margin. The absence of margin tubercles distinguishes it also from *Joania peyrerensis* n. sp.

In shell outline and ornamentation *A. cuneata* resembles *Megathiris detruncata*, being, however, easily distinguishable internally from the latter species; *M. detruncata* has three septa on the dorsal valve.

Argyrotheca bitnerae Dulai in Dulai & Stachacz, 2011 (Fig. 5A-M; Table 5)

Argyrotheca bitnerae Dulai in Dulai & Stachacz, 2011: 285-291, figs 3, 4.

Argyrotheca cistellula – Barczyk & Popiel-Barczyk 1977: 161, 162, pl. 1, figs 1-3. — Popiel-Barczyk & Barczyk 1990: 172, 173, pl. 2, figs 11, 13.

Argyrotheca sp. – Barczyk & Popiel-Barczyk 1977: 164, pl. 1, figs 6, 7.

MATERIAL EXAMINED. — Peyrère: 13 complete specimens, 2 ventral and 7 dorsal valves, MNHN.FA46513, A46514. — Abesse: eight complete specimens and six dorsal valves, MNHN.FA46515-A46517. — Estoti: three complete specimens, two ventral and six dorsal valves, MNHN.FA46518-A46520. — Bélus: five complete specimens, three ventral and one dorsal valves, MNHN.FA46521, A46522.

OCCURRENCE. — This species has been so far recorded from the Middle Miocene of the northern part of the Central Paratethys (Dulai & Stachacz 2011).

DESCRIPTION

Shell small (maximum length 3.3 mm), thin, subtriangular in outline, weakly dorsibiconvex. Dorsal valve nearly semicircular in outline. Shell surface

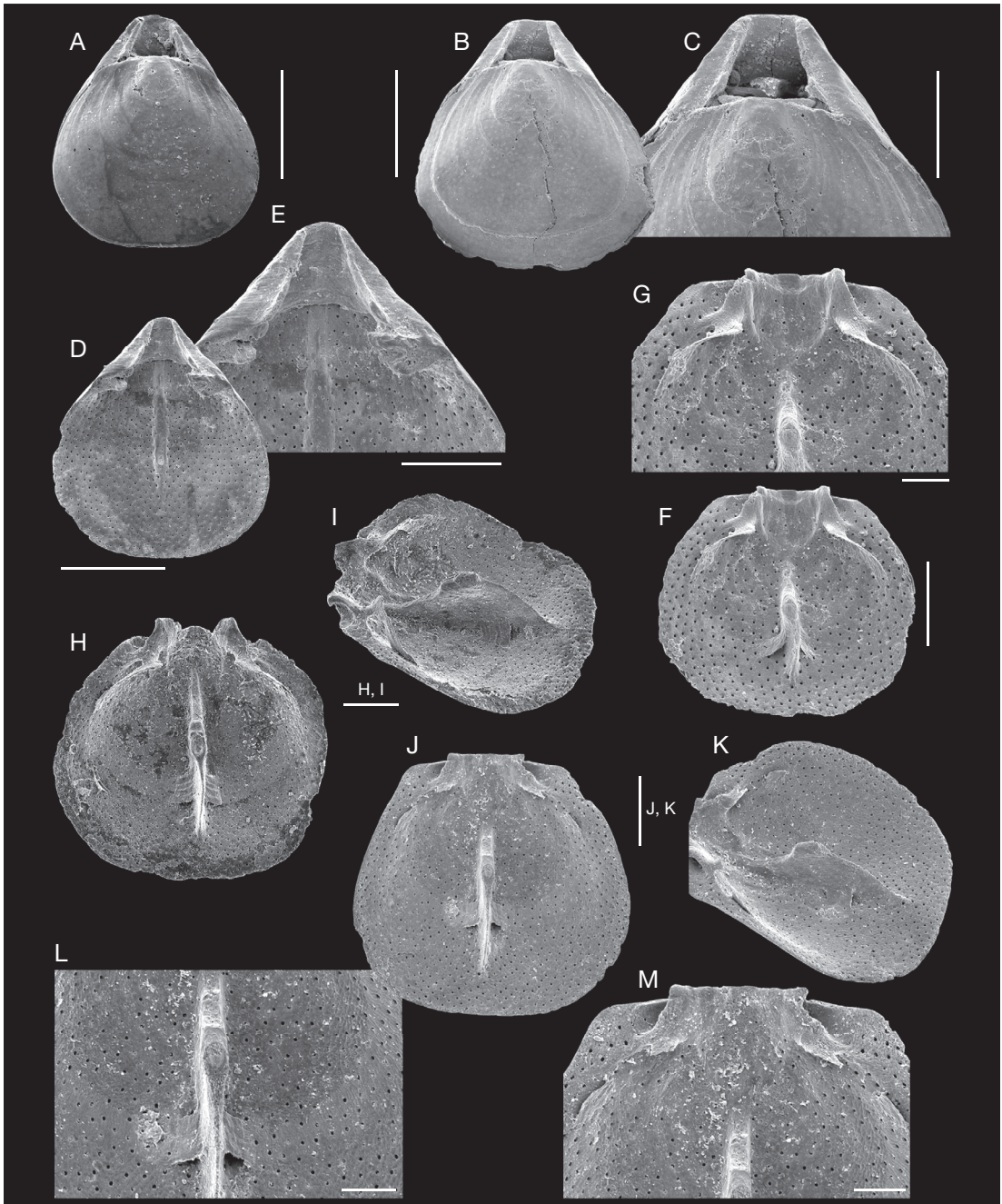


FIG. 5. — *Argyrotheca bitnerae* Dulai, 2011, Upper Oligocene: **A**, dorsal view of complete specimen, Peyrière, MNHN.FA46513; **B, C**, dorsal view of complete specimen and enlargement of the umbonal part to show details of the beak, Abesse, MNHN.FA46515; **D, E**, inner view of ventral valve and enlargement of umbonal part to show details of pedicle collar and teeth, Estoti, MNHN.FA46518; **F, G**, inner view of dorsal valve and enlargement of cardinalia (**G**), Bêlus, MNHN.FA46521; **H, I**, inner and oblique lateral views of dorsal valve, visible high median septum without serrations, Estoti, MNHN.FA46519; **J-M**, inner and oblique lateral views of dorsal valve, and enlargement of descending branches but-tressed the septum (**L**) and cardinalia (**M**), Abesse, MNHN.FA46516. All SEM. Scale bars: A, B, D, 1 mm; C, E, F, H-K, 500 μ m; G, L, M, 200 μ m.

TABLE 5. — Measurements (in mm) of *Argyrotheca bitnerae* Dulai, 2011.

Locality	Length	Width	Thickness
Abesse	2.6	2.0	0.8
Abesse	3.3	2.6	1.3
Abesse	2.1	1.7	0.7
Estoti	3.3	2.9	1.4
Bélus	2.5	2.1	1.0
Bélus	1.4	1.3	0.5

smooth, coarsely punctate with numerous growth lines. Anterior commissure rectimarginate. Hinge line short. Beak high, straight; beak ridges sharp. Interarea very narrow. Foramen large, triangular, hypothryd, bordered by two deltidial plates forming narrow ridges.

Ventral valve interior with small, hooked teeth projecting into delthyrium. Pedicle collar broad, sessile attached valve floor anteriorly. Median septum low, extending from pedicle collar to about mid-valve.

Dorsal valve interior with well developed, narrow inner socket ridges. Dental sockets deep. Cardinal process as small depression. Crura very short, as are crural processes (see Fig. 5F-I). Descending branches fuse with valve floor (Fig. 5F, H), and emerge to attach to median septum. Median septum high, triangular in profile, without serrations (Fig. 5I, K).

REMARKS

This species is relatively common in the studied material being found in four localities. The investigated specimens correspond well, both externally and internally, to those described as *Argyrotheca bitnerae* by Dulai *in* Dulai & Stachacz (2011) from the Middle Miocene of Poland. The Oligocene specimens differ from the Miocene ones in being slightly larger and having the septum without serrations. Dulai *in* Dulai & Stachacz (2011) observed 2-3 weak serrations at the anterior slope of the septum.

This brachiopod was earlier attributed to the species *A. cistellula* (Searles-Wood, 1841) by Barczyk & Popiel-Barczyk (1977) and Popiel-Barczyk & Barczyk (1990). However, *A. cistellula* has a shell transversely subrectangular in outline, with a wide straight hinge line (Logan 1979). In addition, the pedicle collar in *A. cistellula* is excavated anteriorly,

TABLE 6. — Measurements (in mm) of *Joania cordata* (Risso, 1826).

Locality	Length	Width	Thickness
Abesse	3.3	3.0	1.2
Abesse	3.3	2.7	—
Abesse	3.0	2.5	1.1
Bélus	2.5	2.3	—
Bélus	2.3	2.0	0.9

while in *A. bitnerae* the pedicle collar is close to the valve floor.

In shell shape, smooth surface, sessile pedicle collar and short crura with blunt crural processes *A. bitnerae* bears a close resemblance to the Early Miocene species *A. kupei* Hiller, Robinson & Lee, 2008 from New Zealand, differing, however, in having smooth slope of the dorsal septum (Hiller *et al.* 2008; Hiller 2011). In *A. kupei* the anterior slope of septum has 2-3 knob-like extensions.

Externally, in smooth surface and triangular outline with a short hinge margin, the studied specimens resemble *Joania cordata* but they differ strongly from the latter species internally. *Joania cordata* possesses a prominent cardinal process and marginal tubercles on inner surface of both valves (Logan 1979; Álvarez *et al.* 2008).

Genus *Joania* Álvarez, Brunton & Long, 2008

TYPE SPECIES. — *Terebratulina cordata* Risso, 1826, by original designation of Álvarez *et al.* (2008: 401).

Joania cordata (Risso, 1826) (Fig. 6A-I; Table 6)

Terebratulina cordata Risso, 1826: 389.

Argyrotheca cordata — Logan 1979: 50-54, text-figs 13, 14, pl. 5, figs 1-12. — Taddei Ruggiero 1985: 371, 372, pl. 7, figs 10-14; 1994: 208, pl. 2, fig. 1-3; 1996: 202. — Bitner 1990: 140-143, text-figs 7, 8, pl. 5, figs 1-14, pl. 7, fig. 1; 1993: 150, pl. 4, figs 1-5; pl. 5, figs 1-8. — Bitner & Pisera 2000: 9-10, pl. 2, figs 1-9. — Bitner & Dulai 2004: pl. 3, figs 9, 10. — Bitner & Kaim 2004: 196, 197, figs 2D-K, 3A-E. — Álvarez & Emig 2005: 155-158, figs 25F, G, 47, 48. — Dulai 2007: 4-5, fig. 4.1-9.

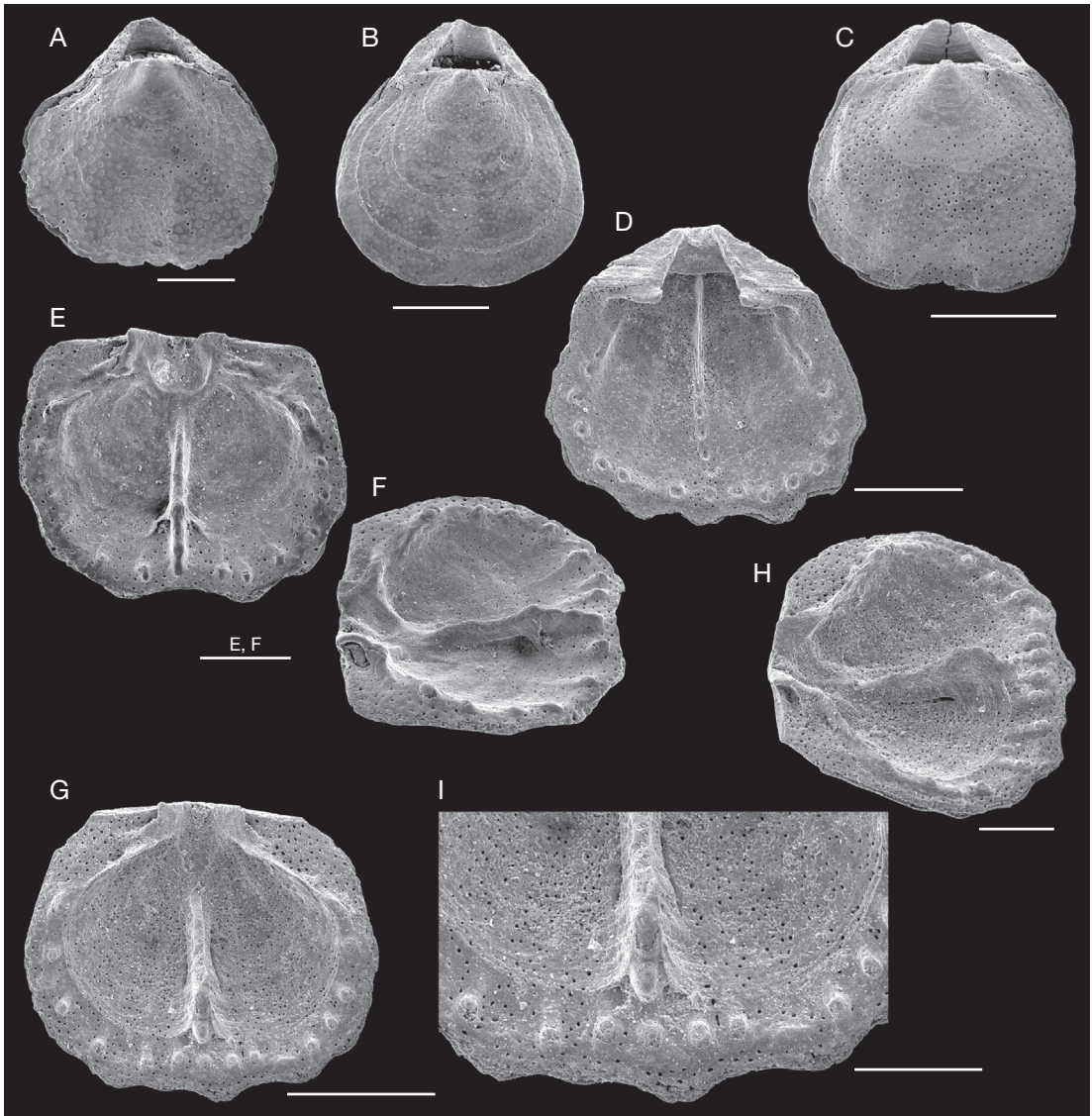


FIG. 6. — *Joania cordata* (Risso, 1826), Upper Oligocene: **A-C**, dorsal views of complete specimens; **A**, Estoti, MNHN.FA46523, **B, C**, Abesse, MNHN.FA46526-A46527; **D**, inner view of ventral valve, Bélus, MNHN.FA46529; **E, F**, inner and oblique lateral views of dorsal valve, young individual, Estoti, MNHN.FA46524; **G-I**, inner, oblique lateral views of dorsal valve, and enlargement of anterior part to show septum and connection with a loop, Bélus, MNHN.FA46530. All SEM. Scale bars: A, E, F, H, I, 500 μ m; B-D, G, 1 mm.

Joania cordata – Álvarez, Brunton & Long 2008: 400-402, fig. 4C-D, 5A-F, 11-13.

MATERIAL EXAMINED. — Peyrère: three complete specimens, three ventral and one dorsal valves. Abesse: seven complete specimens, four ventral and two dorsal valves, MNHN.FA46526-A46528 and A46551. Estoti: one

complete specimen MNHN.FA46523 and five dorsal valves MNHN.FA46524-A46525. Bélus: four complete specimens, three ventral and four dorsal valves, MNHN.FA46529-A46531.

OCCURRENCE. — This species is common in the Neogene of the Central Paratethys and the Mediterranean

TABLE 7. — Measurements (in mm) of *Joania peyrerensis* n. sp.

Locality	Length	Width	Thickness
Bélus	2.3	2.3	1.0
Bélus	2.9	3.0	1.3
Peyrère (holotype)	2.5	2.7	1.3

province, living today in the north-eastern North Atlantic and the Mediterranean Sea (Logan 1979, 1983, 1988) at the depth of 3 to 600 m (Logan 2007).

REMARKS

The genus *Joania* was recently established by Álvarez *et al.* (2008) for those *Argyrotheca* species that have a narrow hinge line, prominent cardinal process and tubercles on the inner margin.

The specimens from the Aquitaine Basin agree well with those described from the Miocene of the Central Paratethys (Bitner 1990, 1993; Bitner & Pisera 2000; Bitner & Kaim 2004), differing from the Recent ones described and illustrated by Logan (1979) in having a lower median septum. The shell is small, smooth or covered with poorly defined, shallow ribs. The large foramen is triangular with a wide pedicle collar supported by a low median septum. The inner socket ridges are narrow but high, and the cardinal process is prominent. The specimens bear tubercles on the inner margin of both valves.

Joania peyrerensis n. sp. (Fig. 7A-I; Table 7)

TYPE MATERIAL. — Holotype MNHN.FA46532: specimen figured in Fig. 7A-C; paratypes MNHN.FA46533, A46534: specimens figured in Fig. 7D-I.

ETYMOLOGY. — Referring to the name of type locality, Peyrère.

MATERIAL EXAMINED. — Peyrère: one complete specimen. — Bélus: three complete specimens and one dorsal valve.

TYPE HORIZON AND LOCALITY. — Upper Oligocene, Peyrère, Aquitaine Basin, SW France.

DIAGNOSIS. — Small, rounded subrectangular *Joania* with surface ornamented by six to eight distinct ribs; teeth triangular; dorsal septum high, triangular in profile with serrations; tubercles on inner margin of both valves.

DESCRIPTION

Shell small, not exceeding 3 mm in length, rounded subrectangular in outline with maximum width at mid-valve, weakly biconvex. Shell surface covered with 6 to 8 distinct ribs. Hinge line shorter than maximum width, slightly curved. Anterior commissure rectimarginate. Beak high with distinct beak ridges. Interarea narrow. Foramen large, triangular, hypothrid flanked by elevated, narrow deltidial plates.

Ventral valve interior with plate-like, triangular teeth (Fig. 7F-H). Pedicle collar wide, excavate anteriorly, supported by a slender septum that extends beyond mid-valve. On inner surface radial ridges terminating in tubercles (Fig. 7I).

Dorsal valve interior with narrow but high inner socket ridges. Dental sockets deep. Cardinal process distinct. Septum high, triangular in profile, with 4 serrations. Numerous tubercles on inner margin (Fig. 7D, E). Loop not preserved.

REMARKS

Álvarez *et al.* (2008) created *Joania* as a monospecific genus, however, since that time several *Argyrotheca* species have been transferred into the genus *Joania*, based mostly on the important diagnostic character – numerous radial ridges terminating anteriorly in tubercles on the inner margin. The presence of marginal tubercles in the specimens from the Aquitaine Basin supports their attribution to the genus *Joania*.

In the ornamentation of 6-8 distinct, sharp ribs *J. peyrerensis* n. sp. can be easily distinguished from other so far described *Joania* species. The shell surface of *J. cordata* is smooth or covered with almost imperceptible costae (Logan 1979; Bitner 1990; Álvarez *et al.* 2008). In addition, both species differ in the nature of the teeth; in *J. peyrerensis* n. sp. the teeth form a triangular plate, while in *J. cordata* they are hooked.

The shell of a Recent Indo-Pacific species *J. arguta* (Grant, 1983) is also completely smooth without any costae (Bitner 2008; Simon 2010). The teeth in this species are, similarly like in *J. cordata*, hooked given off dorsally, thus differing clearly from *J. peyrerensis* n. sp.

The studied specimens differ strongly from the Lower Pleistocene species from southern Italy,

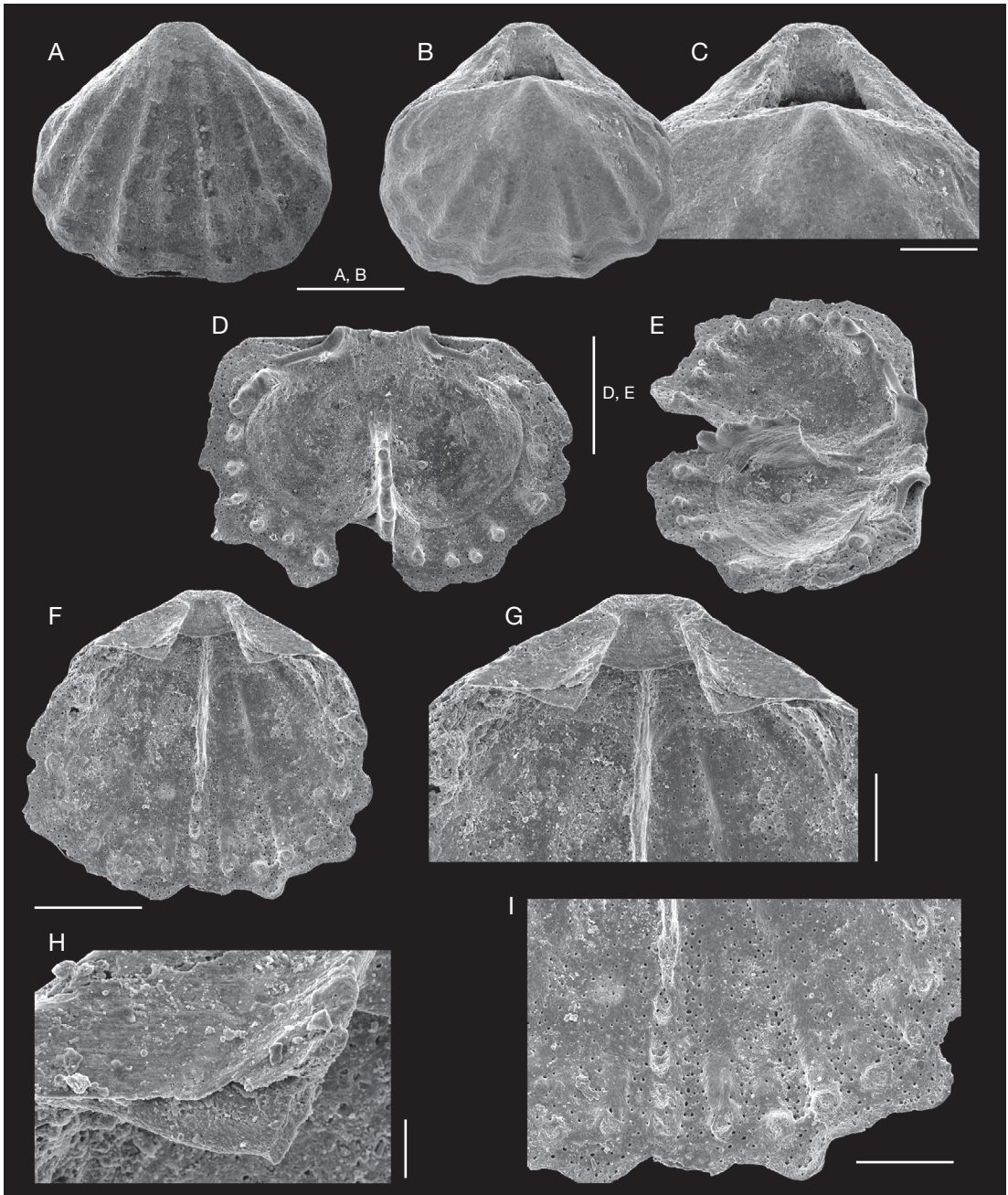


FIG. 7. — *Joania peyrerensis* n. sp., Upper Oligocene: **A-C**, ventral and dorsal views of complete specimen, and enlargement of posterior part to show details of the beak, holotype MNHN.F.A46532, Peyrère; **D, E**, inner and oblique lateral views of dorsal valve, paratype MNHN.F.A46533, Bélus; **F-I**, inner view of ventral valve, enlargement of posterior part (**G**) and details of left tooth (**H**) and enlargement of anterior part (**I**) to show radial ridges terminating anteriorly in tubercles, paratype MNHN.F.A46534, Bélus. All SEM. Scale bars: A, B, D-F, 1 mm; C, G, I, 500 μm; H, 100 μm.

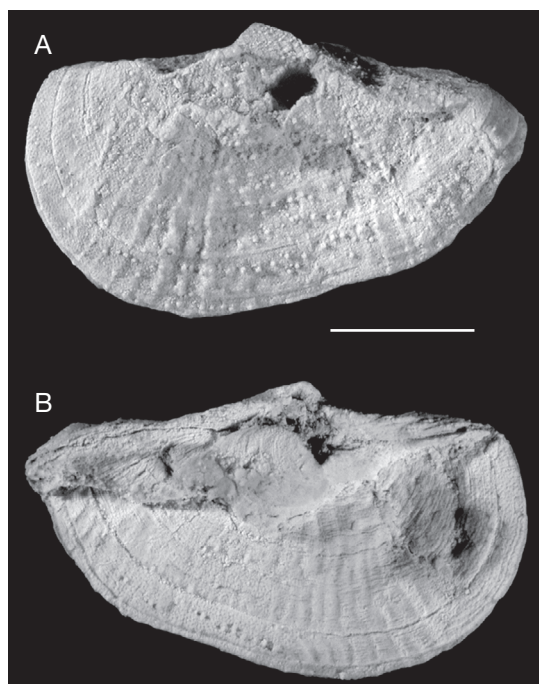


FIG. 8. — *Megerlia truncata* (Linnaeus, 1767), Upper Oligocene, Peyrère (MNHN.FA46535), complete specimen in ventral (A) and dorsal (B) views. Scale bar: 3 mm.

Joania ageriana, originally described as *Argyrotheca ageriana* by Taddei Ruggiero (1993). *Joania ageriana* is much larger, reaching 7 mm in length, and ornamented by 14 to 18 rounded ribs (Taddei Ruggiero 1993, 1994)

Dulai (2010a) attributed a single dorsal valve from the Late Miocene of Italy to *Joania* aff. *falunica* (de Morgan, 1915), recognizing in this brachiopod diagnostic characters of the genus. The poor material prevents any formal description of a new species.

Superfamily KRAUSSINOIDEA Dall, 1870

Family KRAUSSINIDAE Dall, 1870

Genus *Megerlia* King, 1850

TYPE SPECIES. — *Anomia truncata* Linnaeus, 1767, by the original designation of King (1850: 145).

TABLE 8. — Measurements (in mm) of *Megerlia truncata* (Linnaeus, 1767).

Locality	Length	Width
Peyrère	76.3	10.1
Peyrère	10.3	–
Peyrère	6.7	9.3

Megerlia truncata (Linnaeus, 1767)

(Fig. 8A, B; Table 8)

Anomia truncata Linnaeus, 1767: 1152, no. 229.

Megerlia truncata – Logan 1979: 68-72, text-fig. 21; pl. 9, figs 1-23. — Taddei Ruggiero 1985: 372-374, pl. 8, figs 1-6, pl. 9, figs 1-5, pl. 10, figs 1-11, pl. 11, figs 1-10; 1994: 210, pl. 3, figs 3, 4. — Bitner 1990: 145-147, text-fig. 10, pl. 2, figs 6-9, pl. 7, figs 3-6, pl. 8, figs 1-7. — Álvarez & Emig 2005: 167, 168, figs 25J-M, 53F, 71. — Dulai 2010a: 28, pl. 3, figs 4, 5.

Megerlia montruosa – Taddei Ruggiero 1985: 374, 375, pl. 1, figs 7-11; 1994: 210, pl. 3, fig. 5.

MATERIAL EXAMINED. — Peyrère: four complete specimens, one ventral and two dorsal valves, MNHN.FA46535, A46536. Material is strongly crushed.

OCCURRENCE. — This is one of the commonest species in the Miocene of the Central Paratethys and the Mediterranean region, being also very common today in the Mediterranean and the western Atlantic with the wide depth range from 8 to 1086 m (Logan 2007). *Megerlia truncata* is also recorded from the Indian Ocean (Cooper 1981; Bitner *et al.* 2008).

REMARKS

Megerlia truncata is very rare in the investigated assemblage, found only in one locality. The material is poorly preserved, all specimens are crushed, preventing examination of internal structure. However, the size and characteristic ribbed ornamentation support attribution to this species. This is the first record of this species from the Oligocene but the genus *Megerlia* was already reported from the Oligocene of Hungary (Dulai 2010b).

Order THECIDEIDA Elliott, 1958
Superfamily THECIDEOIDEA Gray, 1840

Family THECIDEIDAE Gray, 1840
Subfamily LACAZELLINAE Backhaus, 1959

Genus *Lacazella* Munier-Chalmas, 1880

TYPE SPECIES. — *Thecidea mediterranea* Risso, 1826, by original designation of Munier-Chalmas (1880: 279).

Lacazella mediterranea (Risso, 1826)
(Fig. 9A-L; Table 9)

Thecidea mediterranea Risso, 1826: 394, pl. 12, fig. 183.

Thecidea (Lacazella) mediterranea – Peyrot 1932: 487, pl. 17, figs 7-10.

Lacazella mediterranea – Pajaud 1970: 128, text-figs 50, 52, pl. 1, fig. 4, pl. 5, fig. 4, pl. 7, fig. 3, pl. 10, figs 1-6, pl. 11, fig. 3, pl. 12, fig. 2, pl. 16. — Logan 1979: 73, text-fig. 22, pl. 10, figs 1-8. — Taddei Ruggiero 1985: 376, 377. — Álvarez & Emig 2005: 117-119, fig. 34A-C. — Bitner & Dieni 2005: 109, 110, fig. 4I-K. — Bitner & Dulai 2008: 40, fig. 5.7-8. — Dulai 2010a: 28, pl. 3, fig. 3a, b.

MATERIAL EXAMINED. — Peyrère: 306 complete specimens, 105 ventral and 72 dorsal valves, MNHN.FA-46537-A46543 and A46552. — Abesse: 97 complete specimens, 104 ventral and 47 dorsal valves MNHN.FA46544-A46547, A46554 and A46556. — Estoti: four ventral valves, MNHN.FA46548. — Bélus: one complete specimen, one ventral and one dorsal valves, MNHN.FA46549. — Bezoye: ten complete specimens, 22 ventral and 12 dorsal valves, MNHN.FA46550. — Escornebéou: 17 ventral valves, Larralde Collection.

OCCURRENCE. — The stratigraphical range of this species is from the Upper Paleocene (Pajaud & Plaziat 1972) to Recent. Its Recent representatives are living in the south-western part of the Mediterranean Sea at the depth of 1-110 m (Logan 2007) and are regarded as a neoendemic species (Logan *et al.* 2004). It is in fact a relict distribution because in the Eocene it is recorded throughout Europe but in the Neogene it is known only from the Mediterranean region.

REMARKS

This species dominates in the studied assemblage and is represented by more than 800 specimens. Its presence was already reported from the Oligocene of the Aquitaine Basin (Peyrot 1932; Pajaud 1974; Lozouet 2004).

TABLE 9. — Measurements (in mm) of *Lacazella mediterranea* (Risso, 1826).

Locality	Length	Width	Thickness
Peyrère	10.1	6.7	5.4
Peyrère	9.2	6.5	4.2
Peyrère	8.5	6.8	5.4
Peyrère	8.5	6.3	4.5
Peyrère	8.4	7.2	4.4
Peyrère	8.1	6.4	4.0
Abesse	3.8	3.1	2.1

Although consistent with the hitherto described specimens (see Pajaud 1970; Logan 1979; Álvarez & Emig 2005) the specimens from southern France are much larger, reaching about 10 mm of length, thus being even three times as long as those living today, which rarely exceed 3 mm (Logan 1979; Álvarez & Emig 2005). The shell is variable in outline, usually subtriangular, with large interarea and wide, triangular pseudodeltidium. The hemispondylium takes the form of two prominent prongs and is supported by a small median septum (Fig. 9E). The cardinal process is large and subrectangular, extending beyond the margin. The median septum is divided forming a trifurcating structure, and the margins of interbrachial lobes are denticulated (Fig. 9G-L).

PALEOECOLOGICAL REMARKS

The Brachiopoda are very abundant in the marls of Peyrère and calcareous sands of Abesse but are scarcely represented in the other five outcrops (Fig. 1). From an ecological point of view the outcrops of the Upper Oligocene of the Aquitaine Basin can be divided into four main groups (Lozouet 2004): a shallow-water calcareous facies outcropping in the vicinity of Dax (Abesse, Bezoye, Estoti), a muddy sand assemblages (Escornebéou, Bélus), a mud assemblage localized in the paleocanyon and the Peyrère fauna. The shallow-water calcareous facies contains numerous faunistic elements of the littoral zone indicating the proximity of the shore line; otherwise the assemblage is particularly rich in macro-fossils (molluscs, hermatypic corals, bryozoans, serpulids). The muddy sand assemblages are characteristic of the sublittoral zone

TABLE 10. — Drill hole data for the Upper Oligocene brachiopods from the Aquitaine Basin.

Species	Number undrilled	Number drilled (% drilled)	Drilled on ventral	Drilled on dorsal	Drilled on both valves
<i>Novocrania anomala</i> (Müller, 1776)	12	0 (0.0%)	0	0	0
<i>Terebratulina retusa</i> (Linnaeus, 1758)	101	8 (7.3%)	3	5	0
<i>Megathiris detruncata</i> (Gmelin, 1791)	401	25 (5.4%)	6	18	1
<i>Argyrotheca cuneata</i> (Risso, 1826)	15	0 (0.0%)	0	0	0
<i>Argyrotheca bitnerae</i> Dulai, 2011	56	0 (0.0%)	0	0	0
<i>Joania cordata</i> (Risso, 1826)	36	1 (2.8%)	1	0	0
<i>Joania peyrerensis</i> n. sp.	4	1 (20%)	0	1	0
<i>Megerlia truncata</i> (Linnaeus, 1767)	7	0 (0.0%)	0	0	0
<i>Lacazella mediterranea</i> (Risso, 1826)	775	24 (3.0%)	5	18	1
Totals	1407	59 (4.0%)	15	42	2

up to the depth of 80 m as indicated by the presence of gastropods with bathyal habitats: Seguenziidae Verrill, 1884, *Benthonella* Dall, 1889, *Benthonellania* Lozouet, 1990 (Lozouet 1990). The mud assemblages correspond to the distal part of the shelf and the top of the continental slope. The Peyrère fauna deserves special explanation. The originality of the Peyrère associated fauna, including gastropods, bivalves, annelids, corals with a very common species of the genus *Epiphaxum* Lonsdale, 1850 (Octocorallia) (Lozouet & Molodtsova 2008), is clearly in abundance of elements characteristic for hard substrates and cryptic habitats (Lozouet 2004). Otherwise there are very characteristic forms, restricted today only to the submarine cave environments. The gastropod families Neritopsidae Gray, 1847, Neritiliidae Schepman, 1908 and Pickworthiidae Iredale, 1917 are the most emblematic. The micromorphic megathyridid and thecideidae brachiopods commonly occur together, both today and in the fossil record (Meile & Pajaud 1971), in shallow-water, tropical and subtropical environments (Logan 2005, 2008; Lüter *et al.* 2008). The thecideides display the greatest density in light-poor, cryptic habitats as overhangs, crevices, caves and subreef tunnels (Lee & Robinson 2003; Logan 2004). Thus, their abundance in the Peyrère assemblage supports the earlier interpretations of the whole fauna as a cave biocenosis. In turn, the protected, stable environments of cryptic habitats may explain much larger size of *Lacazella mediterranea* from Peyrère than hitherto reported for this species.

DRILLING PREDATION

Gastropod predation intensity, with only few exceptions (see e.g., Baumiller & Bitner 2004; Baumiller *et al.* 2006), is usually very low in most Cenozoic brachiopod populations (Taddei Ruggiero & Bitner 2008), as here. Among 1466 specimens examined 59 specimens (4.0%) were drilled (see Table 10). Such a low frequency may be explained by the fact that brachiopods are not the prime target where molluscs are very abundant. Drillings were observed on *Terebratulina retusa*, *Megathiris detruncata*, *Joania cordata*, *J. peyrerensis* n. sp. and *Lacazella mediterranea*. No drilling predation was observed on *Novocrania anomala*, *Argyrotheca cuneata*, *A. bitnerae* or *Megerlia truncata*. Taxonomic selectivity for particular species is difficult to explain and does not depend on amount of specimens. Drill holes were found on ventral and dorsal valves but the dorsal valve was drilled at a higher frequency (see Table 10); in two specimens drill holes occur on both valves (Fig. 10).

Drill holes on calcareous exoskeletons are for the most part due to two families of gastropods: Naticidae Guilding, 1834 and Muricidae Rafinesque, 1815 (Carriker & Yochelson 1968). Drilling predation is known also in the scavenger family Nassariidae Iredale, 1916 (but it is exceptional) and in the Cassidae Latreille, 1825, which feed exclusively upon echinoderms (Riedel 1995). Naticidae and Muricidae are widespread in the Upper Oligocene of the Aquitaine Basin but the Naticidae are less common, being infaunal gastropods more common

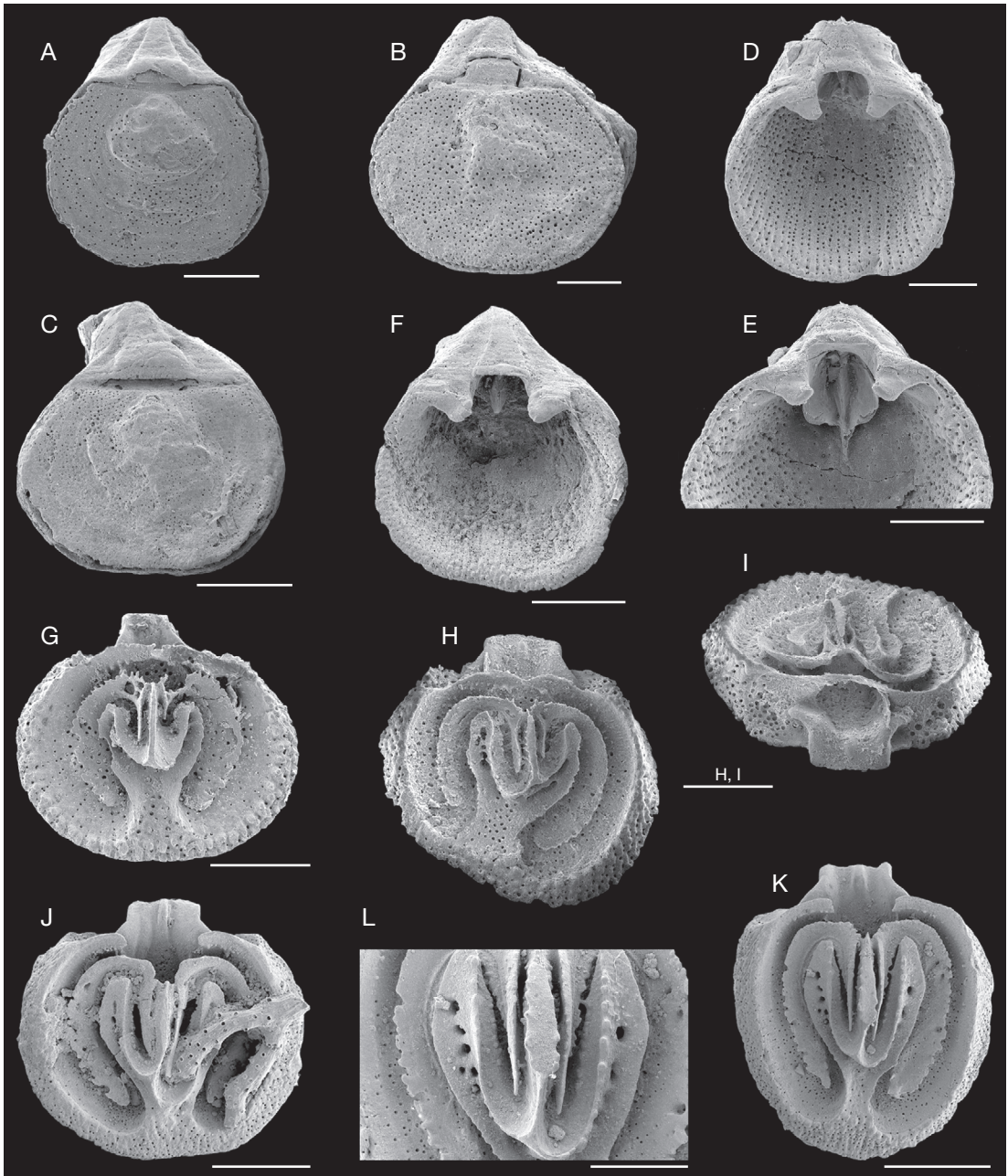


FIG. 9. — *Lacazella mediterranea* (Risso, 1826), Upper Oligocene: **A-C**, dorsal views of complete specimens: **A, C**, Peyrère, MNHN.F.A46537-A46538; **B**, Abesse, MNHN.F.A46544; **D, E**, inner view of ventral valve and tilted enlargement (**E**) to show hemispondylium, Abesse, MNHN.F.A46545; **F**, inner view of ventral valve, Peyrère, MNHN.F.A46539; **G**, inner view of dorsal valve, Abesse, MNHN.F.A46546; **H, I**, inner and posterior views of dorsal valve, Peyrère, MNHN.F.A46540; **J**, inner view of dorsal valve, Peyrère, MNHN.F.A46541; **K, L**, inner view of dorsal valve and enlargement (**L**) of the trifurcating median ramus-ramuli complex, Peyrère, MNHN.F.A46542. All SEM. Scale bars: A, B, D, E, G-I, L, 1 mm; C, F, J, K, 2 mm.

in littoral sandy deposits. In the outcrop of Peyrère where the Brachiopoda are especially common and very well preserved a bulk sample has permitted us to obtain 413 species of gastropods (Lozouet 2004) including two species of Naticidae (36 specimens) and 19 species of Muricidae (133 specimens). The Muricidae generally feed upon sedentary epifaunal prey and the Naticidae only bore when the prey is buried in sediment.

It is possible to differentiate boreholes produced by Muricidae or by Naticidae based on morphological criteria. The bore hole of Naticidae is neat and circular with a wide conical shape while those of Muricidae are more irregular; the hole is also straight-sided, or tapers slightly inwards (Taylor 1970). The holes reported in the studied brachiopod shells correspond clearly to muricid attacks (Fig. 10A, D-L). This is in good agreement with ecology of brachiopods and muricids, and diversity of muricids in the Peyrère outcrop.

STABLE ISOTOPE ANALYSIS

Brachiopods secrete a shell in oxygen isotopic equilibrium with surrounding seawater (Carpenter & Lohmann 1995; Buening & Spero 1996; Buening 2001; Brand *et al.* 2003). As their shell, composed of low-Mg calcite, is resistant to diagenesis they are good fossils for isotopic studies and are often used as a proxy for the environmental conditions of an ancient ocean (Brand *et al.* 2011). Carbon isotopic equilibrium in brachiopod shells is still uncertain and needs further investigations (Buening 2001; Brand *et al.* 2003).

For isotope analysis the three most abundant taxa in the studied species assemblage were chosen, *Terebratulina retusa*, *Megathiris detruncata* and *Lacazella mediterranea*. Under a scanning electron microscope (SEM) their shells appear to be very well preserved, suggesting that this material is suitable for isotopic studies. The $\delta^{18}\text{O}$ values of *M. detruncata* range from -0.41 to -0.03‰ PDB (mean -0.24‰ PDB), of *L. mediterranea* from -2.70 to 0.07‰ PDB (mean -1.29‰ PDB) and of *T. retusa* from -0.55 to -0.25‰ PDB (mean -0.40‰ PDB). The $\delta^{13}\text{C}$ values of *M. detruncata*

range from -0.82 to 2.55‰ PDB (mean 1.27‰ PDB), of *L. mediterranea* from -4.95 to 0.79‰ PDB (mean -1.30‰ PDB) and of *T. retusa* from 1.09 to 1.66‰ PDB (mean 1.37‰ PDB). Plots $\delta^{18}\text{O}$ versus $\delta^{13}\text{C}$ values for those species are shown in the Fig. 11. The results display substantial variability, with five samples of *L. mediterranea* having clearly more negative values than other samples. As both species, *M. detruncata* and *L. mediterranea* live in similar ecological conditions, possible explanations of those large differences in the isotopic values can comprise unrecognized diagenetic effects, different skeletal ultrastructures or vital effects. $\delta^{13}\text{C}$ values can be additionally affected by dissolved inorganic carbon. Nevertheless, a major difference in $\delta^{13}\text{C}$ values in co-occurring brachiopod species was already reported (Buening *et al.* 1998).

The shell in thecideide brachiopods is composed almost entirely of the microgranular primary layer. In the shell of terebratulides the primary layer constitutes a thin, outer layer, while the fibrous secondary layer dominates and this latter layer incorporates oxygen in isotopic equilibrium with the ambient seawater (Carpenter & Lohmann 1995; Buening 2001; Brand *et al.* 2003). The primary layer is considered to be precipitated out of the equilibrium with the seawater (Carpenter & Lohmann 1995; Buening 2001), however, Brand *et al.* (2003) in their detailed work on geochemistry of modern brachiopods concluded that the Thecideida, although built of the primary layer, incorporate oxygen isotopes in equilibrium with the ambient sea water. In turn, vital effects refer to the fact that some organisms may biologically control the incorporation of isotopes into skeletal calcium carbonate, thus precipitating shells in isotopic disequilibrium with surrounding seawater. These preliminary results of isotopic analyses are difficult to interpret at the moment and more studies, especially investigation of diagenetic effects, are necessary.

Nevertheless, we used the $\delta^{18}\text{O}$ values of *M. detruncata* and *T. retusa* to estimate paleotemperatures. The oxygen isotope data of carbonate shells can be used only if the oxygen isotope composition of the seawater is known. Today's seawater has a mean composition of 0‰ SMOW. In open

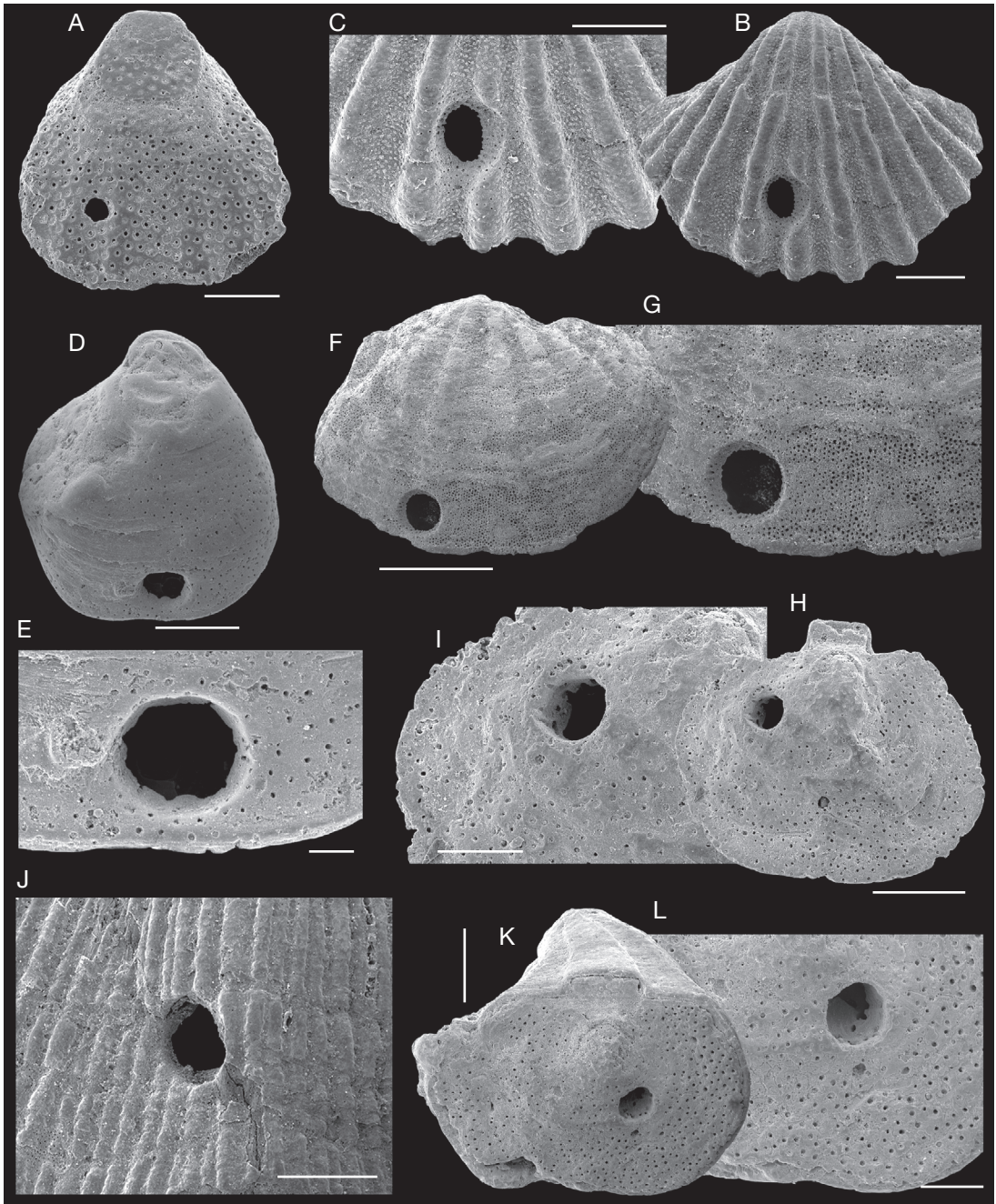


FIG. 10. — Examples of drilled brachiopods from the Upper Oligocene of the Aquitaine Basin, SW France: **A**, *Joania cordata* (Risso, 1826), ventral valve, Abesse, MNHN.FA46551; **B, C**, *Megathiris detruncata* (Gmelin, 1791), ventral valve and a close-up image of drill hole, Bélus, MNHN.FA46506; **D, E**, *Lacazella mediterranea* (Risso, 1826), ventral valve and close-up of drill hole, Peyrère, MNHN.FA46552; **F, G**, *M. detruncata*, dorsal valve and close-up of drill hole, Peyrère, MNHN.FA46554; **H, I**, *L. mediterranea*, dorsal valve and close-up of drill hole, Abesse, MNHN.FA46553; **J**, *Terebratulina retusa* (Linnaeus, 1758), dorsal valve, Peyrère, MNHN.FA46555; **K, L**, *L. mediterranea*, dorsal view of complete specimen and a close-up image of drill hole, Abesse, MNHN.FA46556. All SEM. Scale bars: A, I, L, 500 µm; B-D, G, H, J, K, 1 mm; E, 200 µm; F, 2 mm.

ocean environments the isotopic composition is controlled by global climate, however, in marginal seas or nearshore environments such factors as evaporation and/or freshwater input can change significantly the oxygen isotope value of seawater. Calculating temperatures with an assumed $\delta^{18}\text{O}$ of 0‰ SMOW the results received show the range 17–19°C. These results are too low and are in disagreement with the paleotemperatures obtained from the paleontological data; for the Upper Oligocene a subtropical to tropical climate is proposed (Lauriat-Rage *et al.* 1993; Lozouet 2004).

A similar discrepancy between temperatures obtained from paleontological and isotopic sources was observed by Latal *et al.* (2006) for the Middle Miocene sea of the Central Paratethys, thus they proposed for coastal environments the higher $\delta^{18}\text{O}$ value of +1‰ SMOW; this value is characteristic for the Mediterranean Sea, for instance. Using this value they obtained temperatures that fit well with other paleotemperature proxies.

Although the Upper Oligocene sea of the Aquitaine Basin cannot be compared with the epicontinental sea of the Central Paratethys, the Aquitaine Basin constituted during the Oligocene a narrow embayment, having character of marginal, nearshore environment with reduced exchange with the ocean. Thus, when assuming a value of +1‰ SMOW for the Oligocene sea in the Aquitaine Basin the paleotemperatures calculated for *M. detruncata* vary from 21 to 23°C, and for *T. retusa* from 22 to 24°C. These temperatures fit much better with the paleoenvironmental interpretation based on faunal data. Because in marginal, nearshore marine settings the isotopic composition of seawater can be influenced by different factors (mostly evaporation and freshwater input) a combination of several independent methods, including isotopes, should be applied for a paleotemperature interpretation as presented by Latal *et al.* (2006) and Nehyba *et al.* (2008). In comparison, the higher $\delta^{18}\text{O}$ values (*c.* 1.1‰ PDB) of late Oligocene benthic foraminifera from the Deep Sea Drilling Project (DSDP) Site 119 in the Bay of Biscay (Miller & Curry 1982; Miller 1983) point to a lower temperature that may be expected in more open ocean environment.

CHARACTERISTICS OF BRACHIOPOD FAUNA AND ITS AFFINITIES

The Upper Oligocene brachiopod fauna from the Aquitaine Basin, southwestern France that belongs to the Atlantic Province, contains nine species belonging to seven genera. They include both inarticulate and articulate brachiopods. Inarticulate brachiopods are represented by one cementing species, *Novocrania anomala*. Among articulate brachiopods there is one representative of the short-looped brachiopods, a member of the family Cancellothyridae, *Terebratulina retusa*. Also the families Kraussinidae and Thecideidae are represented by one species each, *Megerlia truncata* and *Lacazella mediterranea*, respectively. More diverse is the family Megathyrididae with five species recognized, namely *Megathiris detruncata*, two species of *Argyrotheca*, *A. cuneata* and *A. bitnerae*, and two species of *Joania*, *J. cordata* and *J. peyrerensis* n. sp. The latter species has been described as a new taxon. Two species, *Megathiris detruncata* and *Lacazella mediterranea* dominate in the studied assemblage, constituting more than 80% of the material. All species, except *M. detruncata* and *L. mediterranea*, are reported for the first time from this region; however, the presence of the genus *Argyrotheca* without specific attribution was already announced (Lozouet 2004). The occurrence in the studied assemblage of *Novocrania anomala*, *Terebratulina retusa*, *Argyrotheca cuneata*, *A. bitnerae*, *Joania cordata*, and *Megerlia truncata* extends the stratigraphical range of those species from the Miocene to the Oligocene. In the case of *Joania* and *Megerlia* there are the oldest occurrences of those genera.

The species composition in particular localities differs considerably. The most diverse localities are Peyrère and Bélus where nine and six species were found, respectively. It may be explained by the peculiarity of the paleoenvironment in the region of Peyrère and Bélus. Both outcrops are located near the head of the paleocanyon with abundance of hard substrates and cryptic habitats, suitable environment for megathyridid and thecideid brachiopods. The two localities of Escornebéou and St-Étienne-d'Orthe show the lowest diversity with one species only. In the region of Dax five species were recognized.

The Chattian brachiopods contain one form potentially endemic to the Aquitaine Basin, *J. peyrerensis* n. sp. and other species having wide stratigraphical and geographical range. In taxonomic composition the brachiopod fauna from the Aquitaine Basin displays low affinity with preceding Eocene faunas (e.g. Davidson 1870; Fabiani 1913; Calzada *et al.* 1988; Bitner 2000; Bitner & Dieni 2005; Bitner & Dulai 2008; Dulai *et al.* 2010; Dulai 2011; Bitner *et al.* 2011); only two species, *M. detruncata* and *L. mediterranea* are in common. In the Eocene, like the Oligocene, megathyrinids dominate, with *M. detruncata* and numerous species of *Argyrotheca* represented, however, by different species than those in the Oligocene. There are also few species of craniid brachiopods, rhynchonellids represented by the genera *Erymnaria* Cooper, 1959 and *Streptaria* Cooper, 1959, and short-looped terebratulines like *Gryphus* and *Leymerithyrus* Calzada, 1988. Restricted to the Eocene seemed to be two micromorphic cancellothyrids, *Terebratulina tenuistriata* (Leymerie, 1846) and *Orthothyris pectinoides* (von Koenen, 1894), however, recently the latter species has been found in the Lower Oligocene deposits of eastern Germany (Müller 2011b).

In turn, there is a great resemblance of the investigated brachiopod fauna to the Miocene faunas of the Mediterranean Province and Central Paratethys. Apart from *J. peyrerensis* n. sp., all species described here are known from one or both of these regions (e.g., Davidson 1864, 1870; Dreger 1889; Zilch 1934; Julien 1940; Bărbulescu & Rado 1984; Gaetani & Saccà 1985; Marras & Ventura 1985; Bitner 1990, 1993; Taddei Ruggiero 1994; Bitner & Pisera 2000; Bitner & Dulai 2004; Logan *et al.* 2004; Dulai 2007, 2010a; Bitner & Schneider 2009). *Lacazella mediterranea* common in the Miocene of the Mediterranean region (Davidson 1864; Julien 1940; Pajaud 1974; Logan *et al.* 2004) was not found in the Central Paratethys. The only thecideid brachiopod recognized in the Paratethys was *Thecidellina* Thomson, 1915 from Bulgaria (Bitner 1993). *Argyrotheca bitnerae* described originally from the Miocene of the Central Paratethys (Dulai & Stachacz 2011) is recorded from the Oligocene of the Aquitaine Basin (this paper) but was not found in the Mediterranean province.

The low affinities to the Eocene brachiopod faunas may be explained by the dramatic changes in the

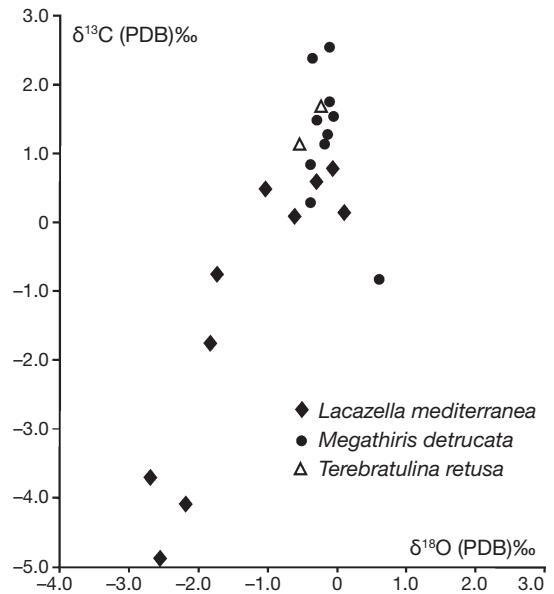


Fig. 11. — Stable carbon and oxygen isotopic values from brachiopod samples.

paleogeographical and paleoenvironmental conditions in Europe at the Eocene/Oligocene boundary, provoked by plate tectonic movements and formation of the Alpine chain (Meulenkamp & Sissingh 2003; Ivany *et al.* 2003). In the earliest Oligocene the origin of the Paratethys began, and till the Middle Miocene two distinct basins, the Mediterranean Sea and the intercontinental Paratethys Sea in the North, existed. A drop of sea level and climatic cooling in the early Oligocene had a significant effect on a variety of most taxonomic groups (see Berggren & Prothero 1992; Dockery & Lozouet 2003); many forms became extinct and many new taxa appeared for the first time, and a similar pattern is visible among brachiopods. In the late Oligocene the climate again became warm (tropical to subtropical) and remained warm through the Miocene (Lauriat-Rage *et al.* 1993).

The Recent Mediterranean and Atlantic brachiopod faunas are clearly a continuation of those Oligocene-Miocene faunas as shown by the fact that seven of nine species described here are still living in the Mediterranean Sea and/or north-eastern Atlantic (Logan 1979, 1993, 2007; Logan *et al.* 2004; Álvarez & Emig 2005).

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